CHAPTER

3

Cognitive Components of Insect Behavior

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INTRODUCTION

Cognition is the integrating process that utilizes many different forms of memory (innate and acquired), creates internal representations of the experienced world, and provides a reference for expecting the future of the animal's own actions.[1,2] It thus allows the animal to decide between different options in reference to the expected outcome of its potential actions. All these processes occur as intrinsic operations of the nervous system, and they provide an implicit form of knowledge for controlling behavior. None of these processes need to—and certainly will not—become explicit within the nervous systems of many animal species (particularly invertebrates and lower vertebrates), but their existence must be assumed given the animal's specific behavioral output. Here, we focus on cognitive components of insect behavior and analyze behavioral outputs that refer to several forms of internal processing. In doing so, we aim to relate the complexity of the insect nervous system to the level of internal processing, which is a major goal of comparative animal cognition.

ACTING UPON THE ENVIRONMENT: EXPLORATION, INSTRUMENTAL LEARNING, AND OBSERVATIONAL LEARNING

Insects, like all animals, explore the environment and by doing so acquire relevant sensory, motor, and integrative information that facilitates learning about relevant events in such environments.[3–5] Honeybees, for instance, explore the environment before they start foraging,[6,7] and they learn the spatial relations of environmental objects during these exploratory flights.[8–10] Fruit flies (*Drosophila melanogaster*) also respond to their placement within a novel open-field arena with a high level of initial activity,[11–13] followed by a reduced stable level of spontaneous activity. This initial elevated component corresponds to an active exploration because it is independent of handling prior to placement within the arena, and it is proportional to the size of the arena.[14] Furthermore, visually impaired flies are significantly impaired in the attenuation of initial activity, thus suggesting that visual information is required for the rapid decay from elevated initial activity to spontaneous activity within the novel open-field arena.[14]

Exploratory behavior facilitates learning by associating the animal's action to the resulting outcome. For example, a hungry animal searching for food in a particular sensory environment learns upon a successful search the relationship between its own actions, the external conditions signaling the outcome, and the valuating signal of the food reward. This kind of association constitutes the basis of operant (instrumental) learning.[15] Operant learning has been intensively studied in insects. A classic protocol for the study of this learning form is the flight simulator in which a *Drosophila* is suspended from the thorax in the middle of a cylindrical arena that allows the presentation of visual landmarks (Figure 3.1). The tethered fly flies stationary and if some of these landmarks are paired with the aversive reinforcement of an unpleasant heat beam pointed on the thorax, the fly learns to fly toward a safe direction, avoiding the dangerous-landmark directions (Figure 3.1).[17,18] The fly learns to control reinforcement delivery as its flight maneuvers determine the switching-off of the heat beam if the appropriate

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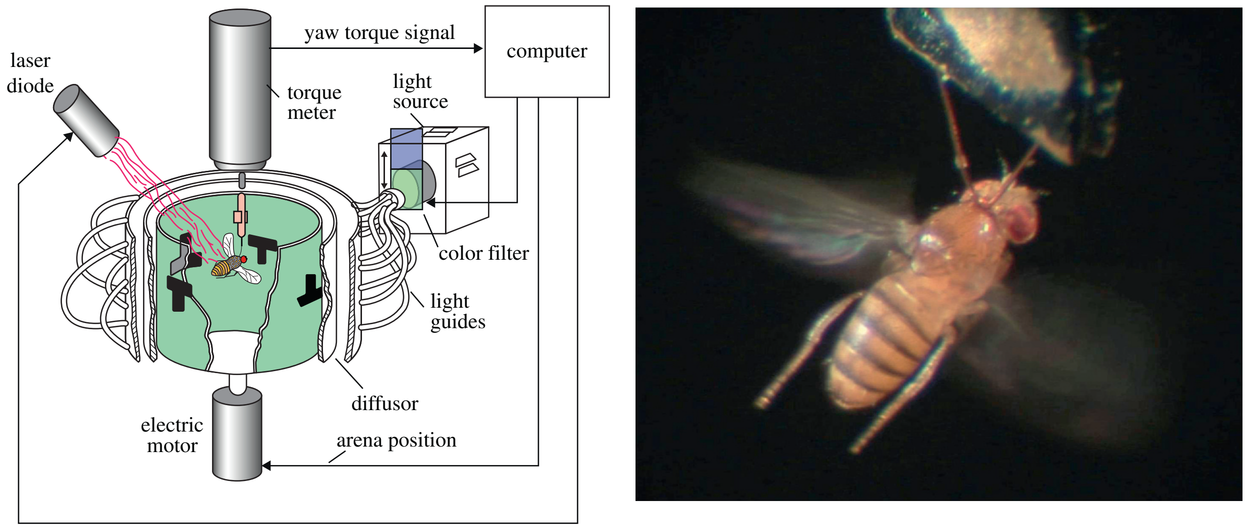

FIGURE 3.1 **The flight simulator used for visual conditioning of a tethered fruit fly.**[16] (Left) A *Drosophila* is flying stationary in a cylindrical arena. The fly's tendency to perform left or right turns (yaw torque) is measured continuously and fed into a computer, which controls arena rotation. On the screen, four 'landmarks,' two T's and two inverted T's, are displayed in order to provide a referential frame for flight direction choice. A heat beam focused on the fly's thorax is used as an aversive reinforcer. The reinforcer is switched on whenever the fly flies toward a prohibitive direction. Therefore, the fly controls reinforcer delivery by means of its flight direction. (Right) Detail of a tethered fly in suspended flight within the simulator. Source: *Courtesy of B. Brembs.*

flight directions are chosen,[18] thus constituting a case of operant learning (see Chapters 2 and 28).

