

Visual Cognition in Social Insects

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Abstract

Visual learning admits different levels of complexity, from the formation of a simple associative link between a visual stimulus and its outcome, to more sophisticated performances, such as object categorization or rules learning, that allow flexible responses beyond simple forms of learning. Not surprisingly, higher-order forms of visual learning have been studied primarily in vertebrates with larger brains, while simple visual learning has been the focus in animals with small brains such as insects. This dichotomy has recently changed as studies on visual learning in social insects have shown that these animals can master extremely sophisticated tasks. Here we review a spectrum of visual learning forms in social insects, from color and pattern learning, visual attention, and top-down image recognition, to interindividual recognition, conditional discrimination, category learning, and rule extraction. We analyze the necessity and sufficiency of simple associations to account for complex visual learning in Hymenoptera and discuss possible neural mechanisms underlying these visual performances.

INTRODUCTION

Visual learning refers to an individual's capacity of acquiring experience-based information pertaining to visual stimuli so that adaptive responses can be produced when viewing such stimuli again. This capacity admits different levels of complexity, from the establishment of a simple associative link connecting a visual stimulus (e.g., a specific color) and its outcome (e.g., a reward or a punishment) to more sophisticated performances such as learning to categorize distinct objects (e.g., animal versus nonanimal) or apprehending abstract rules applicable to unknown visual objects (e.g., "larger than," "on top of," or "inside of").

The first situation, the establishment of univocal, unambiguous links between a visual target and its outcome, constitutes a case of elemental learning. For instance, what is learned for a color is valid only for that color and not for different ones. In contrast, learning about categories or rules constitutes a case of nonelemental learning, as appropriate responses can be transferred to unknown stimuli for which the subject has no personal experience, as long as the stimuli satisfy the learned category or rule. In these cases, the subject's response is flexible and relatively independent of the physical nature of the stimuli considered.

Social Hymenoptera, particularly bees (*Apis* spp. and *Bombus* spp.), ants, and wasps (several genera), which are at the center of this article, are interesting models for the study of visual learning because in their natural context they have to solve a diversity of visual problems of varying complexity. For instance, these insects learn and memorize the local cues characterizing the places of interest, which are essentially the hive and the food sources (27, 28, 68, 71, 85, 112). Honey bees (*Apis mellifera*), and to a minor extent bumble bees (*Bombus terrestris*), are flower constant, which means that they forage on a unique floral species as long as it offers a profitable nectar and/or pollen reward (14, 40, 46). This capacity is based partly on visual cues provided by flowers such as colors or patterns. Learning and memorizing the visual cues

of the exploited flower through their association with a nectar and/or pollen reward are what allow a bee forager to track a particular flower species in the field (68). Similarly, learning abilities for landmark constellations, complex natural scenes, and celestial cues used in navigation (e.g., azimuthal position of the sun, polarized light pattern of the blue sky) ensure a safe return to the nest and enhance foraging efficiency (15, 16, 24, 74, 103).

Visual capacities are highly developed in social Hymenoptera. Bees, wasps, and some ant species see the world in color (3, 8, 9, 12, 21, 60, 61, 63, 70), perceive shapes and patterns (23, 33, 60, 61, 84, 102), and resolve movements with a high temporal resolution (86). One of the reasons why bees, ants, and wasps constitute an attractive model for the study of visual learning resides precisely in the existence of controlled experimental methods for the study of these capacities in the laboratory.

VISUAL CONDITIONING OF BEES

Visual conditioning of honey bees (98) has uncovered the perceptual capabilities of these insects and has been used to this end for nearly a century. This protocol exploits the fact that free-flying honey bees learn visual cues such as colors, shapes, patterns, depth, and motion contrast, among others (33, 34, 59, 98, 102), when these cues are presented together with a reward of sucrose solution. Each bee is individually marked by means of a color spot on the thorax or the abdomen so that individual performances can be recorded. The marked bee is generally displaced by the experimenter toward the experimental site, where it is rewarded with sucrose solution to promote its regular return. Such pretraining is performed without presenting the training stimuli in order to avoid uncontrolled learning. When the bee starts visiting the experimental place actively (i.e., without being displaced by the experimenter), the training stimuli are presented and the choice of the appropriate visual target rewarded with sucrose. This basic protocol has been used to study visual

learning in other bee species such as bumble bees (24, 63, 82), leaf-cutter bees (9), stingless bees (6, 72), and wasps (3, 60).

In studies on pattern vision, the plane of stimulus presentation is extremely important. Early works (47–49, 98) presented stimuli on the horizontal plane of an experimental table, and the position of the stimuli were varied to verify that bees were indeed choosing a rewarded pattern rather than using position information. In this situation it is difficult to determine which specific information contained in the patterns is used by the insects to make their choices because they can approach the patterns from any possible direction. Later, vertical presentation was preferred because it constrained the approach direction to the patterns (99), thereby forcing a frontal approach and perception. In this way, it was possible to determine whether bees are sensitive to different pattern cues such as orientation, bilateral and radial symmetry, and center of gravity. In all cases, insects have to be trained and tested individually to achieve a precise control of the experience of each subject. It is also important to control the distance at which a choice is made because visual orientation and choice are mediated by different visual cues at different distances or angles subtended by the target (33, 34, 37). The time between visits to the experimental place also has to be recorded, as it reflects the appetitive motivation of the bee (75) and thus its motivation to learn. The associations built in this context can be classical, operant, or both; i.e., they may link a visual stimulus (conditioned stimulus, or CS) and a sucrose reward (unconditioned stimulus, or US), the response of the animal (e.g., landing) and the US, or both, respectively. The experimental framework is nevertheless mainly operant, because the bee's behavior is a determinant for obtaining or not obtaining the sucrose reinforcement.

