



Vision, perception, navigation and ‘cognition’ in honeybees and applications to aerial robotics

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ABSTRACT

This review summarizes research carried out in the author's laboratory investigating the ways in which honeybees use vision to guide their flight and navigate in their environment, and describes how these principles have been used to design, build and test biologically-inspired systems for the guidance and navigation of unmanned aerial vehicles. It also outlines studies investigating the capacities of honeybees in the areas of visual perception, pattern recognition, and ‘cognition’.

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1. Introduction

Honeybees have proven to be a very attractive experimental subject for investigating the general principles that underlie vision, perception, navigation and higher cognition in many organisms, including humans. One reason for this is that bees lend themselves readily to investigation of their behavior. The daily life of a forager honeybee is dedicated solely to gathering nectar and pollen from flowering plants or trees in the surrounding environment. A curious experimenter can attract honeybees to regularly visit a feeder that offers a solution of sugar water. The feeder, together with the visiting bees, can then be slowly moved into in an experimental setup designed to investigate a specific aspect of their behavior. This simple experimental paradigm allows the experimenter to make use of the honeybee's lifestyle in an unobtrusive way, to ask and answer interesting questions. Another attractive feature of this approach is that no bees are harmed or killed in the process. The bees visit the experimental feeder of their own ‘free will’ – there is no coercion – and at the end of the experiment, they are free to resume their original lifestyle of foraging in the natural environment.

This article highlights studies in our laboratory aimed at (i)

understanding the principles of visual guidance of flight in honeybees; (ii) using some of the findings to design novel, biologically-inspired algorithms for the guidance of unmanned aerial vehicles, and (iii) examining features of vision, perception, learning, memory, and ‘cognition’ in these creatures.

1.1. Visual guidance of flight

Safe flight in a cluttered environment requires an ability to gauge the distances to potential obstacles. Humans use stereo vision to do this, through a principle that is based essentially on triangulation. This process works accurately in humans because the two eyes are about 65 mm apart, providing a relatively large ‘stereo baseline’. Insects, however, possess a much smaller interocular separation (only a few millimeters), and much poorer visual acuity [1]. As a result, insects can only use stereo vision for estimating the range to objects that are a few centimeters away, at most [2]. Research over the past few decades has revealed that most insects rely on a different method for estimating object range. When the eye moves in a straight line, the images of nearby objects will move more rapidly past the visual field of the eye, compared those of objects that are farther away. Objects that are very far away (such as distant hills, or the sun, or the clouds in the sky) will generate virtually no image motion. Insects have evolved the ability to translate this image motion into object range. Thus, insects rely on

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an ‘active’ method for perceiving the three-dimensional structure of the world.

1.1.1. Flying safely through narrow passages

Our first insight into this remarkable ability arrived some forty years ago, and was triggered by a chance observation. When bees fly through a hole in a wall, they fly safely through the middle of the hole by balancing the distances to the left- and right-hand rims. How were they measuring and balancing the distance to the two rims, given that they do not possess stereo vision? Even if they did possess stereo, they could not use it in this context, as each rim was being viewed only by one eye. We hypothesized that the bees were flying through the middle of the hole by balancing the speeds of the images of the left- and right-hand rims. If the image of one of the rims was moving at a faster rate, it would imply that rim was closer, and cause the bee to veer away from it. To test this hypothesis, we trained bees to fly through a tunnel to a feeder at its far end, and video-filmed their flight trajectories from above. The bees were observed to fly close to the mid-line of the tunnel, balancing the distance to the two walls. However, when one of the walls was moved against a bee's flight direction, the bee flew further away from that wall. Evidently, the increased image speed generated by that wall signaled a greater proximity, causing the bee to veer away. On the other hand, when the wall was moved in the bee's flight direction, the bee flew closer to the wall. In this case, the moving wall generated a lower image speed, signalling a greater distance, causing the bee to move closer to it. This simple experiment demonstrated that bees negotiate narrow passages safely by balancing the speeds of the images (the ‘optic flow’) experienced by the two eyes [3,4].

