Honey Bees as a Model for Vision, Perception, and Cognition

Mandyam V. Srinivasan

Queensland Brain Institute and School of Information Technology and Engineering,
University of Queensland, St. Lucia, QLD 4072, Australia;
email: M.Srinivasan@uq.edu.au

ARC Centre of Excellence in Vision Science, The Australian National University,
Canberra, ACT 0200, Australia

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Abstract

Among the so-called simpler organisms, the honey bee is one of the few examples of an animal with a highly evolved social structure, a rich behavioral repertoire, an exquisite navigational system, an elaborate communication system, and an extraordinary ability to learn colors, shapes, fragrances, and navigational routes quickly and accurately. This review examines vision and complex visually mediated behavior in the honey bee, outlining the structure and function of the compound eyes, the perception and discrimination of colors and shapes, the learning of complex tasks, the ability to establish and exploit complex associations, and the capacity to abstract general principles from a task and apply them to tackle novel situations. All this is accomplished by a brain that weighs less than a milligram and carries fewer than a million neurons, thus making the bee a promising subject in which to study a variety of fundamental questions about behavior and brain function.

INTRODUCTION

The worker honey bee, by virtue of its lifestyle, is a spectacularly suitable organism for studying fundamental principles of color vision, pattern recognition, learning and memory, flight control, and navigation (55, 75, 78, 84, 89). Gathering nectar and pollen is the raison d'être of a forager's existence. To forage successfully, a bee has to learn and remember the color, shape, and fragrance of flowers that are bountiful in these nutrients, and also how to get to them. Because the flowers that are in bloom are likely to change every few days, the bee needs, and has evolved, an impressive ability to learn (and relearn) colors, odors, shapes, and routes quickly and accurately. A bee can learn a new color in about half an hour (after it has made about five visits to collect a food reward), a new pattern in about half a day (after 20–30 rewarded visits), and a new route to a food source in about 3 to 4 visits (provided the route is not through a complex labyrinth). It can learn to visit different species of flowers at different locations, at different times of the day. The biology of the honey bee thus offers a tailor-made opportunity for studying the mechanisms by which sensory stimuli are perceived, recognized, and categorized, and how navigational strategies are learned and applied. This review concentrates on the female (worker) honey bee, *Apis mellifera*, about which more is known, in these contexts, compared with the queen or the male drone. Hence, we occasionally refer to our subject as "she," rather than "he" or "it."

We begin with a brief description of the structure and optical organization of the honey bee's compound eye, which is essential for a proper appreciation of this animal's visual capacities. We then describe the honey bee's performance in relation to some of the questions posed above.

THE COMPOUND EYE

Most insects, including honey bees, possess two compound eyes. A succinct schematic illustration of the compound eye of a honey bee is given in figure 2.5 of Reference 31. In the female (worker) honey bee, each compound eye consists of about 4500 "little eyes," or ommatidia. Each ommatidium consists of a small lens (approximately 15–20 μ in diameter), which focuses light onto a group of nine photoreceptors. Each ommatidium collects light from a small patch of the world—it accepts incoming light from a cone-shaped region subtending about 2.5° (46). The angular width of this cone is known as the acceptance angle. Neighboring ommatidia view neighboring regions of space, with their optical axes (viewing directions) separated by about 2° (67).

This angular separation is termed the interommatidial angle. The nine photoreceptor cells within each ommatidium can be grouped into three classes according to the spectral sensitivity of the light-sensitive pigment (photopigment) that they contain: UV sensitive (with a peak sensitivity at 340 nm), blue sensitive (peaking at 463 nm), and green sensitive (peaking at 530 nm) (53). Each cell is elongated in shape, aligned radially, and carries a set of slender tubular structures, called microvilli, which contain the photopigment. The microvilli are present throughout the length of the cell body of each photoreceptor and are oriented at right angles to the optical axis of the ommatidium.

Absorption of light by the photopigment causes a chain of events (the so-called phototransduction cascade), which ultimately leads to a change in the electrical potential across the cell membrane (a so-called depolarization). It is this change in potential that is signaled to the brain and which ultimately leads to the perception of light. The microvillar regions of the nine different cells are closely juxtaposed to form a cylindrical, central column that runs along the length of the ommatidium. This cylindrical column, known as the rhabdom, is surrounded by the photoreceptors. It possesses a higher optical refractive index than the surrounding photoreceptors and functions as an optical waveguide, thus confining the incoming light to the rhabdom and encouraging its absorption by the photopigment. As light travels down the rhabdom, it is absorbed (to different extents) by the three different spectral classes of photoreceptors, depending upon its intensity and spectral composition. It is the magnitude and the relative stimulation of the three photoreceptor classes within each ommatidium that convey information on the brightness and the color of the impinging light. Each ommatidium therefore carries information on the brightness and color of the light that it receives. The totality of approximately 9000 ommatidia (about 4500 in each eye) therefore captures a panoramic, pointillistic representation of the surrounding world.

The axons of the nine photoreceptors within each ommatidium project to the next neuropil, the lamina, for further processing. Visual information is then conveyed to the next ganglion, the medulla, for further processing, and eventually to the lobula, where complex analysis of the image takes place, leading to the perception of color, shape, and motion (for a recent review, see Reference 28).

The acceptance angle of the ommatidium, the interommatidial angle, and the distribution of photoreceptor classes within each ommatidium are not constant over the entire compound eye. They show important variations, reflecting regional specializations that serve specific requirements. For example, the frontal region is specialized for high visual acuity (67), the fronto-ventral region of the eye is specialized for color vision, and the region at the dorsal rim of each eye is specialized for the perception of the polarized light patterns in the sky (45, 46).