Visual conditioning of freely flying insects does not allow visual learning to be studied at the cellular level. Because bees freely fly during the experiment, studying neural activity in visual centers in the brain simultaneously remains impossible thus far. Recently, however,

a protocol for visual conditioning of harnessed bees has been developed (50, 51). This protocol, based on pioneer studies by Kuwabara (56), consists of training a harnessed bee to extend its proboscis to colors (50) or motion cues (51) paired with sucrose solution. Hungry bees reflexively extend the proboscis when their antennae are touched with sucrose solution, the equivalent of a nectar reward. In this protocol, colors or patterns are paired with a sucrose reward to create a Pavlovian association in which the visual stimuli are the CS and sucrose is the US. Learning, however, is poor in this protocol. It takes 2 days to reach an acquisition level that is approximately 40%, and this is possible only if bees have their antennae previously cut. The reasons for the apparent interference of the antennae on visual learning remain unknown. Cutting the antennae may affect the general motivation of the bee so that the sucrose reward is not as attractive as expected by the experimenter (19). Improving this protocol is a priority for future research on visual learning as it will allow combining behavioral quantification with access to the nervous system.

VISUAL CONDITIONING OF ANTS

Visual learning in ants has been studied mostly in the context of insect navigation. Experiments with the Sahara desert ant, *Cataglyphis bicolor*, have increased our understanding of navigation strategies based on celestial cues and landmarks (see Reference 103 for a review). In other ant species such as, *Melophorus bagoti* (10, 74), *Gigantiops destructor* (64), and *Formica rufa* (39, 45), similar questions have been investigated, thus placing importance on determining how ants use visual cues to negotiate their spatial environment. These works are not examined here because they rarely focus on the learning process itself, which is the main framework of our review. Although learning of visual cues underlies navigation processes studied in these ants, learning curves or memory retention tests are generally absent from these works, thus making difficult any analysis in terms of the associative

links established during spatial learning in ants. It is therefore difficult to determine what is and what is not elemental in these performances.

Nevertheless, a recent work on *Cataglyphis aenescens* and *Formica cunicularia* has used an experimental design that reproduces basic features of visual training in bees (8), as it focuses on color learning and discrimination. These ants were trained in a Y-maze to choose and discriminate monochromatic lights of constant intensity associated with a food reward. Using this kind of design could help researchers dissect in a more controlled way the nature of associative learning in ants.

ATTENTIONAL AND EXPERIENCE-DEPENDENT MODULATION OF VISUAL LEARNING

The first study on bee learning and memory that used controlled protocols for characterizing individual learning and memory employed colors as rewarding stimuli (66). Free-flying honey bees were trained to choose a rewarded monochromatic light and were then presented in dual-choice situations with the rewarded light versus an alternative color on a horizontal plane. This study reported learning curves for different wavelengths and showed that, under these experimental conditions, bees learned all wavelengths after few learning trials. Some wavelengths, particularly 413 nm, were learned faster than others, requiring only one to three acquisition trials (66; but see below). This result argued in favor of innate biases in color learning, probably reflecting the intrinsic biological relevance of the color signals that are learned faster (66). Indeed, color-naïve honey bees in their first foraging flight prefer those colors that experienced bees learn faster (35), and those colors seem to correspond to floral colors highly associated with profitable nectar reward (35).

Visual learning, as studied in these color-conditioning experiments, is elemental, as bees are just presented with a single color target paired with sucrose solution. It was supposed to

be a fast form of learning (66; see above), compared, for instance, to learning of visual patterns, which usually takes longer (20 or more trials). Recent studies on bumble bee and honey bee color learning (21, 29) have nevertheless introduced a new twist to these conclusions. It was long thought that what an animal sees and visually learns is constrained by its perceptual machinery with no or less place for experience-dependent modulations of perception. Studies on honey bees (22, 29) and bumble bees (21) have shown that this idea is wrong: In some cases, learning one and the same color may occur after few trials but in other cases it may take more than 20 trials (**Figure 1a**). The critical feature is how the bees learn the task. Absolute conditioning, in which a subject is trained with a single color rewarded with sugar water, yields generally fast learning. Differential conditioning, in which the same subject learns to discriminate a rewarded from a nonrewarded color, takes more trials, even if the rewarded color is the same as in absolute conditioning. When these animals are asked to discriminate colors in a test, their performance differs dramatically. Whereas bees trained in differential conditioning discriminate colors that are very similar (**Figure 1c**), bees trained in absolute conditioning do not discriminate the same pair of colors (**Figure 1b**) (21, 29). Similar results were obtained in ants trained to discriminate colors in a Y-maze (8).

Comparable results were obtained in a study on pattern learning and discrimination by honey bees (32, 89). Whereas differential conditioning results in a visual recognition strategy that uses the cues present in the whole pattern, absolute conditioning results in a recognition strategy that restricts cue sampling mainly to the lower half of the pattern. In other words, bees recognize a pattern differently, depending on the kind of learning implicit to the conditioning task. In both cases (color and pattern learning), however, differential conditioning increases the demands imposed on the perceptual system of the bees, which must not only go where a rewarded stimulus is presented (absolute conditioning) but also discriminate