1.1.2. Regulating flight speed

Recording flight behaviour in tunnels has also provided insights into how bees regulate the speed of their flight. When the walls are stationary, doubling or halving the width of the tunnel respectively doubles or halves the flight speed [5–7]. When both walls are moved in or against the direction of flight, the bees respectively increase or decrease their flight speed by about the same amount as the change of wall speed [5–7]. These findings demonstrate that bees regulate flight speed by holding the speed of the image of the environment (the optic flow) constant, at a value of about 300 deg/sec [5,6]. A consequence of this strategy for controlling flight speed is that when bees fly through a tapered tunnel, they slow down as the tunnel narrows, and speed up as it widens [5]. This ensures that the flight speed is automatically adjusted to a value that is safe and appropriate for the environment through which the bee is flying – high for an open environment, and low for a densely cluttered environment. And this speed regulation is achieved without any explicit measurement of the ranges to the objects in the environment.

1.1.3. Odometry

When a forager honeybee returns home after discovering an attractive source of food, she performs a ‘waggle’ dance to indicate, to her nestmates, the location from which she has returned [8]. The waggle dance, performed on the vertical surface of the honeycomb, consists of alternating left-hand and right-hand loops, interspersed by a ‘waggle’ phase in which the bee oscillates her abdomen from side to side. The duration of the waggle phase is proportional to the distance of the food source, and the direction of the waggle axis provides information on the direction. Nestmates observing the dance are then also able to fly to the advertised location to bring in food and bolster the colony's food supply. Our tunnel paradigm has been able to provide insights into how bees estimate the distance they have flown to the food source. The dancing bee needs this

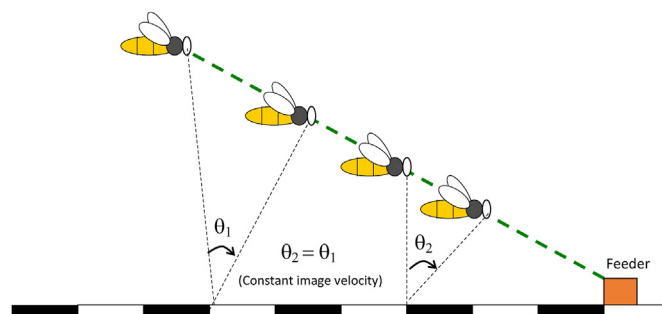


Fig. 1. Investigation of honeybee landing behavior. Details in text.

information not only to orchestrate her dance, but also to make repeated visits to the location that she has discovered. How does the forager bee estimate the distance that she has traveled? We have used the tunnel paradigm to investigate this question. Bees were trained to emerge from their hive, and fly through a narrow, 6 m long tunnel, lined with vertical stripes, to reach a food reward. When these bees returned to their hive, they performed a waggle dance which indicated that they had traveled a distance of 180 m: they had massively overestimated the travel distance [9,10]. We hypothesized that the bees were estimating the distance flown in terms of the total amount of angular image motion (angular velocity of the image, integrated over time) that they had experienced *en route* to the food source. Flight in a narrow tunnel greatly increased the amount of angular motion, because the surrounds (the walls and floor of the tunnel) were very close to the flying bee, compared to what it would encounter during flight in an open outdoor environment. To test this hypothesis, we examined the bees' dances when they flew in the same tunnel, but with the vertical stripes replaced by horizontal ones. Horizontal stripes would generate no visible image motion, because the bees are flying parallel to the stripes. In this case, the bees indicated a travel distance of zero. These experiments, taken together with several others [11–13] reveal that honeybees estimate the distance flown to a destination in terms of the total extent of image motion that they have experienced *en route*. In other words, the honeybee's odometer is visually driven. The advantage of a vision-based cue for odometry (as opposed to measuring energy consumption or flight time, or counting wingbeats) is that the estimate of travel distance is not affected by the speed of flight, or by headwinds or tailwinds.

1.1.4. Making co-ordinated turns

Reconstruction of 3D flight trajectories of bees loitering in the front of their hive reveals that they orchestrate well - coordinated turns [14]. As a bee enters a turn, it progressively decreases its speed and increases the curvature of the turn – and does the opposite while coming out of the turn. At each instant of the turn, the speed is matched to the curvature in such a way that the centrifugal force experienced by the bee is held constant at a value of about 20% of the body weight [14]. This strategy ensures that the turning bee never loses control due to sideslips caused by excessive centrifugal forces.