PERCEPTION AND LEARNING OF COLORS

The honey bee has figured prominently in the history of the study of color vision. After humans, the honey bee was the second nonhuman organism for which the existence of color vision was demonstrated, only a year after the discovery of color vision in fish. Both of these discoveries were made by the Nobel Laureate Karl von Frisch. von Frisch trained a group of individually marked bees to collect a food reward placed on a piece of blue cardboard (83). He then tested whether the bees had learned this color by removing the reward and surrounding the blue card with cards of varying brightness (gray levels), ranging from black to white. He found that the trained bees consistently landed on the blue card in search of the food—although it no longer carried any reward—and regardless of where this card was positioned in relation to the other cards.

The use of cues derived from scents or pheromones was excluded by using a fresh blue card in the tests. The trained bees also found the blue card when it was surrounded by cards of other colors. These experiments demonstrated, clearly and convincingly, that bees perceive color, and that they perceive it as a distinct sensation—one that is different from the sensation of brightness. Convincing as these experiments were, it was a long time before the scientific community was willing to accept this conclusion and to acknowledge that a creature as humble as the bee could distinguish colors. We now know that a bee can learn a color in about half an hour—after it has made about 3 to 4 visits to a food-bearing source (50).

In the decades since this groundbreaking discovery, microspectrophotometric analyses of the visual pigments in the photoreceptors of the honey bee's compound eye have revealed the existence of three different types of photopigments that absorb light maximally in the UV, blue, and green regions of the spectrum, respectively (53, 58). Intracelluar recordings of the electrical responses of these photoreceptors have confirmed this by revealing that the photoreceptors can indeed be grouped into three different spectral classes, with peak sensitivities in the UV (around 350 nm), blue (around 440 nm), and green (around 540 nm) regions of the spectrum, respectively (2, 54). The genes that encode the three different photopigments have now been determined (6, 81).

In the meantime, sophisticated behavioral analysis of color discrimination, using a range of monochromatic colors, as well as color mixtures, has demonstrated that color vision in the honey bee is fully trichromatic, just as it is in humans (17, 18, 50–52, 85). That is, the honey bee's visual system analyzes color by making full use of the information provided by all of its three spectral classes of photoreceptors. The major differences between color vision in honey bees and humans are as follows. First, the visual spectrum of the bee (with its UV, blue, and green photoreceptors) is shifted toward shorter wavelengths (bees see UV, but not red, whereas humans see red, but not UV). The UV sensitivity is useful for bees, enabling them to detect and distinguish between flowers that reflect UV and also to see the so-called nectar guides—UV patterns that some flowers carry, which function as signposts to direct the visiting bees toward the nectar within. Second, the bee's three photopigments are spaced uniformly along the bee's visual spectrum. Presumably, this design is optimal for evaluating the colors of the flora that occur naturally (10, 86). A comprehensive overview of the evolution of color vision in insects is given by Briscoe & Chittka (4).

In humans, two of the photopigments (red and green) are closely spaced and have broadly overlapping sensitivities (with peak sensitivities at 563 nm and 534 nm, respectively), whereas the third pigment, blue, is positioned much farther away (with peak sensitivity at 420 nm) (3). It has been suggested that this arrangement is suitable for assessing the ripeness of fruit against a background of foliage (57, 80).

What are the factors that determine the performance and the accuracy of bees' choices in color discrimination tasks? Chittka et al. (8) and Dyer & Chittka (20) observed that bumble bees are less accurate at discriminating colors that are spectrally closely separated compared with colors that are distinctly different—the choice frequency for the correct color is higher in the latter case. Although this is not surprising, they also found that discrimination performance with the closely spaced colors can be improved if the training paradigm is modified to include a mild punishment when bees make the wrong choice—the incorrect stimulus carries unpleasant-tasting quinine. Thus, with bees, the carrot-and-stick approach to training appears to be more effective than the carrot approach alone. Furthermore, they found that bees spend more time making a decision when the colors are closer. Thus, the harder the task, the longer the bees spend deliberating on it. Another observation was that for a given individual, there appears to be a trade-off between accuracy and decision time—longer decision times are correlated with higher accuracies. Finally, across individuals, bees that made more rapid decisions tended to be less accurate. Longer inspection durations may improve the signal-to-noise ratios underlying the discrimination, and thus enhance the accuracy of performance.

Like humans, bees possess color constancy, which is the ability to determine the true color of an object (that is, its spectral reflectance) more or less independently of the spectrum of the illumination under which it is viewed, although this performance is not 100% robust (19, 49, 92). The spectrum of the light that is reflected from an object can vary dramatically, as the spectrum of the light that illuminates it is varied. Nevertheless, it appears that humans (and bees) "discount the illuminant" and ascertain the true color of the object over a large range of illumination spectra. For bees, this capacity enables accurate identification of the colors of flowers whether they are in the sun or under the shade of a tree—where the spectrum of the illumination can be different because it comes not directly from the sun, but from the sky and from light reflected by foliage.