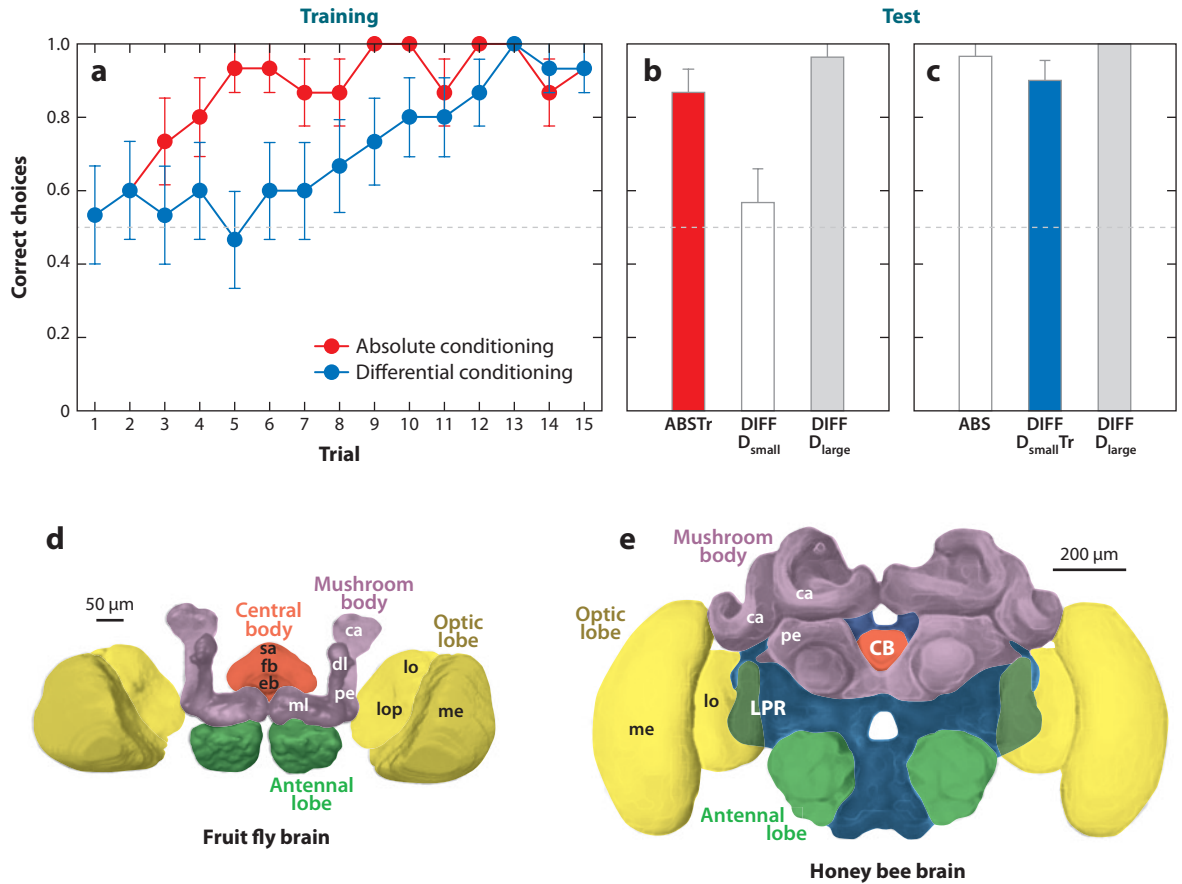


Figure 1

(a, b, c) Attention-like processes in honey bees. Performance of the free-flying bees trained with colors under absolute and differential conditioning. (a) Acquisition along 15 trials (mean \pm standard error; $n = 15$ bees for each curve). (b) Tests of the group trained with absolute conditioning. The red bar depicts the test presenting the trained situation (ABSTr), i.e., the single color that was previously rewarded. The white bar depicts the test presenting a novel differential situation (DIFF D_{small}), i.e., the color that was previously rewarded versus a new color that was similar to the trained one. The gray bar depicts the test presenting a novel differential situation (DIFF D_{large}), i.e., the color that was previously rewarded versus a new color that was different from the trained one. (c) Tests of the group trained with differential conditioning. The blue bar depicts the test presenting the trained situation (DIFF D_{small}Tr), i.e., the previously rewarded and the nonrewarded colors that were similar. The white bar depicts the test presenting just the previously rewarded color (ABS). The gray bar depicts the test presenting the previously rewarded color versus a novel color different from the rewarded one (DIFF D_{large}). (d) Three-dimensional reconstruction of the fruit fly (*Drosophila melanogaster*) brain (courtesy of Armin Jenett). (e) Three-dimensional reconstruction of a honey bee brain. Abbreviations: me, medulla; lo, lobula; lop, lobula plate; ca, calyx; dl, dorsal lobe; ml, medial lobe; pe, peduncle; CB, central body; eb, ellipsoid body; fb, fan-shaped body; sa, superior arch; LPR, lateral protocerebrum. Adapted from Reference 29.

it from a nonrewarding alternative (differential conditioning). The difference in performance therefore suggests that attentional processes are involved because in differential conditioning the bee has to focus on the difference and

not on the mere presence of a visual target, thus making learning slower. In any case, the result goes against the idea that the difference between two colors is an immutable property constrained by the visual machinery.

When Menzel characterized color learning (66, 67; see above), studies on pattern perception were simultaneously performed by Wehner (99–101) and others (e.g., 1), continuing the tradition started by von Frisch's students (47–49, 105–107). In contrast to Menzel's work, these studies focused not on learning but on the perceptual capabilities of bees confronted with pattern discrimination tasks. Visual conditioning was also used in these and later works on pattern perception (for reviews, see References 59, 84, and 102), but a quantification of acquisition curves and/or a characterization of pattern memory was absent from these works. This tradition was continued in the 1970s, 1980s, and even 1990s, as visual learning was used mainly as a tool to answer questions on visual perception and discrimination. Yet, some experiments showed that in pattern vision, as in color vision, what a bee perceives depends on its previous visual experience and of possible attentional processes. Zhang & Srinivasan (115) showed, for instance, that the previous visual experience of a bee can speed up the analysis of the retinal image when a familiar object or scene is encountered. They first attempted to train bees to distinguish between a ring and a disk when each shape was presented as a textured figure placed a few centimeters in front of a similarly textured background. The figures are, in principle, detectable through the relative motion that occurs at the figure borders, which are at a different distance than the background when bees fly toward the targets. Despite intensive training, the bees were incapable of learning the difference between a ring and a disk, a discrimination that usually poses no problems when the bees experience these stimuli as plain (nontextured) shapes. Zhang & Srinivasan then trained a group of bees to this "easy" problem, presenting a plain black disk and ring a few centimeters in front of a white background. The bees could, as expected, easily learn the task. They were then confronted with the difficult problem of learning the textured disk versus the ring, and this time they immediately solved the discrimination. Thus, pretraining with plain stim-

uli primed the pattern recognition system in such a way that it was able to detect shapes that otherwise could not be distinguished. It may be that such pretraining triggers attentional processes that allow better focusing on the targets that have to be discriminated.