1.1.5. Landing

Orchestrating a safe landing is one of the most challenging manoeuvres for a flying insect – or a bird, or an aeroplane. To examine how bees make smooth landings, we trained them to feed from a drop of sugar water placed on a horizontal surface, and filmed them using stereo video cameras as they landed to collect their food (Fig. 1). Reconstruction of the 3D landing trajectories revealed several interesting features. Landing bees reduce their

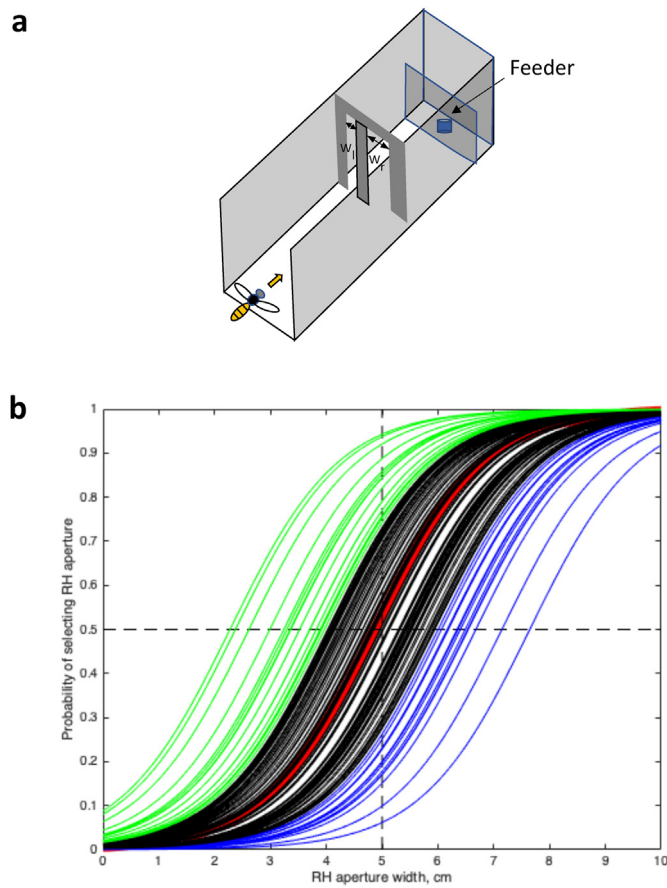


Fig. 2. Investigation of route choice behavior in honeybees. Details in text.

flight speed progressively as they approach the ground. The lower the altitude, the slower the speed. Detailed analysis revealed that the instantaneous speed of flight is strictly proportional to the instantaneous altitude [15]. This critical observation, which has been backed up by further studies, reveals that the bees are achieving the deceleration by adjusting their flight speed in such a way as to hold constant the speed of the image of the ground as they are coming in to land. This ensures that the bee slows down, progressively and automatically, as it approaches the ground, reaching a speed that is close to zero at the point of contact. The simplicity and elegance of this landing strategy is that it does not require knowledge or measurement of the instantaneous height above the ground, or the speed of approach. The bee only needs to measure the speed of the image of the ground and adjust its flight speed, from moment to moment, to ensure that this image speed is held constant as the ground is approached [15]. A generalized form of this strategy can be applied when a bee lands on a surface of any inclination [16].

1.1.6. Route choice

When moving in a cluttered environment, flying insects are constantly faced with the need to choose between alternative routes: some routes may be safer than others, and offer a more rapid passage. Can bees discriminate between wider and narrower passages, and will they choose the wider passage when offered a choice? To explore this question, we trained bees to fly through a tunnel to a feeder at the far end. A transverse wall, placed halfway along the tunnel, carried two apertures (Fig. 2a). The bees had to choose to fly through one of the apertures on the way to the feeder,

which was hidden behind a low wall to prevent it from potentially influencing the bees' choices [17]. The relative widths of the left-hand and right-hand apertures, W_l and W_r , could be varied by changing the position of a partition (P) that was placed inside a window (Fig. 2a). The combined width of the two apertures was 10 cm, and the individual widths could be varied from ($W_l = 0$ cm, $W_r = 10$ cm) when the partition was positioned at the extreme left end, through ($W_l = W_r = 5$ cm) when the partition was placed in the middle, to ($W_l = 10$ cm, $W_r = 0$ cm) when the partition was placed at the extreme right end.