Furthermore, insects are also endowed with the capacity to learn about the actions produced by others, be they conspecifics or not.[19] Wood crickets (*Nemobius sylvestris*), for instance, learn to hide under leaves by observing experienced conspecifics in the presence of a natural predator, the wolf spider.[20] Observer crickets were placed in a leaf-filled arena accompanied by conspecifics (demonstrators) that were either confronted with a wolf spider and therefore tended to hide under leaves or did not experience this predatory threat. Observers that interacted with spider-experienced conspecifics were more likely to hide under leaves than observers that interacted with conspecifics that had no recent spider experience. This difference persisted 24 hr after demonstrators were removed from the experimental arena, thus showing that perception of danger in observers had been altered by the demonstrators' behavior.[20] Crickets did not hide under leaves when separated from demonstrators by a partition that allowed for pheromone exchange between compartments but not visual or physical contact, nor did they increase their tendency to hide when placed in arenas that had previously contained crickets confronted with spiders. Thus, naive crickets learn from experienced demonstrators how to hide under leaves when facing a potential threat, and this learning requires a direct contact between observers and demonstrators.

An important point raised by this example of observational learning is that it would have to take the form of higher order conditioning because the observer cricket would not actually directly experience the unconditional stimulus of a spider attack, which would result in immediate death, thus making learning superfluous. That insects are capable of such higher order conditioning, specifically second-order conditioning, has been shown in various cases. Honeybees and fruit flies learn such second-order associations. Whereas flies exhibit second-order conditioning in an aversive context, in which they learn to associate an odor (conditioned stimulus 1 (CS1)) with shock (unconditioned stimulus (US)) and then a second odor (conditioned stimulus 2 (CS2)) with the previously conditioned CS1,[21] honeybees learn second-order associations in an appetitive context while searching for food. They learn to connect both two odors (odor 1 + sucrose reward; odor 2 + odor 1[22–24]) and one odor and one color.[25] Although these examples refer to the framework of classical (Pavlovian) conditioning in which animals learn to associate different stimuli,[26] similar explanations could be provided for operant learning situations, thus rendering the higher order conditioning explanation of observational learning plausible.

Observational learning even at a symbolic level is exemplified by dance communication in bees (discussed later).[6]

EXPECTATION

Operant learning means that the animal may develop an expectation about the outcome of its actions. Two forms of expectation can be distinguished: conditioned responding to an experienced stimulus, as in associative learning, and planning of behavior in the absence of the stimuli associated with its outcome. Both of these forms of expectation comprising lower and higher cognitive processes interact in navigation and waggle dance communication in honeybees. Bees navigating toward predictable food sources follow routes and develop visual memories of landmarks seen en route and at the locations of food sources.[8] The locations are qualified in the sense that the insect expects the formerly experienced target signals at specific points of its route. For instance, bees trained to fly along a series of three similar, consecutive compartments in which they have to choose between two patterns, one positive (+) allowing passage to the next compartment and one negative (−) blocking passage, choose between combinations of positive patterns according to their expectation of which should be the positive pattern at a given compartment.[27] If, for instance, bees are trained with a white (+) versus a black disk (−) in the first compartment, a blue (+) versus a yellow disk (−) in the second compartment, and a vertical (+) versus a horizontal black-and-white grating (−) in the third compartment, they prefer the positive white disk over the positive vertical black-and-white grating in the first compartment but they revert this preference if the same stimuli are confronted in the third compartment.[27] Furthermore, bees learn the sequence of four landmarks as cues for turns toward the feeder.[28] Thus, bees exhibit specific expectations along a route about the outcome of landmarks that guide them toward the food source. Similarly, bees trained to fly to different locations in the morning and in the afternoon choose the correct homing direction if released at the wrong time of the day at one of these locations, and they integrate this location-specific information when released halfway between these two locations.[29]

A higher form of expectation can be found after latent learning in navigation and dance communication in honeybees. Bees perform novel shortcuts between two or more locations within a previously explored environment.[30,31] They also fly along shortcuts between a learned location and a location communicated by the waggle dance of a hive mate.[32] They do so without reference to beacons or a structured panorama, excluding the possibility that they somehow rely on snapshot memories established at the respective locations.[33] The fact that they are able in certain circumstances to fly such shortcuts between a communicated location and a location memorized on the basis of their own experience implies that both locations have a common spatial reference framework. Such memory structure could store geometric relations of objects in the explored environment and could be conceptualized as a cognitive (or mental) map because the behavior of bees meets the definition of a cognitive map.[8,30] It would include meaningful objects at their respective locations and on the way toward them, and thus the animal would know at any place where it is relative to potential destinations allowing to plan routes to locations whose signifying signals are not available at the moments decisions are made.