Uncovering how attentional processes and learning modulate visual perception constitutes an unexplored and promising research field. The existence of attentional processes in insect brains is not far-fetched, and recent research has located such processes in precise structures of the insect brain. In the fruit fly, *Drosophila melanogaster*, attention can be demonstrated and characterized at the physiological level (96). A fruit fly fixed stationary within a circular arena, and tracking a visual object (a vertical black bar) moving at a constant frequency around it, exhibits anticipatory behavior consistent with attention for the bar tracked. Such an anticipatory tracking has a neural correlate in the form of a transient increase in a 20–30 Hz local-field potential recorded in a region of the brain called the medial protocerebrum (**Figure 1d**) (96). In other words, the 20–30 Hz response in the fly brain is correlated with transitions to behavioral tracking. This response is not only anticipatory, but also selective to the stimulus presented, increased by novelty and salience and reduced when the fly is in a sleep-like state (96). Moreover, the use of mutants showed that a subset of neurons of the mushroom bodies, which are a higher-order structure of the insect brain (**Figure 1d,e**), is required for both the tracking response and the 20–30 Hz response (96). This result is consistent with the finding that mushroom bodies are required for choice behavior of *D. melanogaster* facing contradictory visual cues (90). In this case, individually tethered flies flying stationary are trained in a circular arena in which one kind of visual stimulus (say, a T pattern) represents a permitted flight direction, while another kind of visual stimulus (say, an inverted T pattern) represents a forbidden flight direction associated with a displeasing heat beam on the thorax. Tang & Guo (90) conditioned flies

to choose one of two directions in response to color and shape cues; after the training, flies were tested with contradictory cues. Wild-type flies made a discrete choice that switched from one alternative to the other as the relative saliency of color and shape cues gradually changed, but this ability was greatly diminished in mutant flies with miniature mushroom bodies or with chemically ablated mushroom bodies. In other words, mushroom bodies mediate the assessment of the relative saliency of conflicting visual cues (90, 110) and are also involved in improving the extraction of visual cues after pretraining in *D. melanogaster* (77). The mushroom bodies of hymenopterans may play similar roles (**Figure 1e**), thus favoring attention and better problem solving and discrimination.

Yet, visual learning and the neural circuits mediating it are still poorly understood in the fruit fly. The mushroom bodies, which are the main site for olfactory memories, are not directly involved in visual learning because in *D. melanogaster*, contrary to hymenopterans, there is no direct input from the visual areas of the brain to these structures (108). Recent studies have succeeded in identifying the precise neuronal substrates of two forms of visual memory in the *D. melanogaster* brain outside the mushroom bodies (62). Memories for pattern elevation and orientation were retraced to different neuronal layouts of the central complex, a median structure of the insect brain (**Figure 1d**). Liu et al. (62) showed that two neuronal layers of the central complex are required to achieve visual discriminations based on pattern elevation or orientation. In all cases, visual short-term memory was studied, thus leaving open the question of the localization of visual long-term memory. In bees and wasps, the localization of visual memories may differ from that of *D. melanogaster*. In contrast to the fruit fly, visual areas of the hymenopteran brain provide direct input to the mushroom bodies (26), thus making these structures a candidate for the localization of visual memories in addition to the central complex (**Figure 1d**).

COMPLEX FORMS OF VISUAL LEARNING (THAT MAY NOT BE SO COMPLEX)

Only in the 1990s did researchers become interested in the existence of cognitive processing in insects, and the honey bee was the model chosen to address most of the works performed in that direction. Such a delay with respect to the cognitive revolution, which flourished from the late 1970s to the early 1980s (73), can only be explained by the reluctance to view invertebrates, and therefore insects, as organisms capable of nonelemental, higher-order forms of learning. For instance, the main idea with respect to visual pattern learning, which is still sometimes defended, was that insects can only view isolated spots, blobs, and bars without the capacity of integrating them into a given configuration (52–55). Even a basic capacity of recognition systems such as generalization, the ability of individuals to respond to stimuli that, despite being different from a trained target, are nevertheless perceptually similar to it (81, 83), was and is considered by some researchers as too high-level for a honey bee (54, 55). Yet, dozens of works had already shown that honey bees generalize their choice of visual patterns to novel figures that have some similarity to those that have been trained (e.g., 1, 100). This refusal of generalization capacities is consistent with the preconception that insects have limited plasticity and should be viewed rather as reflex machines reacting to specific features in the environment to which they are tuned.

In the past decade, however, researchers have found evidence showing that bees are not reflex machines and that they exhibit visual learning capabilities that were only suspected in some vertebrates. Some of these capacities are surprising and may be viewed as nonelemental. However, an alternative view could argue that it is possible to explain them based on simple, elemental associations. These experiments, reviewed in the next section, were not conceived to address these opposite views, so that we are currently unable to determine whether these

performances are forms of elemental or higher-order learning.

Visually Based Individual Recognition in Wasps

The capacity of individuals to recognize their distinctive identity has long been dismissed in social insects due to the cognitive requirements that such performance may impose on colonies made of thousand of individuals. For instance, Wilson (104) stated that “. . . insect societies are, for the most part, impersonal . . . The sheer size of the colonies and the short life of the members make it inefficient, if not impossible, to establish individual bonds.” However, not all social insects live in huge, overcrowded societies. Small, relatively primitive colonies of bumble bees, wasp, and some ant species are based on dominance hierarchies where individual recognition may be crucial for responding appropriately to a conspecific. Indeed, recent studies have shown that *Pachycondyla villosa* ant queens recognize each other using olfactory, cuticular cues (20). In the visual domain, studies on the paper wasp, *Polistes fuscatus*, have shown that individual recognition is achieved through learning the yellow-black patterns of the wasp faces and/or abdomens (92). In another species, *Polistes dominulus*, more variable patterns with larger black components were carried by individuals ranking higher in the nest hierarchy. Altering these facial and/or abdominal color patterns induced aggression against such animals, whether or not their patterns were made to signal higher or lower ranking. These results, however, were challenged by another study (9a), which could not find evidence supporting the hypothesis that the facial patterns of *P. dominulus* act as hierarchy or quality signals. Size, on the contrary, was highly correlated with social dominance in this wasp (9a). Although these results question the validity of the hypothesis that posits that visual facial patterns that contain more black areas or more black spots are associated with dominant wasps, they do not exclude the possibility that visual patterns are used as individual identity markers rather

than as status markers. In this scenario, wasps would recognize each other on the basis of their facial features, and each individual mask, regardless of its amount of black areas or spots, would have an unambiguous outcome in terms of its ranking in the social structure (i.e., mask $A \rightarrow \alpha$ individual and mask $B \rightarrow \beta$ individual). Wasps would learn a series of elemental associations between mask patterns and social ranking. Given the small size of colonies, in which 5 to 10 individuals can coexist, storing several memories, one for each individual, seems plausible. If this were the case, a fundamental goal would be to characterize the storage capacity of the visual memory as related to colony size.