101 individually marked bees were trained in the apparatus, and the frequencies of their choices for the two apertures were recorded for various combinations of aperture widths. The data were fitted to logistic curves [17]. The red curve in Fig. 2b shows the variation of the probability of choosing the right-hand aperture (Pright) as a function of its width W_r , for data pooled over the entire population. This choice function shows that when one aperture is twice as wide as the other (6.7 cm vs 3.3 cm), the wider aperture is chosen 85% of the time. Thus, bees discriminate aperture width with high sensitivity. When the two apertures are equally wide, the bees choose them equally frequently: Pright is approximately 50% when $W_r = 5.0$ cm (Fig. 2b). Thus, considering the population as a whole, bees do not exhibit any side bias in this behaviour (i.e. a preference for one side or the other): they do not have an innate 'handedness'. Interestingly, however, individual bees exhibit clear and distinct biases. While some bees show a near-zero bias, others display a preference for the right-hand aperture: they select it even when it is narrower than the left-hand aperture. A third group displays a clear left bias. The variation in bias is evident from the choice functions plotted in Fig. 2b for all of the 101 bees. The bias can be quantified in terms of the width of the right-hand aperture (W_{r0}) at which the two apertures are chosen equally frequently (i.e. Pright = 0.5). $W_{r0} = 5.0$ corresponds to zero bias; $W_{r0} < 5.0$ implies a right bias, and $W_{r0} > 5.0$ a left bias. The choice functions are shown in black for bees with a near-zero bias (defined as $4.0 \leq W_{r0} \leq 6.0$), in green for bees with a clear right bias ($W_{r0} < 4.0$), and in blue for bees with a clear left bias ($W_{r0} > 6.0$). The distribution of W_{r0} varies from 2.28 cm (extreme right bias) to 7.65 cm (extreme left bias). The bias can also be quantified in terms of the probability of choosing the right-hand aperture when the two apertures are equally wide. This ranges from 0.06 (extreme left bias) to 0.94 (extreme right bias). The biases across the bees are distributed approximately symmetrically on either side of the zero-bias point [17]. The bias displayed by each individual bee is robust and consistent; it persists throughout the duration of each experiment - which can continue for up to a week, during which each individual bee is tested ~200 times. We have also observed a similar distribution of aperture-choice biases in birds (Budgerigars [18]).

The observations of near-zero bias across the whole population, but the presence of clear individual biases is unexpected, and intriguing. Most organisms - ranging from humans through various mammals, vertebrates and insects - display a bias that is consistent throughout the population. For example, right-handedness and right-eye dominance is well known in humans [19]. Many birds tend to use their right eye to seek and view food, and the left eye to detect predators [20–22]. Lateralization has also been documented in a large number of invertebrate species - including bees, fruitflies, cockroaches, octopuses, locusts, ants, spiders, crabs, snails, water bugs and cuttlefish, in a wide variety of contexts that include vision, olfaction, hearing, and various aspects of learning and motor behavior [23,24]. Given this broad prevalence of a population bias in sensorimotor behavior across many organisms, why do bees display individually distinct biases in their choice of routes? And is this behaviour advantageous in any way? While there is currently no definitive answer to this question, one

can hazard a speculation. Consider a swarm of bees (or a flock of birds) flying through a cluttered environment, and encountering a situation where they have to choose between two passages - for example, two gaps between tree trunks. It would not be optimal if all of the bees had a right bias (for example), because the left-hand gap would then be scarcely used, and a bottleneck would be created at the right-hand gap, delaying the progress of the swarm. The bottleneck would be particularly severe if the right-hand gap is narrower than the left-hand gap, because the better throughput capacity of the left-hand gap would never be utilised. If the bees had no bias, and all of them simply chose the wider gap, that would also be suboptimal because, again, a bottleneck would be created at the wider gap, and the narrower gap would never be utilised. Quantitative modelling of the scenario [18] reveals that, if the individuals have a spread of biases, distributed uniformly over the range $0 \leq W_r0 \leq 10$, then the number of individuals that choose each gap would be proportional to the width of the gap. Since the time required by a bee to transit a gap is likely to be inversely proportional to its width, both gaps would then complete transmitting their bees at the same time. This would ensure that the bee swarm (or bird flock) uses the two gaps in the best possible way, to minimise the overall transit time. The biases need not be confined to the horizontal domain (left versus right): they can be distributed over a two-dimensional plane, with individuals displaying different preferences: for example, for a gap located in the upper left, the upper right, the lower left or the lower right (Fig. 4 in [18]). This natural spread of preferences among the population would automatically ensure the rapid transit of a flock through a cluttered

environment, without any need for a higher-level process of decision and control. In principle, such a strategy could also be employed to facilitate the progress of a fleet of autonomous drones through a cluttered environment.