SPATIAL ACUITY OF HONEY BEE VISION

How much spatial detail can the eye of a honey bee resolve? The spatial resolving ability of the compound eye is determined primarily by two parameters: the acceptance angle of the ommatidium (symbolized by $\Delta\rho$) and the interommatidial angle (symbolized by $\Delta\phi$). $\Delta\rho$ determines the extent to which the image of the world is smeared, or blurred, by the optics of the compound eye: The larger the value of $\Delta\rho$ is, the greater the blur is, or the lower is the amount of spatial detail that is captured by the optics. $\Delta\phi$ determines the fineness of the visual mosaic of the compound eye: The smaller the value of $\Delta\phi$ is, the greater is the capacity of the eye to sample the detail in the image that is transmitted by the optics. In most compound eyes, including that of the honey bee, these two parameters are closely matched; that is, the optics transmit only as much detail as the mosaic can sample (or represent) accurately. This is good engineering design: Severe distortions of the image, caused by undersampling, can occur if the mosaic is too coarse to resolve all the detail transmitted by the optics (71). In engineering terms, the compound eye seems to have evolved to obey the Sampling Theorem (68, 69). In the frontal region of the honey bee compound eye, $\Delta\rho$ is about 2.6° (24, 44, 46). $\Delta\phi$ is about 2.1° in the horizontal plane (67) and about half this value in the vertical plane (because of the hexagonal arrangement of the ommatidia). Taken together these figures indicate that, in the honey bee, the spatial resolving power is limited primarily by $\Delta\rho$, and not by $\Delta\phi$. From the value of 2.6° for $\Delta\rho$, one can calculate that the eye is capable of resolving angular spatial frequencies of up to about 0.38 cycles per degree, using the criterion developed by Snyder (70).

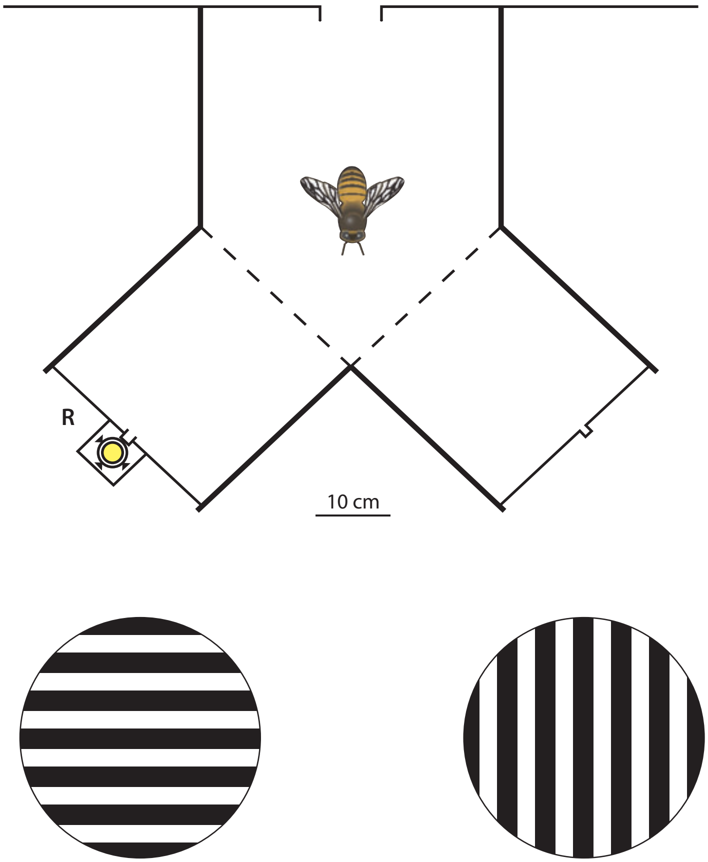

Figure 1

Illustration of a Y-maze apparatus for testing the bees' ability to discriminate visual stimuli using a dual-choice paradigm. The stimuli are presented on the (vertical) end wall of each tunnel. One of the stimuli (usually termed the positive stimulus) offers a reward of sugar solution (R) in a feeder that is placed behind it and is accessible though a short tube in the middle of the stimulus. The other stimulus (usually termed the negative stimulus) carries no reward, but it carries a visually identical tube that is closed at the back end. During training, the positions of the vertical and horizontal gratings and the associated reward are frequently swapped to ensure that the bees learn to choose the pattern with the correct orientation and not simply the arm of the apparatus that carries the reward. The gratings shown illustrate the patterns that have been used to measure the spatial acuity of honey bee vision. The bee is not shown to scale. Modified with permission after Reference 73.

The above figure for the resolving ability of the honey bee's compound eye has been confirmed independently by behavioral measurements of visual acuity (73), in which bees were trained, by reward, to distinguish between vertical and horizontal gratings (striped patterns) in a Y-maze (**Figure 1**). One of the orientations (e.g., horizontal) offered a food reward concealed behind the pattern, whereas the other did not. Once the bees had learned to distinguish the orientations of coarsely striped, easily resolvable gratings, the spatial frequency of the gratings (their fineness) was increased systematically to determine the highest spatial frequency at which the bees were still able to discriminate the horizontal from the vertical orientation. These experiments—which are akin to the vision tests that humans undergo to obtain a driver's license—indicate that the honey bee's visual system is capable of resolving gratings with a spatial frequency of up to 0.35 cycles per degree. By comparison, the human eye can resolve angular spatial frequencies of up to 60 cycles per degree (5), which implies that we can see about 170 times more detail in the world than a honey bee can.