Observatory Learning in Bumble Bees

Recent studies on bumble bees (57, 58, 109) have shown that these insects copy other bees' learned foraging preferences by observing their choices of visual, rewarded targets. Bumble bees, *B. terrestris*, are influenced by other conspecifics when sampling unfamiliar flowers, such that they land on unknown flowers where other bees have been (57). This occurs even when naïve bees are separated from experienced foragers by a transparent screen so that they can neither sample the flowers by themselves nor interact with their foraging conspecifics (109). Similarly, naïve bees abandon an unrewarding species and switch to a more rewarding alternative more quickly if accompanied by experienced foragers (58).

As surprising as this performance may appear, it can be accounted for by an elemental form of associative learning called second-order conditioning (76), which involves two connected associations. In this scenario, an animal first learns an association between a CS and an US (CS1 + US) and then experiences a pairing between a new conditioned stimulus, CS2 and CS1 (CS1 + CS2). In this way, CS2 becomes meaningful, directly through its association with CS1 and indirectly with the US. How would this apply to the observational learning of bumble bees? One could propose that naïve bumble bees would first

associate the presence of a conspecific with reward (CS1 + US) simply by foraging close to experienced foragers. Afterward, observing a conspecific landing on a given color may allow an association between color and conspecific (CS2 + CS1) to be established (58). These connected elemental links may thus underlie the observational learning of bees. This hypothesis is supported by the fact that honey bees can learn second-order associations while searching for food. They learn to connect both two odors (odor 1 + sucrose reward; Odor 2 + Odor 1) (7) and one odor and one color (odor + sucrose reward; color + odor) (42).

Symbolic Matching to Sample and Other Forms of Conditional Discrimination in Honey Bees and Bumble Bees

Symbolic matching to sample is a term used to describe an experimental situation in which the correct response to a problem depends on a specific background or condition. In other words, animals have to learn, for instance, that given condition A, response C is correct, while for condition B, response D is correct. Symbolic matching to sample is a form of conditional discrimination because a given stimulus, the sample (also called the occasion setter), sets the condition for the next choice. Using this design, Zhang et al. (117) trained honey bees to fly through a compound Y-maze consisting of a series of interconnected cylinders. The first cylinder carried the sample stimulus (e.g., a vertical or a horizontal black-and-white grating). The second and third cylinders had two exits apiece. Each exit presented a visual stimulus so that the bee had to choose between them. In the second cylinder, bees had to choose between a blue and a green square. In the third cylinder, they had to choose between a radial sector pattern and a ring pattern. Correct sequences of choices were “Vertical–Green–Ring” and “Horizontal–Blue–Radial.” Only after making a succession of correct choices (i.e., in both the second and the third cylinders) could a bee reach a feeder with

sucrose solution. The bees learned to master these successive associations between different kinds of visual cues (117). This finding was also extended to other sensory modalities, as the same principle applied when visual cues were combined with odors in a similar protocol (87).

Conditional learning allows other variants that, depending on the number of occasion setters and discriminations involved, have received different names. For instance, another form of conditional discrimination 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, C and D. When C is available, stimulus A is rewarded, whereas stimulus B is not (A+ versus B-); the opposite occurs (A- versus B+) when D is available. The transwitching problem is also considered a form of contextual learning because the occasion setters C1 and C2 can be viewed as contexts determining the appropriateness of each choice. Bumble bees 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 (28). Here, the nest and the feeder provide the appropriate contexts defining what has to be chosen. Bumble bees 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: At the nest, access 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 applied (27). In both cases, the potentially competing visuomotor associations were insulated from each other because they were set in different contexts.

Solving this kind of problem can be viewed as a form of nonelemental learning and thus as a sophisticated form of cognitive visual processing. Indeed, as for other forms of conditional discrimination, one could describe this protocol as CA+, CB- (if C then A, but not B), and DA-, DB+ (if D then B, but not A). Each stimulus, A, B, C, and D, therefore is rewarded as often

as it is nonrewarded, such that solutions cannot be based on the mere outcome of A, B, C or D. A higher-order solution then would be to learn the outcome of each particular configuration, CA, CB, DA, or DB. However, an alternative explanation could argue that what the insects do is establish hierarchical simple associations as the ones underlying second-order conditioning (see above). Indeed, one could imagine that bees learn to associate a radial disc with sucrose reward and that they then learn to associate a 45° grating with the radial disc. This is a relatively simple strategy that is probably used by bees for navigational purposes (116, 117) when they are confronted with successions of different landmarks en route to the goal.

A critical factor determining one strategy or the other therefore may be the temporal order of stimulus presentation. If these are presented serially, learning chains of simple associations could be primed, while simultaneous presentation of stimuli may prime learning of configurations and their specific outcome. An example of the latter is the case of honey bees trained to solve a biconditional discrimination, AC+, BD+, AD-, BC-, in which all four stimuli were presented simultaneously and were rewarded as often as they were nonrewarded (80). Four different gratings combining one color (yellow or violet = A or B) with one orientation (horizontal or vertical = C or D) were used in such a way that bees had to learn that, for instance, yellow-horizontal (AC) and violet-vertical (BD) were rewarded while yellow-vertical (AD) and violet-horizontal (BC) were nonrewarded. Bees learned to choose the rewarded stimuli, although the colors and orientations were ambiguous when considered alone. Thus, they learned the configurations and not the specific outcome of the elements (80). Again, cumulative experience is a critical factor promoting configural learning (36). Although few learning trials promote processing of a compound color stimulus made of A and B elements as the sum of A and B, increasing number of trials results in bees treating the compound AB as a unique entity that is different from its composing elements (36).

NONELEMENTAL VISUAL LEARNING

The visual performances of the previous section could be accounted for by elemental associations despite their sophistication. A higher level of complexity, however, is reached when animals respond in an adaptive manner to novel stimuli that they have never encountered before and that do not predict a specific outcome per se based on the animals' past experience. Such a positive transfer of learning (78) is therefore different from elemental forms of learning, which link known stimuli or actions to specific rewards (or punishments). In the cases considered in this section, the insects' responses have in common the transfer to novel stimuli, which cannot be explained based on the previous knowledge that the animal has of these stimuli.