The term *expectation* can be applied at multiple levels of behavioral and neural processes. A low-level process is the efference copy of the neural program initiating the movement that leads to an error signal when compared with the sensory feedback resulting from the movement.[34,35] This error signal is thought to feed into an internal, neural value system leading to associative alterations in the neural circuits initiating the movement. The efference copy can be considered as a neural correlate of expectation because it precedes the conditions of the external world and leads to a correction of neural circuitry. On a formal ground, the neural operation of comparison between the efference copy and sensory feedback is equivalent to the deviation from expectation as derived in computational reinforcement learning by the delta rule.[36] It has been difficult to trace efference copies to neural circuits, but an exciting example exists in insects. A single multisegmental interneuron, the corollary discharge interneuron (CDI), was found in the cricket *Gryllus bimaculatus* that provides presynaptic inhibition to auditory afferents and postsynaptic inhibition to auditory interneurons when the animal produces its own song but not when it hears songs from other animals.[37] When the animal sings without sound (fictive song), the CDI is excited and inhibits the coding of played songs. The authors managed to stimulate CDI intracellularly, resulting in inhibited auditory encoding. They also found that excitation of CDI is specific for self-generated songs and not for other motor patterns, demonstrating that the CDI is both necessary and sufficient for the blocking of sensory input expected to be received from own song production. It will be interesting to determine whether a mismatch between the expected song pattern and the received song produces an error signal that may be used to fine-tune own song production, for example, after some disturbance of the song production by the wings.

The concept of an error signal driving associative learning has a strong impact on neural studies of learning-related plasticity in the nervous system. For example, the dopamine neurons of the ventral tegmentum of the mammalian brain change their response properties to a conditioned stimulus predicting reward (US) according to a modified delta rule.[38] A similar effect was found in an identified neuron in the honeybee brain, which encodes the reinforcing property of the sucrose reward (US) in olfactory learning.[39] This neuron, known as VUMmx1 (ventral unpaired median neuron 1 in the maxillary neuromere), appears to have similar properties as dopaminergic neurons in the mammalian brain (Figure 3.2). During differential conditioning in which a bee is trained to respond to a rewarded odor (CS+) and not to a non-rewarded odor (CS−), intracellular recordings of VUMmx1 activity show that this neuron develops responses to CS+ and stops responding to CS−. If the US is now given after the CS+, one finds no responses to the US anymore, but a US after CS− is well responded to. In other words, the neuron responds to unexpected sucrose presentations but not to an expected one (for further discussion, see Chapter 29).

Octopamine immunoreactive neurons in the *Drosophila* brain correspond to VUMmx1 in structure and function, and they represent the reward function in olfactory learning.[40] Dopaminergic neurons in the *Drosophila* brain act as a value system in the framework of aversive learning.[40] These neurons thus mediate the aversive reinforcing properties of electric shock punishment in odor−shock learning. Signaling from specific subsets of these dopaminergic neurons arborizing at the level of subcompartments of paired, central brain structures called the mushroom bodies, which intervene in the storage and retrieving of olfactory memories,[41−43] are necessary and sufficient to support learning of the odor−shock association.[44] Thus, inhibiting these neurons in genetic mutants impedes aversive learning, whereas artificial activation of these neurons in other types of mutants facilitates odor learning even in the absence of shock.[45−47] Interestingly, dopaminergic neurons in *Drosophila* are weakly activated by odor stimuli before training but respond strongly to electric shocks. However, after one of two odors is paired several times with an electric shock, the neurons acquire the capacity to respond to the odor stimulus.[44] Like VUMmx1, they also respond distinctly to odorants with different outcomes in a differential conditioning experiment with a punished odor (CS+) versus a non-punished odor (CS −): In this case, odor-evoked activity is significantly prolonged only for the CS+. Thus, dopaminergic neurons involved in odor−shock learning not only mediate aversive reinforcing stimulation but also reflect in their activity the training-induced association with the US; in other words, during training they acquire the capability to predict the anticipated punishment (for further discussion, see Chapters 2, 5, 6, 27, and 28). Recently, it was found that a subpopulation of dopamine neurons is involved in coding the reward function in olfactory learning of *Drosophila. In vivo* calcium imaging revealed that these neurons are activated by sugar ingestion and the activation is increased on starvation. These dopamine neurons are selectively required for the reinforcing property of, but not a reflexive response to, the sugar stimulus.[48]

These results support the notion that reward is an intrinsic property of structurally and functionally defined neurons in the insect brain. It is controlled by expectation about their own actions that are relative to specific objects in the external world or that are driven internally in order to fulfill expected outcomes that are absent. The latter component—the driving of behavior by expectations of absent outcomes—has been highlighted in experiments in which *Drosophila* larvae are trained with different kinds of appetitive and aversive associations and afterward are tested in retention tests in which the memories induced by this training should be expressed.[49] These experiments show, for instance, that aversive olfactory memories are not expressed if the test situation is performed under extinction conditions—that is, if the previously punished odor is presented without punishment. It is argued that with the expected outcome of punishment being absent, the corresponding avoidance behavior has no reason to be expressed[49] (see Chapter 5). Conversely, after appetitive learning, memories would be expressed only in extinction conditions because the previously rewarded odor would be, in this case, deprived of the expected reward (see Chapter 33 for additional information about context dependence of extinction learning in honeybees). In this case, it makes sense to initiate appetitive search in order to access the reward expected in association with this odor.[49] Thus, conditioned olfactory behavior would reflect specific expectations and would aim at reaching specific goals associated with these expectations.