SHAPE AND PATTERN VISION

The study of pattern vision in the honey bee has seen three major milestones, or eras (72, 74, 39). The studies of the first era, by Karl von Frisch (83) and Hertz (36), were carried out by cutting two or more patterns out of black paper, placing them flat on a horizontal table, and training a group of bees to collect a reward of sugar water at one of the patterns. The positions of the patterns were varied frequently to ensure that the bees learned to come to a specific pattern, rather than to a specific location on the table. By analyzing the bees' performance in this task, they proposed the so-called flicker hypothesis, namely, that honey bees discriminate between visual patterns in terms of the frequency of on/off stimuli experienced by the compound eye as they cruise above the patterns (37).

The next era commenced with the work of Wehner & Lindauer (91), who began experimenting with patterns presented in the vertical plane (48). Although this may seem a simple modification at first glance, it opened up a whole new dimension in research on pattern recognition in bees. The reason was that one could now ask, for the first time, whether bees can learn the orientation of a pattern. (This could not be done with a pattern laid flat on a table, as the bees could approach such a pattern from any direction.) An interesting observation made in these studies was that, during training, the bees tended to hover stably in front of the training pattern for a second or two before landing on the entrance tube leading to the reward behind the pattern (90). This led Wehner to propose the so-called template hypothesis; that is, bees fixate the pattern and memorize it in a photographic sense. When, after training, the bee is offered a choice between the rewarded pattern and another pattern, the bee evaluates the two patterns by comparing the extent to which each pattern matches the stored template that the bee has acquired of the rewarded pattern during training (87, 89). The template theory of pattern recognition was reinforced by the work of Gould (32, 33), who showed that bees could be trained to distinguish rather small differences between patterns, suggesting that recognition does indeed involve a precise evaluation of the extent to which regions in the viewed pattern match up with corresponding regions in the template.

The third, and most recent, era of pattern recognition in honey bees commenced when people began to ask whether bees could learn abstract features, or properties, of patterns instead of, or in addition to, memorizing them photographically. This was an important step toward gaining insights into the cognitive capacities of the honey bee brain. In the next section, we outline some aspects of the progress made in this era.

LEARNING GENERAL PROPERTIES OF PATTERNS

There can be little doubt that bees use some kind of neural "snapshot" to remember and recognize patterns and landmarks (12, 42). However, is pattern recognition really that simple? In their daily lives, bees are required to remember a number of different patterns and their properties, such as the shape of the nest or hive, shapes representing nectar-bearing flowers, and shapes of important landmarks on the way to the food source and back. If snapshots were the only mechanism for remembering shapes, bees would require a large memory to store all these images. Given that the brains of bees contain far fewer neurons than do ours, it seems unlikely that they can afford the luxury of a large memory.

One might conjecture, therefore, that bees also possess other, more economical means of representing patterns. Can bees abstract the general features of a pattern, such as its orientation, without memorizing the pattern in its entirety? An early paper by Wehner (88) hinted that bees could indeed do so. This question was pursued further by van Hateren et al. (82), who presented random gratings at two different orientations in a Y-maze apparatus, as shown in **Figure 2*a***. In these gratings, the width of