Categorization of Visual Stimuli in Honey Bees

Visual categorization refers to the classification of visual stimuli into defined functional groups (44). 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 (94, 113). A typical categorization experiment trains an animal to extract the basic attributes of a category and then tests it with novel stimuli that were never encountered before and that may or may not present the attributes of the category learned. If the animal chooses the novel stimuli on the basis of these attributes, it classifies them as belonging to the category and exhibits therefore positive transfer of learning.

Several studies have shown the ability of visual categorization in free-flying honey bees trained to discriminate different patterns and shapes. For instance, van Hateren et al. (95) trained bees to discriminate two given gratings presented vertically with different orientations (e.g., 45° versus 135°) by rewarding one of these gratings with sucrose solution. Each bee was trained with a changing succession of pairs of different gratings, one of which was always

rewarded and the other not. 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, which was perpendicular to the rewarded one. Under these circumstances, the bees had to extract and learn the orientation that was common to all rewarded patterns to solve the task. This was the only cue predicting reward delivery. In the tests, bees were presented with novel patterns, all of which were all nonrewarded, and 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. Thus, bees could categorize visual stimuli on the basis of their global orientation.

They can also categorize visual patterns based on their bilateral symmetry. When trained with a succession of changing patterns to discriminate bilateral symmetry from asymmetry, they learn to extract this information from different figures and to transfer it to novel symmetrical and asymmetrical patterns (31). Similar conclusions apply to other visual features such as radial symmetry, concentric pattern organization and pattern disruption (see Reference 5 for a review), and even photographs belonging to a given class (e.g., radial flower, landscape, plant stem) (118).

How could bees appropriately classify different photographs of radial flowers if they vary in color, size, outline? An explanation was provided by Stach et al. (88), who showed that different coexisting orientations can be considered at one time and that they can be integrated into a global stimulus representation that is the basis for the category (88). Thus, a radial flower would be, in fact, the conjunction of five or more radiating edges. In addition to focusing on a single orientation, honey bees assembled different features to build a generic pattern representation, which could be used to respond appropriately to novel stimuli sharing such a basic layout. Honey bees trained with a series of complex patterns sharing a common layout

comprising four edges oriented differently remembered these orientations simultaneously in their appropriate positions and transferred their response to novel stimuli that preserved the trained layout. These results show that honey bees extract regularities in their visual environment and establish correspondences among correlated features. Therefore, they may generate a large set of object descriptions from a finite set of elements.

This capacity can explain recent findings showing that honey bees learn to recognize human faces if trained to do so (23). In this case, bees were rewarded with sugar water to choose and distinguish people's faces from photographs. Bees chose the appropriate photograph, thus showing a capacity to discriminate this particular kind of stimuli. Does this mean that bees realize that two different persons are behind two discriminated photographs? Not really. To the bees, the photographs were merely strange flowers. The question then would be what information from the photographs was used to recognize the right stimulus. This question was tackled by a work that studied whether bees can bind the features of a face-like stimulus (two dots in the upper part representing the eyes, a vertical line below as the nose, and a horizontal line in the lower part as the mouth) and recognize faces using this basic configuration (2). Bees did indeed distinguish between different variants of the face-like stimuli, thus showing that they discriminate between these options, but grouped together and reacted, therefore, similarly to faces if trained to do so. Stimuli made of the same elements (two dots, a vertical line, and a horizontal line) but not preserving the configuration of a face were not recognized as positive, thus showing that bees learn that the rewarded stimulus consists of a series of elements arranged in the specific spatial configuration of a face (2). Furthermore, if trained with real faces, bees can learn to recognize novel views of a face by interpolating between or averaging views they have experienced (25).

In any case, honey bees show positive transfer of learning from a trained to a novel

set of stimuli, and their performances are consistent with the definition of categorization. Visual stimulus categorization therefore is not a prerogative of certain vertebrates. However, this result might not be surprising as it allows an elemental learning interpretation. To understand this elemental interpretation, the possible neural mechanisms underlying categorization should be considered. If we allow that visual stimuli are categorized on the basis of specific features such as orientation, the neural implementation of category recognition could be relatively simple. The feature(s) allowing stimulus classification would activate specific neuronal detectors in the optic lobes, the visual areas of the bee brain. Examples of such feature detectors are the orientation detectors whose orientation and tuning have already been characterized by means of electrophysiological recordings in the honey bee optic lobes (111). Thus, responding to different gratings having a common orientation of, say, 60° is simple, because all these gratings elicit the same neural activation in the same set of orientation detectors despite their different structural quality.

In the case of category learning, the activation of an additional neural element is needed. Such an element would be a reward neuron whose activity would substitute for sucrose reward. Such a neuron has been identified in the honey bee brain, VUM_{mx1} (ventral unpaired median neuron located in the maxillar neuromere 1) (43). VUM_{mx1} mediates olfactory learning in the honey bee because it contacts the olfactory circuit at its key processing stages in the brain. In other words, when an odor activates the olfactory circuit, concomitant sucrose stimulation activates VUM_{mx1} , thus providing the basis for neural coincidence between odor and reward. The branching of VUM_{mx1} makes it specific for the olfactory circuit and thus for olfactory learning (43). Other VUM neurons whose function is still unknown are present in the bee brain (79). Some of them could provide the neural basis of reward in associative visual learning.

Category learning could thus be reduced to the progressive reinforcement of an

associative neural circuit relating visual-coding and reward-coding neurons, similar to that underlying simple associative (e.g., Pavlovian) conditioning. From this perspective, even if categorization is viewed as a nonelemental learning form because it involves positive transfer of learning, it may simply rely on elemental links between conditioned and unconditioned stimuli.