GENERALIZATION, CATEGORIZATION, AND CONCEPT LEARNING

Extracting information from experienced events and applying it to solve novel situations is a distinctive behavior of 'intelligent' systems. Indeed, experiments showing that animals respond in an adaptive manner to novel stimuli that they have never encountered before and that do not predict a specific outcome based on the animals' past experience are the hallmark of higher forms of flexible behavior. Such a positive transfer of learning (also called stimulus transfer)

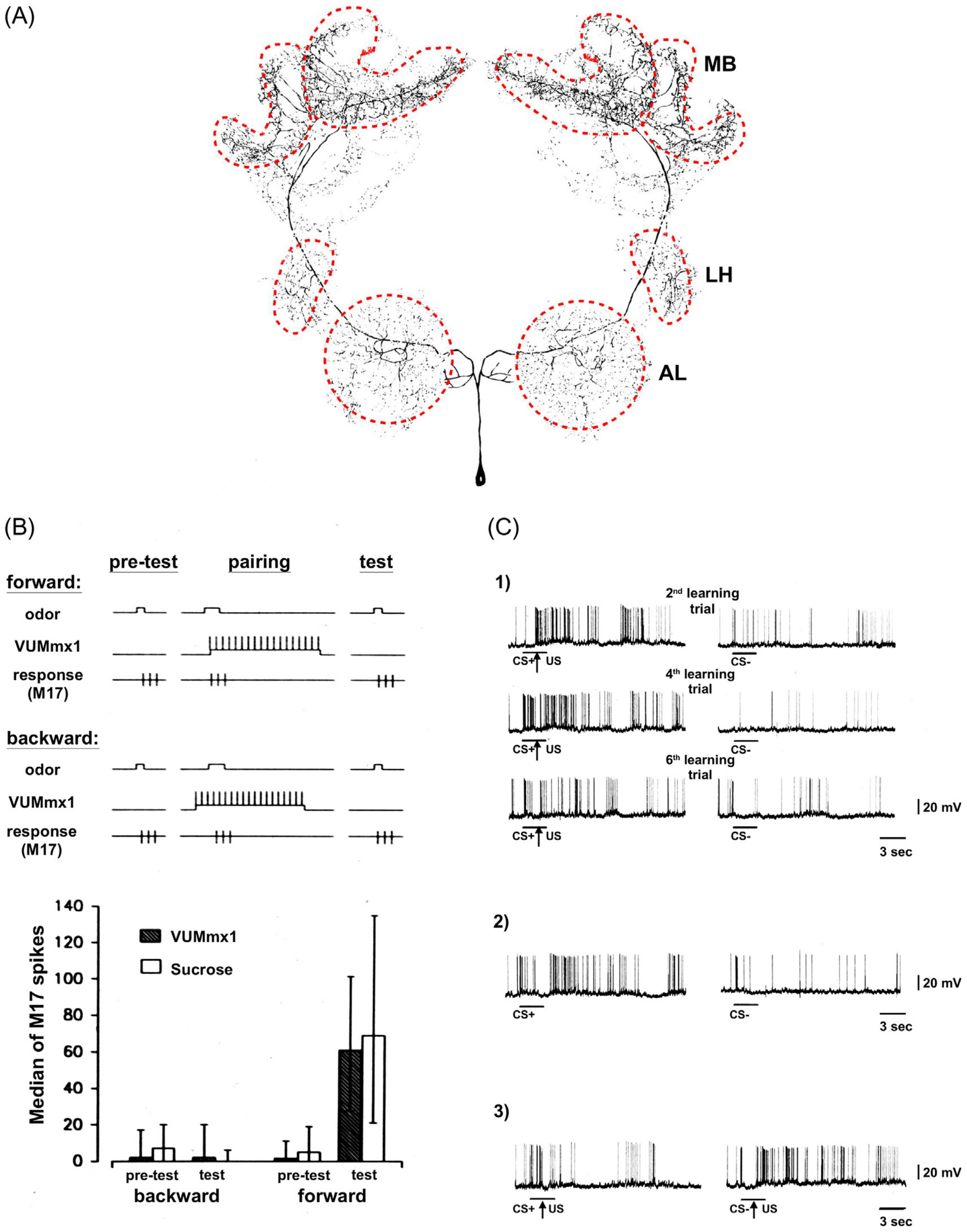

FIGURE 3.2 (A) The VUMmx1 neuron.[39] The soma is located in the maxillary neuromere, and the dendrites arborize symmetrically in the brain and converge with the olfactory pathway at three sites (delimited by a red dashed line), the primary olfactory center, the antennal lobe (AL), the secondary olfactory integration area, the lip region of the mushroom bodies (MB), and the output region of the brain, the lateral horn (LH). VUMmx1 responds to sucrose solution both at the antenna and at the proboscis with long-lasting spike activity and to various visual, olfactory, and mechanosensory stimuli with low-frequency spike activity. (B) Olfactory learning can be induced by substituting the sucrose reward in PER conditioning by an artificial depolarization of VUMmx1 ('sucrose signaling') immediately after odor stimulation. If depolarization precedes olfactory stimulation (backward pairing), no learning is observed. The same forward–backward effect is seen in behavioral PER conditioning. The bees' response is quantified in terms of the number of spikes of M17, a muscle controlling the movement of the proboscis. The results thus show that VUMmx1 constitutes the neural correlate of the US in associative olfactory learning. (C) Intracellular recordings of VUMmx1 during training and tests with a reinforced (CS+; carnation) and a non-reinforced odor (CS−; orange). Such a conditioning leads to an enhanced response of VUMmx1 to CS+ but not to CS−. If the US follows the presentation of the CS+, the response of VUMmx1 to the US is greatly reduced and even inhibited. In contrast, the response of VUMmx1 to the US after the presentation of the CS− remains normal. This indicates that differential conditioning leads to different reward-related responses, depending on whether the reward is expected (after CS+) or not (after CS−).

therefore brings us to a domain that differs from that of elemental forms of learning.[50]