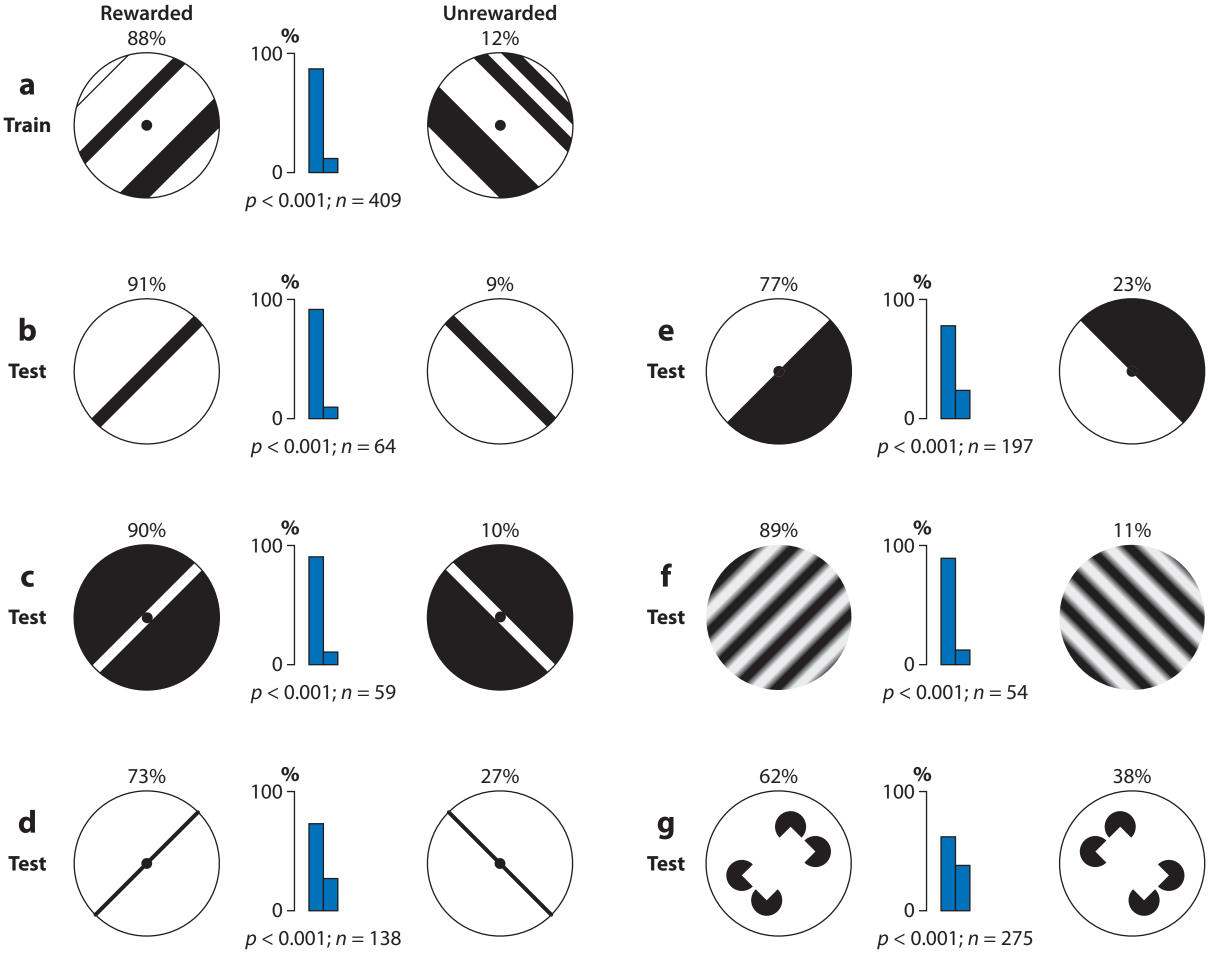

Figure 2

Illustration of some of the training and test stimuli used to investigate orientation discrimination in honey bees. Bees, trained on several pairs of random gratings, as in (*a*), are subsequently able to discriminate the orientations of similarly oriented patterns (*b–f*), which they have never previously experienced, including patterns that display illusory contours (*g*). The percentages represent the relative choice frequencies for the two patterns, *n* denotes the number of choices analyzed, and *p* is the result of a test for statistically significant difference from the random-choice level of 50%. Modified with permission from Reference 82.

each bar (black or white) was distributed randomly over a prescribed range, and the widths of successive bars were statistically independent. Two properties of the apparatus and training paradigm prevented the bees from acquiring a template of the positive pattern. First, the bees had to choose between the two stimuli at a considerable distance away from them; the stimuli could not be fixated at this distance. Second, the gratings were frequently replaced by other random gratings that were similarly oriented but had different spatial structures. Thus, to identify the positive stimulus correctly, the bees had to abstract its orientation and not merely memorize a pattern in a photographic way.

Van Hateren et al. found that bees could be trained in this way to distinguish between vertical and horizontal orientations, as well as between two oblique directions (+45° and −45°). Furthermore, bees trained to distinguish between two mutually perpendicular orientations discriminated the orientations of other, similarly oriented patterns that they had never encountered previously—such as sinusoidal gratings, single stripes, edges, and even figures that produced illusory contours in the appropriate orientations (**Figure 2*b*–*g***). Thus, pattern recognition in honey bees is not restricted to matching photographically memorized images. This notion has been supported by several subsequent studies (23, 27).

Further work has revealed that bees can detect and learn other general properties of patterns, such as radial, circular, and bilateral symmetry. They appear to be particularly adept at distinguishing between patterns that represent radial and circular symmetry, presumably because such patterns represent different classes of flower shapes (47). Bees can also learn to detect bilateral symmetry in patterns, as well as to discriminate the axis of symmetry (29, 38, 40). Indeed, bumble bees have been shown to prefer symmetrical flowers to asymmetrical flowers, and there is evidence to indicate that symmetry in a flower is an indicator of good health and a bountiful nectar supply (56).

Bees can also abstract characteristics of objects, such as their color and size, without having to memorize the objects' images literally (41, 63, 64). There is also evidence that bees are particularly good at distinguishing between patterns that are topologically distinct, such as a disc versus a ring (7). Honey bees can be trained to recognize and discriminate between images of human faces and can evidently commit faces to long-term memory (21). They can recognize faces from novel viewpoints by interpolating between images learned from views already experienced (22). This has striking parallels with some models of face recognition in humans (43). In parallel with human perception, bees discriminate familiar faces poorly when the images are presented upside down (21).

Studies of color and shape perception in other invertebrate species are described, for example, in References 4, 53, 59, and 89.

HIGHER-LEVEL PERCEPTION AND COGNITION

Until relatively recently, insect behavior has been assumed to be rather rigid, stereotyped, and inflexible. Even if certain insects demonstrate the ability to learn, their learning capacity has been considered to be fully preprogrammed. Over the past decade, however, new evidence is beginning to suggest that at least some insects may be more sophisticated than we had originally imagined. Here we describe a few examples of what is known about the cognitive capacities of honey bees.

Perceiving Camouflaged Objects

One study investigated whether honey bees use previously acquired knowledge to detect and distinguish between objects that are otherwise poorly visible or camouflaged. It is difficult to train bees to distinguish between textured objects of different shapes, when these shapes are presented against similarly textured backgrounds. However, if bees are initially trained, in a Y maze, to distinguish between uncamouflaged versions of the same shapes (say, black shapes against white backgrounds, which they learn quickly and well), they can then readily distinguish between the camouflaged versions (98, 99). Evidently, the trained bees use prior knowledge, or top-down processing, to break the camouflage and discriminate between objects that were previously indistinguishable. Thus, bees can learn to look at their world in novel ways and to detect objects that are normally invisible to them.

Learning Mazes and Labyrinths

The ability to learn mazes has been investigated extensively in a number of vertebrates, notably rats, mice, pigeons, and fish. However, until recently, relatively few studies have explored the capacity of invertebrates to learn to navigate mazes.