1.2. Biologically inspired robotics

Our studies of vision-based flight guidance in honeybees have also led to the development of novel, biologically-inspired algorithms for the guidance and control of autonomous aerial vehicles [25–28]. Fig. 3a illustrates the essential elements of one of our drones. This is a fixed-wing model airplane in which the propeller and engine have been translocated to a position above the wing, to make room for the vision system which is mounted at the nose of the fuselage to obtain unobstructed views of the environment in the frontal, dorsal, ventral and lateral directions.

The near-panoramic visual field that is captured by the two compound eyes of the honeybee is replicated by two wide-angle video cameras positioned back to back (Fig. 3b). An example of a panoramic image captured by the vision system, remapped into azimuth and elevation coordinates, is shown in Fig. 3c. The video stream acquired by the vision system is analyzed in real time in an on-board computer to compute the optic flow field (yellow lines, Fig. 3c). This optic flow field is used to estimate the direction of flight (yellow circle), to regulate the height above the ground, to compute the distance traveled (odometry), and to perform smooth landings. The shape of the horizon profile (Fig. 3c) provides information on the instantaneous attitude (roll and pitch) of the aircraft.

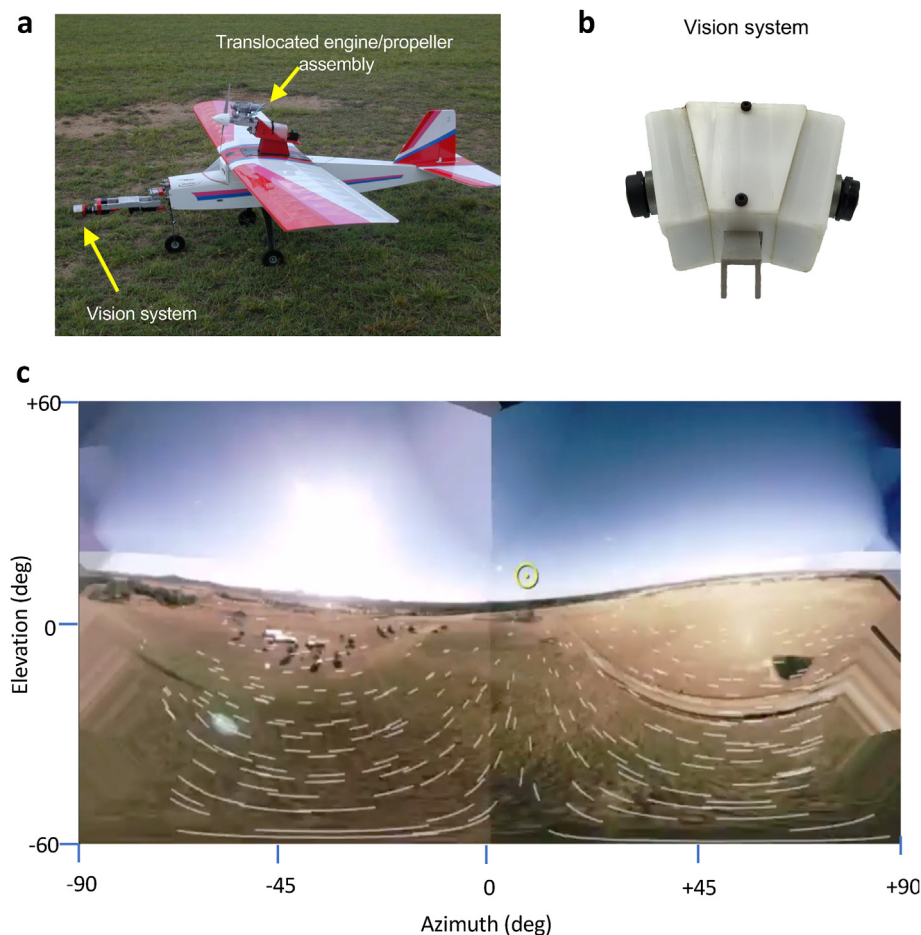


Fig. 3. Application of the principles of visually guided flight in honeybees to the design of vision systems for the guidance of autonomous aircraft. Details in text.