Stimulus transfer admits different levels of complexity that refer to the capacity of transferring specific knowledge to novel events based either on stimulus similarity, and thus on specific physical traits that are recognized in the novel events, or on more abstract relationships that constitute the basis for decisional rules.[51] The first basic process that needs to be mentioned in this context is that of stimulus generalization. Most animals, including insects, have the capacity to record events related with relevant consequences and to signal their reappearance. This requires learning, memorization, and evaluation of perceptual input in relational terms and the capacity of coping with possible distortions of the original stimuli due to noise, extrinsic or intrinsic environmental interferences, positional or developmental changes, etc. Generalization allows for flexible responding when the animal is confronted with these possible interferences because it involves assessing the similarity between the present perceptual input and the previous experience.[52] The evaluation of similarity is performed along one or several dimensions such that stimuli that lie close to each other along a perceptual scale or in a perceptual space are treated as equivalent. As a consequence, generalization processes imply a gradual decrease in responding along a perceptual scale correlated with a progressive decrease in stimulus similarity.[53−55] Stimulus generalization has been shown in insects in perceptual domains as different as the olfactory one,[56−61] the visual one,[62−66] and the gustatory one.[67,68]

The next level of stimulus transfer corresponds to categorization, which is 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.[51,69] Categorization thus deals with the extraction of these defining features from objects of the animal's environment. Labeling different objects as belonging to the same category implies responding similarly to them; as a consequence, category boundaries are sharper than those corresponding to the gradual decrease of responding along a perceptual scale underlying generalization.[70]

Numerous examples have shown that bees categorize visual stimuli based on unique features or on arrangements of multiple features.[71] For instance, bees categorize visual patterns based on the presence or absence of bilateral symmetry.[72] Bees were trained with triads of patterns in which one pattern was rewarded with sucrose solution and the other two were non-rewarded. For the bees trained for symmetry, the rewarded pattern was symmetric and the non-rewarded patterns were asymmetric. For the bees trained for asymmetry, the rewarded pattern was asymmetric and the two non-rewarded patterns were symmetric. To avoid learning of a specific pattern or triad, bees were confronted with a succession of changing triads during the course of training. Transfer tests presenting stimuli that were unknown to the bees, all non-rewarded, were interspersed during the training with the triads.

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 categorize 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 categorizing symmetry. Such a predisposition can either be innate and could facilitate a better and faster learning about stimuli that are biologically relevant[73] or can be based on the transfer of past experience from predominantly symmetric flowers in the field. A specific ecological advantage would arise from flower categorization in terms of symmetrical versus asymmetrical. The perception of symmetry would be important for pollinators because symmetry of a flower may signal its quality and thus influence mating and reproductive success of plants by affecting the behavior of pollinators.[74] As bees discriminate between symmetry and asymmetry, they should also be capable of performing selective pollination with respect to floral symmetry even within a patch of flowers. This may indicate that plants may have exploited such cognitive capabilities of the pollinators during the evolution of flowers.

A further level of stimulus transfer is termed *concept learning*, which, contrary to categorization based on specific physical features, occurs independently of the physical nature of the stimuli considered (colors, shape, size, etc.)[75,76] and relies on relations between objects.[51,77] Examples of such relations are 'same as,' 'different from,' 'above/below of,' and 'on the left/right of.' Extracting such relations allows transferring a choice to unknown objects that may differ dramatically in terms of their physical features but that may fulfill the learned relation.

Various recent reports have indicated that honeybees learn relational rules of different sorts. These include 'sameness/difference,'[78] 'above/below,'[79] and the mastering of two rules simultaneously—'above/below' (or left/right) and 'different from.'[80]

Learning of the concepts of sameness and difference was demonstrated through the protocols of delayed matching to sample (DMTS) and delayed non-matching to sample (DNMTS), respectively.[78] Honeybees foraging in a Y-maze (Figure 3.3A) were trained in a DMTS experiment in which they were presented with a changing