An even simpler alternative may account for this performance. The mechanism explained above could be viewed as a form of supervised learning, in which a visual network is instructed by the external signal of the reinforcement neuron to respond to the right combination of features. Recent modeling work on the vertebrate visual system has shown that visual networks can learn to extract the distinctive features of a category without any kind of supervision (65). The model relies on spike-timing-dependent plasticity (STDP), which is a learning rule that modifies synaptic strength as a function of the relative timing of pre- and postsynaptic spikes. When a neuron is repeatedly presented with similar inputs, STDP has the effect of concentrating high synaptic weights on afferents that systematically fire early, while postsynaptic spike latencies decrease. Masquelier et al. (65) showed that a network that exhibits STDP and is repeatedly presented with natural images of a given category becomes progressively tuned to respond better to the features that correspond to prototypical patterns of the category. Those features that are both salient and consistently present in the images are highly informative and enable robust object recognition. Testing whether similar neural mechanisms underlie object categorization in the insect visual system would be a fascinating endeavor.

Rule Learning in Honey Bees

In rule learning, the animal learns relations between objects, not the objects themselves. Typical examples are the so-called rules of sameness and of difference. Sameness and difference rules are demonstrated through the protocols of delayed matching to sample (DMTS) and

delayed nonmatching to sample (DNMTS), respectively. In DMTS, animals are presented first with a sample and then with a set of stimuli, one of which is identical to the sample and is reinforced. Because the sample is changed regularly, animals must learn the sameness rule, i.e., “always choose what is shown to you (the sample), independent of what else is shown to you.” In DNMTS, the animal must learn the opposite, i.e., “always choose the opposite of what is shown to you (the sample).” Honey bees foraging in a Y-maze learn both rules (38). Bees were trained in a DMTS problem in which they were presented with a changing nonrewarded sample (i.e., one of two different colored disks or one of two different black-and-white gratings, vertical or horizontal) at the entrance of a maze (**Figure 2**). 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 unknown black-and-white gratings 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. Transfer was not limited to modalities within the visual domain (pattern versus color) but could also operate between different domains such as olfaction and vision (38). Furthermore, bees also mastered a DNMTS task, thus showing that they learn a rule of difference between stimuli (38). The capacity of honey bees to solve a DMTS task has recently been analyzed with respect to the working memory underlying it (114). It was found that the sample is stored for approximately 5 s (114), a period that coincides with the duration of other visual and olfactory short-term memories characterized in simpler forms of associative learning in honey bees (69; see above). Moreover, bees trained in a DMTS task can learn to pay attention to one of two different samples presented successively in a flight tunnel and can transfer the learning of this sequence weight to novel samples (114).

Despite the honey bees' 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 bee from solving 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 (4). In this problem, animals must learn a transitive rule, i.e., $A > B$, $B > C$, then $A > C$. Preference for A over C in this context can be explained by two strategies: (a) deductive reasoning (97) in which the experimental subjects construct and manipulate a unitary and linear representation of the implicit hierarchy $A > B > C$, and (b) responding as a function of reinforced and non-reinforced experiences (91), in which animals choose among stimuli on the basis of the effective number of reinforced and nonreinforced experiences (A is always reinforced whereas C is always nonreinforced).

To determine whether bees can learn a transitive rule, they were trained with five different visual stimuli (A, B, C, D, and E) in a multiple discrimination task: A+ versus B-, B+ versus C-, C+ versus D-, D+ versus E- (4). Training involved overlapping 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 no reinforcement during training. Thus, if bees were guided by the stimulus' associative strength, they should choose randomly between B and D. If, however, bees used a transitive rule, they should prefer B to D.

Honey bees learned the premise pairs as long as these were trained as uninterrupted, consecutive blocks of trials (4). 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

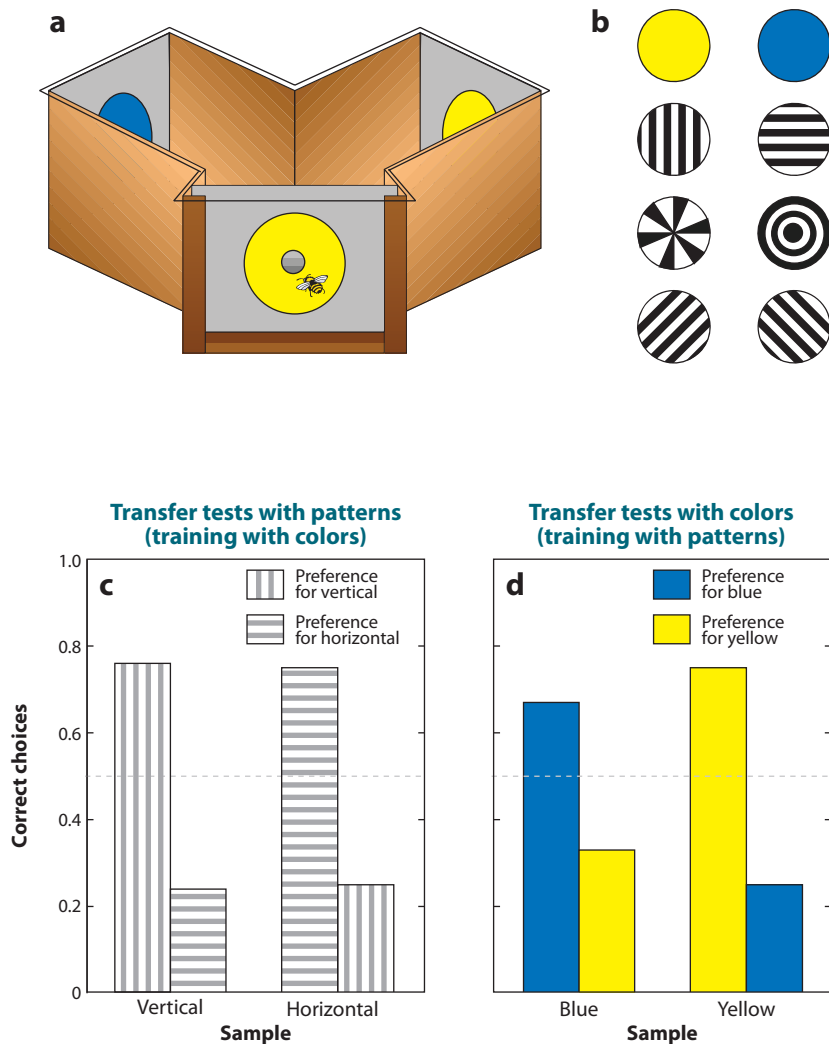


Figure 2

Rule learning in honey bees. Honey bees trained in a delayed matching-to-sample task to collect sugar solution in (a) a Y-maze on a series of (b) patterns or colors learn a rule of sameness. (c, d) Transfer tests with novel stimuli. (c) In Experiment 1, bees trained on the colors were tested on the patterns. (d) In Experiment 2, bees trained on the patterns were tested on the colors. In both cases, bees chose the novel stimuli corresponding to the sample, although they had no experience with such test stimuli. Adapted from Reference 38.