This information is used to monitor and stabilize the attitude in the way that insects are known to do [29–31]. We have demonstrated that the horizon profile can also be used to guide aerobatic maneuvers such as loops, rolls and Immelmann turns [32]. Fully autonomous flights, comprising takeoff, cruise, controlled turns and landing, are achieved without the use of any external information such as GPS or radar [32]. Like a flying insect or a bird, the prototype aircraft relies solely on its own sensors. These studies provide a proof of concept for the design of a backup for the navigation system of a conventional aircraft, when there is a dropout of GPS or radar information.

1.3. Vision, perception, learning, memory, and ‘cognition’

Anyone who has observed a honeybee set out from its hive, fly a meandering course in search for food, and literally make a ‘beeline’ back home after finding the food, and signal the position of the food source to its nestmates would realise that these creatures possess impressive faculties of perception, navigation, and ‘cognition’, despite carrying a brain that weighs a mere milligram.

One of the pioneers to investigate these capacities was Karl von Frisch [8], who won the Nobel prize for his work in 1973. In a simple, elegant study in 1914 [33], he trained bees to collect a food reward from a colored dish, and then presented the trained bees with an array of discs in which the colored dish was situated among a number of other dishes—which were all grey, but of different reflectances, ranging from black to white. None of the dishes carried a reward. He found that the trained bees consistently landed only on the colored disc, regardless of where it was positioned within the constellation. Thus, the bees were perceiving and learning the *color* of the dish on which they had been trained, and not simply its brightness. This finding clearly demonstrated that honeybees possess color vision. Bees were the first invertebrate, and the second non-human organism in which color vision was discovered. One year earlier, von Frisch demonstrated that fish (minnows) possess color vision [34].

1.3.1. Pattern discrimination

In honeybees, pattern discrimination was first investigated by von Frisch [35] and Mathilde Hertz [36], who offered bees a variety of patterns presented on the horizontal plane. They found that bees showed a greater preference to land on ‘busy’ patterns, such as stars, than on smooth patterns, such as discs. It was suggested that this was because the bees experienced more fluctuations of light intensity as they flew over the busy pattern [36]. If this was the case, then the bees were not discriminating the patterns *per se*, but only distinguishing between the frequencies of the fluctuating light intensities registered by their photoreceptors.

Many decades later, Lindauer and Wehner [37–39] explored the ability of bees to distinguish between patterns that were presented in the vertical plane. This opened up a new chapter of investigation because one could now examine discrimination across a large variety of patterns, including patterns that had different orientations. In these experiments, bees were trained to visit a pattern by landing at its center, and walking through an entrance tube to access a chamber that carried a food reward [39,40]. The bees tended to hover stably in front of the entrance tube for a few seconds before landing on it [35,41], which presumably gave them an opportunity to inspect and learn the pattern at a close range. The trained bees were then tested by presenting them with two patterns - neither of which carried a reward - and measuring the bees’ relative preference for the two patterns by recording the number of landings and antennal touches attracted by each pattern [42]. These studies, as well as others, led to the hypothesis that the bees were learning the training pattern in a largely ‘photographic’ or ‘eidetic’

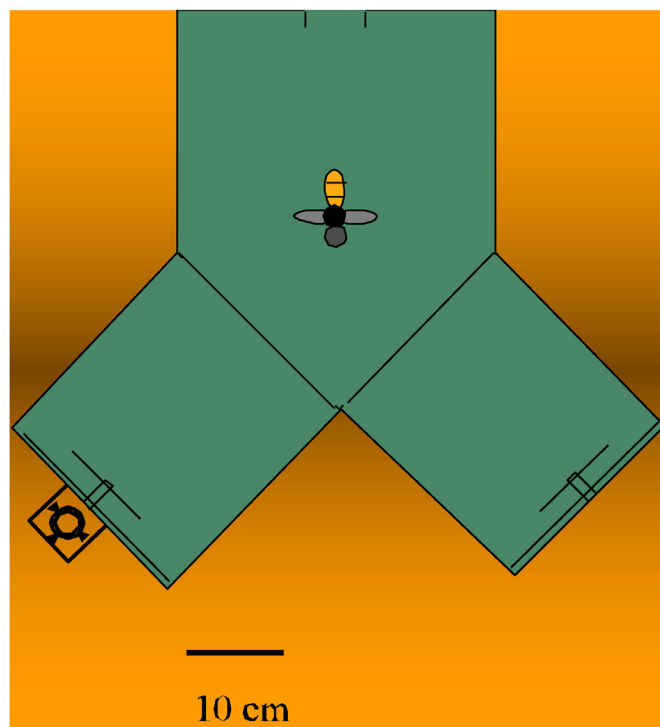


Fig. 4. Y-maze apparatus for training and testing visual pattern discrimination in honeybees.