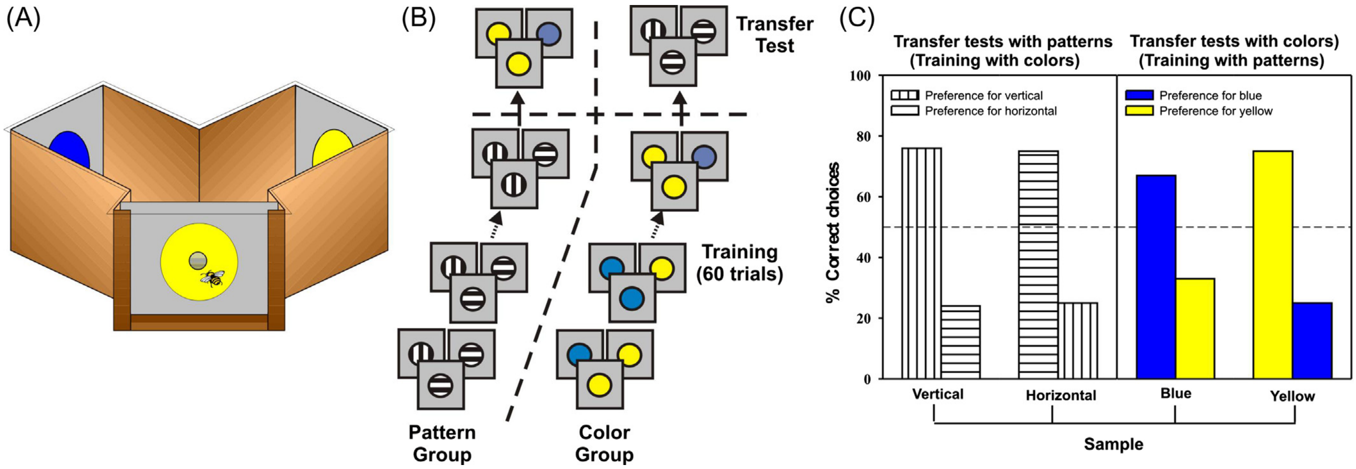

FIGURE 3.3 (A) Y-maze used to train bees in a delayed matching-to-sample task.[78] Bees had to enter into the maze to collect sugar solution on one of the back walls of the maze. A sample was shown at the maze entrance before bees accessed the arms of the maze. (B) Training protocol. A group of bees were trained during 60 trials with black-and-white, vertical and horizontal gratings (pattern group); another group was trained with colors, blue and yellow (color group). After training, both groups were subjected to a transfer test with novel stimuli (patterns for bees trained with colors, and colors for bees trained with patterns). (C) Performance of the pattern group and the color group in the transfer tests with novel stimuli. Both groups chose the novel stimulus corresponding to the sample, although they had no experience with such test stimuli.

non-rewarded sample (i.e., one of two different color disks ('color group') or one of two different black-and-white gratings, vertical or horizontal ('pattern group')) at the entrance of a maze (Figure 3.3B). 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 black-and-white gratings that they had not experienced before 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 color corresponding to that of the sample grating at the maze entrance (Figure 3.3C). Transfer was not limited to different types of visual stimuli (pattern vs. color) but could also operate between drastically different sensory modalities such as olfaction and vision.[78] Bees also mastered a DNMTS task, thus showing that they learn a rule of difference between stimuli as well.[78] These results document that bees learn rules relating stimuli in their environment. They were later verified in a study showing that the working memory underlying the solving of the DMTS task lasts for approximately 5 sec,[81] a period that coincides with the duration of other visual and olfactory short-term memories characterized in simpler forms of associative learning in honeybees.[82]

More recently, bees were shown to process two concepts simultaneously, which presupposes an even higher level of cognitive sophistication than dealing with one concept at a time. Following a training in which they had to learn to choose two distinct objects in a specific spatial relationship (above/below or right/left), they mastered two abstract concepts simultaneously, one based on the spatial relationship and another based on the perception of difference.[80] Bees that learned to classify visual targets using this dual concept transferred their choices to unknown stimuli that offered a best match in terms of dual-concept availability: Their components presented the appropriate spatial relationship and differed from one another. These results thus demonstrate that it is possible for a bee to extract at least two different concepts from a set of complex pictures and combine them in a rule for subsequent choices.

MEMORY PROCESSING

Learning does not produce the final memory trace immediately. Time- and event-dependent processes, conceptualized as consolidation processes, form the memory trace. Short-term memory is transformed into midterm and long-term memory, and the molecular, cellular, neural, and systemic processes underlying this transformation are currently intensively studied (see Chapter 27). Stable memory traces need to be moved from a silent into an activated state by retrieval processes. Internal conditions of the animal, external cues, and a neural search process shift a silent memory into an active memory. The expression of the active memory may undergo selection processes before its content is expressed. Animals need to decide between different options as they reside in memory, and the decision process requires access to the expected outcomes. The expected outcomes are also stored in memory, and only when the respective memory contents are retrieved will they be accessible to selection processes. This network of interactions between retrieval, selection, and execution is conceptualized in a particular form of memory—working memory.

Memory systems are also categorized according to their contents. In vertebrates, different contents are related with particular brain structures—for example, procedural memory (cerebellum), episodic memory (hippocampus and prefrontal cortex), and emotional memory (amygdala). Whereas procedural memory certainly exists to a large extent in insects in their ventral ganglia, it is unknown whether memories qualifiable as ‘emotional’ exist in insects and, if so, whether they reside in modulatory neurons related to reward and punishment and/or in other sets of the widely branching peptidergic neural networks. Higher order forms of memory are usually related to the mushroom bodies (see Chapter 28), but the level of higher order processing mediated by these structures is unknown. Do insects possess a form of episodic memory—the ability to carry out long-term recall of sequences of events or narratives?[83] In humans, birds, and mammals, this property is intimately related to the functions of the hippocampus and cerebral cortex. It is argued that food-storing birds may develop an episodic-like memory about a kind of food stored at a certain place and at a certain time.[84] Pollinating insects certainly control their foraging activities according to the kind of food they collect at a particular place and at a specific time of day, but it is unknown whether they make decisions between options integrating the what, where, and when of potential food sites.

Memory systems are highly dynamic and content sensitive. Any retrieval from the memory store will change its content due to the updating process in working memory. It is precisely this updating process that may lead to extracting rules that underlie implicit forms of abstraction in the visual domain (discussed previously). Furthermore, retrieval from memory store also induces re-learning and consequently consolidation into a new memory form, a process referred to as “reconsolidation.”[85] This process has been demonstrated in the honeybee (see Chapter 33).

From an evolutionary standpoint, one may expect that memory dynamics are adapted to choice behavior under natural conditions. Foraging in pollinating insects has a highly regular sequential structure of events ranging from actions within seconds to those separated by months. It thus offers the opportunity to relate memory structure and ecological demands.[82] Choices between flowers within the same patch quickly succeed each other and are performed during early short-term memory. Choices between flowers of different patches occur after the transition to late short-term memory. Successive foraging bouts are interrupted by the return to the hive so that flower choices in a subsequent bout require retrieving information from midterm memory. Finally, interruptions of days, weeks, and months (the latter in the case of overwintering bees) require retrieval from long-term memory.