Zhang et al. (93) explored the ability of bees to learn to fly the correct route through a complex labyrinth, consisting of several chambers, to get to a reward at the destination. The labyrinth was assembled from a 4 × 5 rectangular array of boxes. Each box carried a transparent lid through which the bees' flights through the maze could be observed. The path through the maze was created by leaving open some of the holes between boxes and blocking others. Bees had to learn to fly through a specific sequence of boxes to reach their goal—a feeder containing sugar solution.

In one experiment, bees had to find their way through the maze by learning to follow a mark that signaled the correct exit in each box. The mark was a small green square, placed immediately below the appropriate exit in each box to indicate the correct path. The bees learned this task within half a day (after about 20 rewarded trials) and showed good performance. After training, over 70% of the bees flew through the maze without making even a single error. Performance continued to be good when the bees were tested on a new path, created by rearranging the boxes and marks. Evidently, the trained bees had learned to follow the mark to get to the goal and immediately used this rule to trace novel paths through the maze.

In another experiment using the same configuration of boxes, Zhang et al. investigated whether bees could learn to negotiate mazes by using a symbolic cue. Left and right turns were signaled by different colors placed on the back wall of each box where a turn had to be made: For example, blue meant "turn left" and yellow meant "turn right." The results revealed that bees learn this task well, too—in fact, just as well as the task of simply following a mark. Here again, bees, trained to use the symbolic cue on a particular route, immediately used the cue to trace novel paths through the maze.

A final experiment in this study explored the ability of bees to learn to navigate unmarked mazes. Here bees were trained step-by-step through the entire path, from the entrance to the reward box. The bees' performance in these experiments was not as good as in the experiments described above. Nevertheless, the performance of the trained bees was significantly better in the training maze than in a control maze that offered an unfamiliar route (93). Thus, bees can learn routes through completely unmarked mazes. Presumably, this is accomplished by memorizing the sequence of turns that have to be made at each point (box) along the route.

When bees that have learned to negotiate a maze with the aid of marks or symbolic cues are tested on the same routes with the marks or cues removed, their performance is substantially poorer than when the bees are trained on unmarked routes in the first place. It appears that, when bees are given marks or symbolic cues, they rely almost entirely on these signals for navigation: They hardly pay any attention to the route they take through the maze—in contrast to the bees that are forced to learn an unmarked route. In this respect, bees appear to be similar to humans—when we drive to an unfamiliar destination, we are less likely to learn the route if we are guided by a passenger or by a GPS-based navigation system.

Bees can also be trained to choose specific visual patterns at specific stages of a multistage maze. Thus, they can learn to navigate through a maze by choosing pattern A over pattern B at stage 1, B over C at stage 2, D over E at stage 3, and so on (13). Other work, using unmarked mazes, has shown that bees are better at learning mazes that involve regular patterns of turns—if they are able to recognize such patterns—compared with random mazes (96). For example, bees readily learn to navigate through constant-turn mazes, such as right-turn mazes (where the goal is reached by making a right turn in each chamber) or left-turn mazes (where the goal is reached by always making a left turn). Bees can also learn zigzag mazes, where the goal is reached by alternately turning left and right.

Learning Complex Associations

Mazes are useful not only for studying the learning of complex routes, but also for probing the ability of animals to perform a variety of perceptual tasks. One example of such an application is the so-called Delayed Match to Sample

LEARNING COMPLEX ASSOCIATIONS

Reinhard et al. (60, 61) took the investigation of complex, cross-modal associative recall one step further by showing that scents can trigger recall of navigational memories in foraging honey bees. They trained bees to forage alternately at a rose-scented feeder at an outdoor location A and at a lemon-scented feeder at a different location B. Bees trained in this way could then be triggered to visit location A or B simply by blowing the associated scent into the hive, even when A and B no longer carried the food or the scents. This finding demonstrates that scent can trigger the recall of specific, complex navigational memories.

(DMTS) task. Here an animal is shown a sample stimulus and shortly afterward is presented simultaneously with two comparison stimuli, of which one is identical to the sample and the other is different. The animal is required to choose the comparison stimulus that matches the sample. This task requires memorizing the sample that is encountered (on a short-term basis, i.e., place it into working memory), and then comparing this memorized sample with each of the comparison stimuli to determine which one of them is appropriate. Learning the task itself—that is, learning the matching rule—would be the province of long-term memory, which is obviously also involved in this exercise.

Until recently, only humans, monkeys, and pigeons were known to perform DMTS tasks. In 2001 this capacity was explored for the first time in an invertebrate, the honey bee (30). Bees were trained in a Y-maze, which presented the sample stimulus at the entrance and the comparison stimuli at the ends of the two arms of the maze. In one experiment, a group of bees was trained to match colors: When the sample was yellow, the bees had to choose the yellow comparison stimulus to get a food reward; when the sample was blue, they had to choose the blue stimulus. Bees learned the DMTS task well, choosing the matching color 70% of the time after 60 rewarded visits. The trained bees were then tested with a novel set of sample and comparison stimuli: vertical and horizontal gratings. These bees immediately showed a clear and statistically significant preference (of over 75%) for the comparison grating that matched the sample grating at the entrance. Thus, bees that have been trained to match colors are capable of learning the concept of matching and applying it to deal with stimuli that they have never previously been trained upon or even encountered. Experiments in which the distance (and therefore the delay) between the sample stimulus and the comparison stimuli is systematically increased reveal that the sample stimulus can be held in working memory for a duration of up to 5 s (94).