fashion, by forming a template [37,39,41,43,44]. In its simplest form, template-based pattern recognition involves comparing the learned image, ommatidium by ommatidium, with the image that is currently being viewed, to evaluate the extent of overlap. The greater the overlap, the greater the similarity between the viewed image and the training image. This form of template-based pattern recognition requires the training and test patterns to always be viewed by a fixed region of the eye. The bees were achieving this by hovering stably in front of the entrance tube at the center of the stimulus. There was, however, some additional evidence that bees are also capable of learning the orientations of the contours of patterns (e.g. [45,46]).

Inspired by these early findings, our laboratory set out to study honeybee pattern recognition in greater detail. One of the first questions we posed was whether bees learn patterns purely in a template-based fashion, as described above, or whether they are also capable of learning more general, abstract properties of these patterns.

Our studies were conducted using a Y-maze apparatus [47], illustrated in Fig. 4. Bees were trained to enter a decision chamber where they had to choose between two visual stimuli, each of which was presented at the back wall of one of the arms. One of the stimuli (termed the ‘positive’ stimulus) bore a food reward, which a bee could access by landing at the center of the stimulus and walking through a tube to a feeder enclosed in a box. The other stimulus (termed the ‘negative’ stimulus) offered no reward. This paradigm allowed us to investigate whether bees could learn to distinguish between any two arbitrary visual stimuli, by associating one of them (the positive stimulus) with a food reward. During the training the positions of the positive and negative stimuli were frequently interchanged, to ensure that the bees were forced to learn the stimuli *per se*, and not simply the arm (left or right) that offered the reward. After the training phase, the bees were tested by removing the reward and recording the frequencies with which

the trained bees chose the arm that carried each stimulus (the positions of the positive and negative stimuli were also swapped during the testing phases). A choice frequency of 100% for the positive stimulus (and 0% for the negative stimulus) would indicate that the bees were perfectly capable of distinguishing between the two stimuli. On the other hand, a choice frequency of 50% for the positive stimulus would indicate that the bees were unable to discriminate between the two stimuli, and were choosing between them at random. Because the bees were making their choices in the decision chamber, at a considerable distance from the stimuli, they had no opportunity to fixate the rewarding stimulus or acquire a template of it [48].

1.3.2. Discrimination of pattern orientation

We began by asking whether bees could learn the orientation of a pattern without memorizing the pattern as a whole, in a template-like fashion. This question was addressed by attempting to train bees to distinguish between random gratings oriented in two orthogonal directions - for example, vertical versus horizontal, as shown in Fig. 5a [48]. The black and white stripes in these gratings had randomly varying widths, as determined by a random number generator. During the training, the gratings representing the positive and negative stimuli were frequently replaced by other random gratings, with the same orientations. This training procedure ensured that the bees had no opportunity to form templates (literal images) of the gratings. Bees trained in this way were able to distinguish between the positive and negative stimuli very well - even in tests in which the bees were presented with a pair of novel random gratings that they had never previously encountered during the training (Fig. 5b) [48]. This experiment reveals that bees are capable of the learning the orientation of a pattern as an abstract property of the pattern, without needing to memorize the entire pattern as a template. Bees that have been trained on these random gratings can even discriminate the orientation of entirely different patterns that they have never been trained on, or previously encountered. Some examples of these novel patterns are single stripes (Fig. 5c), semicircles (Fig. 5d), and periodic gratings with square-wave or sinusoidal profiles (Fig. 5e) [48]. Thus, bees are clearly capable of learning orientation as an abstract geometrical property, and applying it to distinguish between novel patterns. This capacity to learn patterns in terms of their general features, rather than as templates, has also been documented in subsequent studies (e.g. [49]).