Internal processing at the level of working memory can be understood as an indication of rudimentary forms of explicit processing and may exist in insects (and cephalopods; see Chapters 23–25) within the context of observatory learning and social communication. Paper wasps recognize each other on an individual basis (see Chapter 42); the ant *Temnothorax albipennis* informs colony members about a new food site by a particular behavior termed tandem running and that has been assimilated to a form of teaching (see Chapter 40); and bees employ a symbolic form of social communication for the transfer of information about spatial food locations. Key components in all these forms of learning and teaching are the retrieval of remote memory and the incorporation of the new information into the existing memory. Working memory provides implicit forms of representation as a substrate for various kinds of neural operations. These may include evaluation of the new information on the background of existing memory, extraction and updating of rules connecting the contents of memory, and decision making in relation to the expected outcome of the animal’s actions.

Addressing the properties and functioning of active working memory requires for each paradigm a careful evaluation of whether elemental forms of learning and memory retrieval are sufficient to explain behavioral performances. The tradition of the most parsimonious explanation provides a strong tool in science and is well observed in behavioral studies, particularly in those performed with insects. However, the rigidity of some experimental designs frequently used in laboratory studies of insect behavior might result in the danger that the animal in its restriction can only do what the experimenter allows it to do. The conclusion from such experiments is often that because the animal did what was expected from it, this is the only behavior it possesses. 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 small brain of an insect. For example, will it be more difficult to follow a navigation strategy based on route following or on using a cognitive-map? Is it easier to store many sequential images defining a long route or to extract a rule connecting these images? Are neural processes derived from behavioristic learning theory less demanding than those derived from cognitive concepts? The answer at this stage is that we simply do not know, and that the only way to find out is to search for neural mechanisms within a broader conceptual frame. We also need to acknowledge that potential behavioral acts that are not performed by an animal are equally important as expressed behavior. Only by accepting that an attentive brain is constantly producing potential behaviors, most of which are not expressed, will we be able to search for the neural basis of the 'inner doing' as a prerequisite of decision-making processes.

INSECT INTELLIGENCE AND BRAIN STRUCTURE

Thinking about the basic design of a brain subserving the cognitive functions discussed previously, one recognizes a structure of essential modules and their interconnectivity (Figure 3.4).[86] This modular architecture seems to be shared by a broad range of animal species and may even apply to the wormlike creature at the basis of the evolutionary division between protostomes and deuterostomes. These species possess various kinds of perceptual and motor control systems, which constitute the input and output, respectively, of the architecture presented in Figure 3.4. Premotor centers convey information to motor control systems and therefore act as action planning systems. 'Desire' is used here to represent the expected outcomes of behavior, either appetitive or aversive, available to animals via specific signaling pathways. 'Belief,' on the other hand, refers to innate or experience-dependent memories—that is, to the knowledge that the animal has at its disposition and that drives its actions and decisions.

Although the modules depicted in Figure 3.4 may be multiple (multiple perceptual systems, multiple belief-generating systems, multiple desire-generating systems, multiple action-planning systems, and multiple motor control systems), the basic idea of this scheme is that perceptual systems feed onto three downstream systems arranged both serially and in parallel that converge on the action-planning systems,[86] which in turn drive the motor systems. Thus, perceptual systems can reach the action-planning systems directly; in addition, the desire- and belief-generating systems receiving the same perceptual information will act in parallel onto action planning, as well.

When we talk about 'modules' and 'systems,' we mean, in essence, neurons and neural networks. Therefore, if such a scheme should be of any heuristic help in understanding the insect brain, its skeleton needs the flesh of neurons and their functions. The chapters on the insect brain in this volume document such a fleshing out (see Chapters 4, 27, 29, and 41). Sensory systems (vision, olfaction, and mechanosensory) connect to premotor areas via two pathways—a more direct pathway and one via the mushroom body. This is well illustrated in the olfactory circuit of the honeybee, in which olfactory information processed in the first olfactory neuropile, the antennal lobe, is conveyed to the mushroom body and then to the lateral horn, a suspected premotor area, via a medial tract of projection neurons or directly to the lateral horn and then to the mushroom bodies via a lateral tract of