DMTS: Delayed Match to Sample

DSMTS: Delayed Symbolic Match to Sample

In a further extension of this experiment, conducted using a slightly different apparatus (30), bees were trained to match scents (lemon and mango). They learned this task well. The trained bees were then tested with colors (blue and yellow). They immediately matched the colors. Thus, bees can learn the concept of matching in one sensory modality and apply it to a task in an entirely different modality.

Finally, bees can also learn the concept of nonmatching. That is, bees can be trained, using the paradigm described above, to choose the comparison stimulus that does *not* match the sample. Furthermore, as in the matching task, they can transfer the concept of nonmatching to novel stimuli (30).

A task of greater complexity is the Delayed Symbolic Match to Sample (DSMTS) task. Here the experimental subject has to use the identity of a sample stimulus (which can be A or B) to choose between two other comparison stimuli (C and D) that are presented simultaneously in a subsequent chamber. The subject has to learn to choose stimulus C if the sample is A, and stimulus D if the sample is B. In other words, the subject has to learn to associate A with C, and B with D. In this task, neither of the comparison stimuli matches the sample in a literal sense: the matching is symbolic.

Until recently, only vertebrates—humans, monkeys, dolphins, and pigeons—were known to be able to learn DSMTS tasks (1, 16, 65, 62). Zhang et al. (95) explored this capacity in honey bees, using a multilevel maze with two stages of decision chambers and with a sample stimulus presented at the entrance. The sample stimulus was a black-and-white grating that was oriented horizontally or vertically. The first decision stage presented comparison stimuli consisting of colors (blue and green discs), and the second decision stage presented comparison stimuli consisting of patterns (a sectored pattern and a pattern composed of concentric rings). When the sample stimulus was a horizontal grating, the bees had to learn to choose blue in Chamber 1, and the sectors in Chamber 2, to get to the food reward. On the other hand, when the sample stimulus was a vertical grating, the bees had to learn to choose green in Chamber 1 and the rings in Chamber 2. The bees learned this task, choosing the correct stimulus at each stage at a rate significantly better than that corresponding to random choice. This type of associative recall helps the bees make the correct decision at each stage of this elaborate maze and find their way through it. In nature, exposure to one landmark along a particular foraging route, for instance, would trigger recollection of all the other landmarks that are expected on the way.

Associative recall can extend across stimulus modalities. It is a common human experience that a whiff of perfume or cologne, for example, can remind us of an old friend, and that listening to a piece of music can trigger recall of a long-forgotten event. The scent that is associated with a food source can trigger recall of its color and vice versa. In a Y-maze configuration, bees could be trained to choose the color blue (for example) in a decision chamber if they encountered the scent of lemon at the entrance, and the color yellow if they encountered the scent of mango. Conversely, bees could also be trained to choose a particular scent in the decision chamber, depending upon the specific color that they encountered at the entrance (79).

Learning What to do Where and When

Collett & Kelber (14) were perhaps the first to demonstrate that bees learn tasks in a context-specific way. That is, the choice that a bee makes can be driven by the context in which she finds herself. Collett & Kelber placed an identical, square constellation of four cylinders (two blue cylinders on one side, and two yellow cylinders on the other) in each of two huts, 33 m apart. A group of individually marked bees was trained to find a food reward placed between the two yellow cylinders in Hut 1, and to the east of the two blue cylinders in Hut 2. Tests conducted after training, with the reward removed, showed that the bees searched for the food between the two yellow cylinders in Hut 1, and to the east of the two blue cylinders in Hut 2. Even though the constellations in the two huts were identical, the identity of the hut (defined by its location relative to the hive) determined the choices that the bees made.

The choices that a bee makes can also be set by the time at which the decision has to be made. Gould & Gould (34) trained a group of individually marked bees is to visit a blue, triangular, peppermint-scented feeder between 9 and 10 AM. The same group of bees was then trained to visit a yellow, circular, lemon-scented feeder at the same location between 10 and 11 AM. After this training pattern had been repeated daily for four to five days, the bees were presented with both feeders full and placed side by side, and their behavior was observed during the course of the entire morning. The trained bees first appeared at the site at around 8:45 AM, indicating that they had learned the schedule. Between 8:45 and about 9:45 AM, they landed exclusively on the blue triangle. Between 9:45 and 10:15 AM, the bees switched to the yellow circle and thereafter fed exclusively at this site even though the blue circle continued to offer food. More amazingly still, all the trained bees ceased to visit the setup after 11:15 AM, even though both stimuli continued to offer food. These observations indicate that bees can learn tasks in a time-dependent way.

The ability to learn to make flexible choices that vary with changes in space and time is invaluable to a flower forager like the honey bee, as the availability of nectar-bearing flowers in the environment can vary with location as well as time of day. A number of studies have extended these findings by showing that bees can be trained to make diametrically opposite choices of colors (or patterns) depending upon whether they are visiting a feeding site or returning to the hive (11, 26, 77, 97). Furthermore, bees can be trained to reverse this entire ensemble of preferences at a different time of day. Bees are quicker at learning opposite tasks at the feeding site and at the nest if they are made to learn these two tasks sequentially (e.g., feeder task first, nest task later). Interference effects occur, initially, when one attempts to train bees on both tasks concurrently (25).