was significantly influenced by their experience with the last pair of stimuli (D+ versus 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 more often visited

B when it was rewarding (B+ vs. C-) than D when it was rewarding (D+ vs. E-), 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 of 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 while the latter supports choice of B, equal choice of B and D in the tests could be explained (4). 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. Recently, Cheng & Wignall (11) demonstrated that failure to master several consecutive visual discriminations is due to response competition occurring when animals are tested. This may explain why bees in the transitive inference protocol were unable to master the successive short blocks of training with different premise pairs.

Counting

Counting could be useful in navigation tasks where the number of landmarks encountered during a foraging trip or near the hive may contribute to efficient orientation of free-flying bees. Furthermore, it could also improve foraging through evaluation of food source profitability (e.g., number of flowers in a patch). Whether or not honey bees estimate numerosity has been addressed recently by two different works that reached similar conclusions (18, 41).

Dacke & Srinivasan (18) were inspired by Chittka & Geiger's (13) pioneering work suggesting that bees may count landmarks en route to the feeder. In Dacke & Srinivasan's protocol, bees were trained to fly into a tunnel to find a food reward after a given number of landmarks. The shape, size, and positions of the landmarks were changed in the different testing conditions in order to avoid any confounding factor(s). Bees showed a stronger preference to land after the correct number of landmark in nonrewarded tests. This behavior was observed when bees were trained to collect reward after one, two, three, or four landmarks but not

more, thus indicating a limit in their counting capacity.

A similar limit was found in a DMTS protocol (41; see above) in which bees had to choose the stimulus containing the same number of items as a sample. The authors controlled for low-level cues such as cumulated area and edge length, configuration identity, and illusionary shape similarity formed by the elements. Their results showed that honey bees have the capacity to match visual stimuli in a DMTS task as long as the number of items does not exceed four. Together with Dacke & Srinivasan's work (18), this result indicates that the bee brain can deal with a real numerosity concept, even if it is limited to a number of four. Interestingly, the same limit was found in humans when time exposure of items to be counted is limited (17).

CONCLUSION

Almost one hundred years of research on visual learning in bees and other social Hymenoptera, starting with Karl von Frisch's (98) first demonstrations on color and pattern learning in bees, have yielded an impressive amount of information about how honey bees, bumble bees, and wasps see the world and learn about visual cues in their environment. New discoveries in this field have shown that, in addition to simple forms of visual learning, social Hymenoptera also master complex forms of visual learning, from conditional discriminations and observational learning to rule learning. Although the cognitive capabilities of bees and wasps may surprise owing to their sophistication, limitations related to natural life seem inescapable. For instance, in the case of wasps learning facial mask patterns of conspecifics, one could imagine that interindividual recognition is certainly possible but probably has limitations in terms of the number of individuals that can be learned and remembered. Similarly, mastering several different associations simultaneously would be facilitated if these are organized serially or hierarchically in chains of associations that can mediate successful navigation in a complex environment. But if these associations

have to be mastered simultaneously at the same place, learning them would probably be difficult given the bees' biological specialization as a serial forager. In this case, learning configurations of stimuli may be more adaptive than learning each component separately.

If bees and wasps exhibit such a high degree of complex forms of visual learning, which kind of limitation do they present as a model for unraveling the mechanisms of these phenomena? The main limitation resides so far in the impossibility of addressing questions related to the cellular and molecular mechanisms underlying these learning forms. Learning protocols have exploited the advantage of not restraining the animals' movements so that the behaviors recorded express all the potential of the insect brain. However, they are limiting because no access to the brain is so far possible in a flying bee. As mentioned above, new

protocols in which bees learn color-reward and motion cues-reward associations under restrained conditions (50, 51) are promising because they allow the neural circuits involved in these learning forms to be accessed (30). The critical question would be then to what extent do restraining conditions limit the expression of more complex forms of visual learning?

Why should bees and wasps continue to be attractive for research on visual cognition despite this technical limitation? The answer is simple: They exhibit sophisticated visual performances that cannot at this time be uncovered in a fruit fly. Future research in social insects should benefit from a comparative analysis between the visual performances and mechanisms of bees and flies and overcome the historic burden of not having a window open to the neural and molecular basis of visual learning, irrespective of the level of complexity considered.

SUMMARY POINTS

1. Visual learning admits different levels of complexity, from the formation of a simple associative link between a visual stimulus and its outcome (elemental learning), to more sophisticated performances such as object categorization or rules learning, which allow flexible responses beyond simple forms of learning (nonelemental learning). Social insects excel at visual learning in a foraging and navigation context.
2. Honey bees, ants, and bumble bees learn to associate different kinds of visual cues such as colors or patterns with food reward. Even if these associations remain elemental, performance can be modulated by the complexity of the task, thus suggesting attentional processes in these insects. Attention- and experience-dependent changes in visual discrimination can be traced to the neural level. Studies in the fruit fly suggest that these processes can be located at the level of mushroom bodies, a structure of the insect brain involved in learning and memory.
3. Social insects exhibit sophisticated visual abilities. Wasps recognize each other on the basis of facial marks, bumble bees learn to choose profitable food sources by observing the choice of other bees, and honey bees and bumble bees learn to solve different kinds of conditional discriminations. These performances admit both elemental and nonelemental explanations.
4. Depending on their past experience, honey bees respond in an adaptive manner to novel stimuli that they have never encountered before. Such a positive transfer of learning, characteristic of nonelemental forms of learning, has been shown in studies demonstrating categorization, learning of rules such as sameness or difference, and basic counting abilities in bees.

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