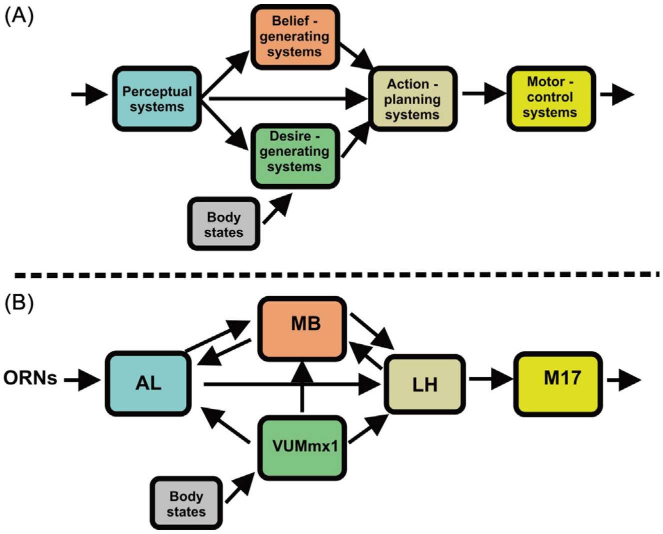

FIGURE 3.4 (A) The cognitive architecture of a generic brain based on interconnected modules for perception, desire- and belief-generating systems, action-planning systems, and motor control systems.[86] Action planning can either be generated by direct inputs from the perceptual systems or result from processes that are generated in parallel pathways weighting the perceptual inputs with respect to learned expectations (belief-generating systems) and signaling of appetitive or aversive outcomes (desire-generating systems). These modules can either be rather basic (as in more simple nervous systems) or highly complex, but their basic structure, particularly with respect to direct and indirect pathways and the necessity of operations between modules, may apply to any nervous system. (B) The cognitive architecture of a honeybee brain illustrated in the case of the olfactory circuit. Olfactory receptor neurons (ORNs) send information about odors to the antennal lobe (AL), which further conveys this information via a direct tract of projection neurons (m-ACT) to the mushroom body (MB), which hosts long-term, olfactory memory traces, and to the lateral horn (LH), a premotor center, via a different tract of projection neurons (l-ACT). The m-ACT tract further projects to the LH and the l-ACT tract to the MB. MBs send feedback neurons to the AL. VUMmx1 is a neuron whose activity mediates the reinforcing properties of appetitive stimuli (e.g., sucrose reward). VUMmx1 contacts the olfactory circuit at the level of the AL, the MB, and the LH, thus favoring the association between odor and sucrose, which is at the basis of olfactory learning. The motor output is represented here by M17, a muscle controlling the appetitive response of proboscis extension, which the bees exhibit to sucrose and/or to an odorant that has been learned to predict sucrose.

projection neurons. The ‘desire’-generating systems are multifold and can be retraced to octopamine- and dopamine-containing neurons, signaling appetitive and aversive outcomes, respectively, and to widely branching peptidergic neurons. The VUM neurons are known to feed into three subsystems in parallel—the action-planning systems such as the lateral horn, the belief-generating system (the mushroom body), and the perceptual system (particularly the olfactory antennal lobe). Less is known about the wiring of the dopamine neurons, and it will be interesting to determine whether they also follow this scheme. The inputs from body states onto the desire-generating systems have not yet been identified, but because their function is modulated by body states (e.g., the levels of satiation, sleep, arousal, and attention), we must assume that such input does exist. In brief, such a ‘boxicology’ of general brain functions, as developed for mammalian brains,[86] applies surprisingly well to the insect brain, and the chapters on insects in this book provide ample evidence for the working of the neurons and networks as components of these boxes.

MINIATURE BRAINS

It is sometimes assumed that ‘simple’ and ‘miniature’ nervous systems such as those of arthropods and (most) mollusks implement cognitive faculties by radically different mechanisms compared to vertebrates, relying predominantly or exclusively on innate routines and elemental forms of associative learning. However, as exemplified previously, constructing a great divide between simple and advanced nervous systems will lead us astray because the basic logical structure of the processes underlying spontaneity, decision making, planning, and communication are similar in many respects in large and small brains. Therefore, it seems more productive to envisage differences in quantitative rather than qualitative terms, providing us with a wealth of ‘model systems’ to elucidate the essence of the basic cognitive processes.

In contrast to studies in mammals and birds,[87] criteria on brain–behavior relations have not been applied systematically to insects. However, it can be tentatively concluded that relatively large insect brains, particularly those with complex mushroom bodies such as those occurring in social Hymenoptera, are equipped with more behavioral flexibility. In the search for neural correlates of behavioral flexibility, features such as ‘information processing capacity’ (IPC) based on the specific neural features have been invoked.[88–90] These features are, for instance, the number of neurons, dendritic structures, the packing density of synaptic connections, and axonal conduction velocity.[90] However, there is no linear relationship between IPC and these measures because brains are organized to reduce wiring costs and smaller brains require fewer material and less energy for construction and maintenance.[91] Long-distance communication within the brain appears to be a major component of IPC, but it also consumes a high amount of energy for spike propagation, again favoring miniaturization. Splitting information across parallel pathways, reducing feedback neural connections, sparse coding, and synchronous activity are a few of many probable neural processes that keep energy consumption low and information capacity high.[91] Such additional processes could be (1) a globular organization of the neuropil (as found in birds and invertebrates) rather than a sheeted organization (as in the cerebral cortex in mammals); (2) large and widely branching neurons whose dendritic branches may participate in different forms of neural processing, either simultaneously or sequentially; and (3) direct oxygen supply via tracheas, which may make energy consumption more efficient and reduce the size and weight of insect brains. Taken together, these processes may endow small brains with relatively higher IPC compared to large brains.

CONCLUSION

It has often been said that neuroscience lacks a theory (or theories) of the brain.[92,93] Indeed, there appears to be no concept at the level of the neurons, the networks, or the whole brain that is able to provide enough generality for developing such a theory. Potentially, the ‘boxicology’ of Carruthers[86] (Figure 3.4), together with the hard facts obtained from anatomy, physiology, and behavioral analysis, may provide a path toward developing a theory about how small brains work. Such a theory would need to include the ‘inner doing’ of the brain—its operations that are not (yet) expressed in behavioral acts and that include operations on representations meaning neural processes at the level of working memory (see Chapter 2). As stated by Carruthers in his book *Architecture of the Mind*,[86]

> To be a believer/desirer . . . means possessing distinct content-bearing belief-states and desire-states that are discrete, structured, and causally efficacious in virtue of their structural properties. These are demanding conditions. But not so demanding that the nonhuman animals can be ruled out as candidates immediately. Indeed we propose to argue, on the contrary, that many invertebrates actually satisfy these requirements. (p. 68)

Future studies on insect brains will gain by incorporating these concepts and by relating them to specific neural modularity and connectivity.

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