Counting

Chittka & Geiger (9) posed the intriguing question of whether bees are capable of counting landmarks on the way to a food source. They placed four large landmarks (yellow tents) equidistantly along a line leading away from a beehive, and trained bees from the hive to find a food reward placed halfway between the third and the fourth tents. After training, the feeder was removed and the bees' ability to pinpoint the correct former location of the feeder (between Landmarks 3 and 4) was evaluated in a series of tests in which the positions and separations of the landmarks were varied, and the visits of the trained bees were counted at a number of dummy feeders, carrying no reward, placed along the training route. In these tests, the trained bees did indeed show a significant tendency to search for the food at a location between Landmarks 3 and 4. This finding suggested that the bees were indeed capable of keeping track of the number of landmarks that they had passed to get to the food source during the training. This apparent ability to count objects sequentially was a first for invertebrates. However, the majority of the bees in the tests did not search after they had passed the correct landmark, Landmark 3. Rather, they searched at a position that corresponded to the distance that the bees had flown to get to the feeder during the training. It is well known that bees are capable of learning the distance that they need to fly to get to a food source, and that they report this distance to their nestmates through the so-called waggle dance when they return to the hive (84). Thus, in these experiments, the odometric signal may have been in conflict with the counting signal, leading to a seemingly less-than-optimum counting performance.

Dacke & Srinivasan (15) repeated the above study by training bees to fly in a tunnel and to obtain a food reward after passing a fixed number of landmarks. However, in these experiments, the separation between the landmarks was frequently varied during the training. This procedure ensured that the food was always present at the correct landmark, but randomized the distance that the bees had to travel to get to it. When trained in this way, the bees showed a strong and dominant tendency to search at the correct landmark, and not at any particular distance along the tunnel. Evidently, the bees had learned from the training that the landmark count was the critical cue and that flight distance was irrelevant.

Training and testing experiments with the feeder placed successively at Landmarks 1, 2, 3, 4, and so on revealed that bees can count up to a maximum of four objects when they are encountered sequentially during flight. Furthermore, bees trained in this way counted novel objects that they had never previously encountered, thus demonstrating that they are capable of object-independent counting.

Recently, Gross et al. (35) have shown that bees are also capable of assessing numerosity, that is, of comparing numbers of objects. By training bees to discriminate between different numbers of objects in a delayed match to sample task, and controlling for the use of extraneous cues such as object area, perimeter, shape, and configuration, they showed that bees can distinguish between one and two objects, between two and three objects, and between three and four objects, but not between four and five objects, or higher numbers.

It is interesting to note that the upper limit of four appears in sequential counting, as well as numerosity determination. Whether this is of some significance, or simply a coincidence, remains to be examined.

CONCLUDING REMARKS AND OUTLOOK

Research over the past thirty years or so is beginning to suggest that learning and perception in insects are more intricate and flexible than originally imagined. Honey bees are capable of a variety of visually guided tasks that involve cognitive processes that operate at a surprisingly high level. Bees can abstract general properties of a stimulus, such as orientation or symmetry, and apply them to distinguish between other stimuli that they have never previously encountered. They can be taught to use new cues to detect camouflaged objects. They can learn to use symbolic rules for navigating through complex mazes and to apply these rules in flexible ways. Honey bees form concepts to group and recall stimuli associatively. The associations that are formed and recalled can be complex. Although the processes of learning and perception are undoubtedly more sophisticated in primates and mammals than in insects, there seems to be a continuum in these capacities across the animal kingdom, rather than a sharp distinction between vertebrates and invertebrates. The abilities of an animal seem to be governed largely by what it needs to pursue its lifestyle, not by whether it possesses a backbone.

Unfortunately, our current knowledge of the behavioral capacities of honey bees greatly surpasses our insights into how the nervous system realizes them. Despite all the effort that has been directed toward investigating the principles of visual processing in a wide variety of animals, ranging from insects to cats to primates, it is probably fair to say that we still know little about the language of pattern recognition. What are the features of the image that are extracted by the visual system, and how are they assembled to form a compact and reliable representation of an object that can be used to recognize it when it is encountered again? How does the nervous system set up associations between sights, smells, and navigational routes, and recall these associations when needed? The honey bee, with its impressive behavioral repertoire and a relatively small nervous system comprising fewer than a million neurons, offers a promising model in which to pursue these challenges.

Owing to space constraints, this review has not addressed a number of additional, important aspects of honey bee vision, such as the perception of movement and its role in visually guided flight, polarizational sensitivity, and navigation. Some of these topics, and the applications of the emerging principles to the design of biologically inspired aerial vehicles, are described, for example, in References 76 and 78. This review has concentrated on the cognitive capacities of individual honey bees and not discussed the collective intelligence of the colony as a whole—an important and fascinating topic that has been covered extensively in, for example, Reference 66.

SUMMARY POINTS

1. Bees, like humans, possess trichomatic color vision and exhibit a degree of color constancy. The visual spectrum of bees is shifted toward shorter wavelengths, compared with that of humans.
2. The visual acuity of honey bees is about 170 times poorer than that of humans.
3. Bees can be trained to discriminate visual patterns. They can abstract general properties of the training patterns (such as orientation or symmetry) and use them to distinguish novel patterns.

4. Bees can be trained to detect camouflaged patterns and to distinguish between them.
5. Bees can learn to use signposts (literal as well as symbolic) to navigate through complex mazes. They can also learn complex routes through unmarked mazes.
6. Bees are capable of complex associative recall. Colors can trigger recall of patterns, and scents can trigger recall of colors.
7. Bees can learn tasks in a context-dependent and time-dependent way.
8. Bees can count up to a maximum of four objects presented sequentially or simultaneously.

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