Bees that have been trained to discriminate orientation using the random gratings are also able to perceive and discriminate the orientations of the white rectangles shown in Fig. 6a, as well as the orientations of the illusory rectangles shown in Fig. 6b [48]. Evidently, bees perceive the illusory contours, just as humans do. Rotating the 'Pacmen' in the corners by 90 deg (Fig. 6c) eliminates the illusion for humans, as well as bees. Similar findings were reported later in [50]. Illusory contours are believed to constitute a process of 'contour completion' whereby the human visual system detects and recognizes partially occluded objects by filling in the missing segments of their boundaries. This is completion accomplished by perceptually connecting together visible segments that are parallel and collinear. Indeed, some neurons in the macaque cortex respond to illusory contours, and are believed to play a role in contour completion [51]. Given the general importance of recognizing partially occluded objects, it is not inconceivable that similar principles underlie visual processing in bees, as well as many other invertebrates. Indeed, higher-order neurons that respond to illusory contours have been discovered in the dragonfly [50], and the existence of processes involved in contour completion has been documented in vertebrates such as chicks [52] and fish [53].

Do bees analyse the orientation of a pattern in terms of its geometrical properties, or do they use a simpler cue? Given the sensitivity of the bee's visual system to movement of the image, and the many ways in which this is used to guide flight, the orientation of a pattern could, in principle, be inferred from the movement signals that it generates in the visual system. For example, vertical stripes would induce primarily horizontal image motion as a bee approaches or flies by them, whereas horizontal stripes would generate primarily vertical motion [54]. However, bees can be trained to distinguish pattern orientation even when these potential motion cues are eliminated by presenting the patterns briefly on display monitors (for 25 ms, every 0.5 s) [55]. Thus, orientation can be discriminated even in the absence of motion cues. Bees trained to discriminate the orientation of random gratings (as in Fig. 5a) were readily able to distinguish between a pattern comprising two vertical rows of dots, and another comprising two horizontal rows of dots (Fig. 7a). The bees were then tested with dynamic versions of these patterns in which the dots were moved along the vertical direction in the vertical-row pattern, and along the horizontal direction in the horizontal-row pattern (Fig. 7b). This should confound the induced motion signals, because the motions of the dots are perpendicular to those induced by the bees' self-motion. However, inclusion of this motion did not compromise the bees' orientation discrimination [55]. This indicates that the bees did not rely on motion cues to discriminate the orientations of these patterns when they were stationary. On the other hand, bees trained to discriminate the orientation of random gratings were unable to distinguish between two patterns of randomly arranged dots (Fig. 7c) - as one might expect, because neither pattern bears a clear geometrical orientation. Furthermore, this lack of discrimination persisted when the random dot patterns were moved in orthogonal directions (one pattern vertically, and the other horizontally, as in Fig. 7d) [55]. These observations again argue against the use of motion cues for discriminating pattern orientation.

The above findings suggest that bees analyse the orientations of patterns based purely on their geometry, as does the human visual cortex. In humans and other primates, pattern orientation is analyzed at the cortical level by a set of neurons that respond to bars or edges [56]. Each neuron is tuned to a different orientation, and the orientation of the observed feature is signaled by the neuron that produces the strongest response [57]. Does the bee's visual pathway analyse orientation in a similar fashion? While there is no definitive answer as yet, there are some useful leads. Bees can easily be trained in a Y-maze to distinguish between a vertical bar and a bar that is inclined at 45 deg by rewarding them on the vertical bar, as shown in Fig. 8a, or between a 45 deg bar and a horizontal bar [58]. That is, they can easily resolve orientation differences of 45 deg. However, bees cannot be trained in a Y-maze to discriminate between a 'plus' shape and a 'cross' shape - even though the cross is again a 45 deg rotated version of the plus (Fig. 8b) [58]. This interesting observation could shed some light on the properties of the orientation-sensitive neurons, if such neurons indeed exist in the bee. If an orientation-sensitive neuron is sharply tuned to a particular orientation, its response would display a strong modulation with four maxima as the plus shape is rotated through 360 deg. On the other hand, if the neuron is broadly tuned, the response would show little or no modulation as the shape is rotated. Specifically, if the orientation tuning curve is a raised cosine function with an angular half-width of 90 deg, rotation of the shape would generate no modulation at all in the neuron's response [58]. These findings therefore suggest that, if orientation-tuned neurons exist in the visual pathway of the bee, they should possess tuning half-widths of about 90°. These behavioral experiments do not reveal the *number* of orientation-tuned neurons, or their individually preferred orientations - that would require

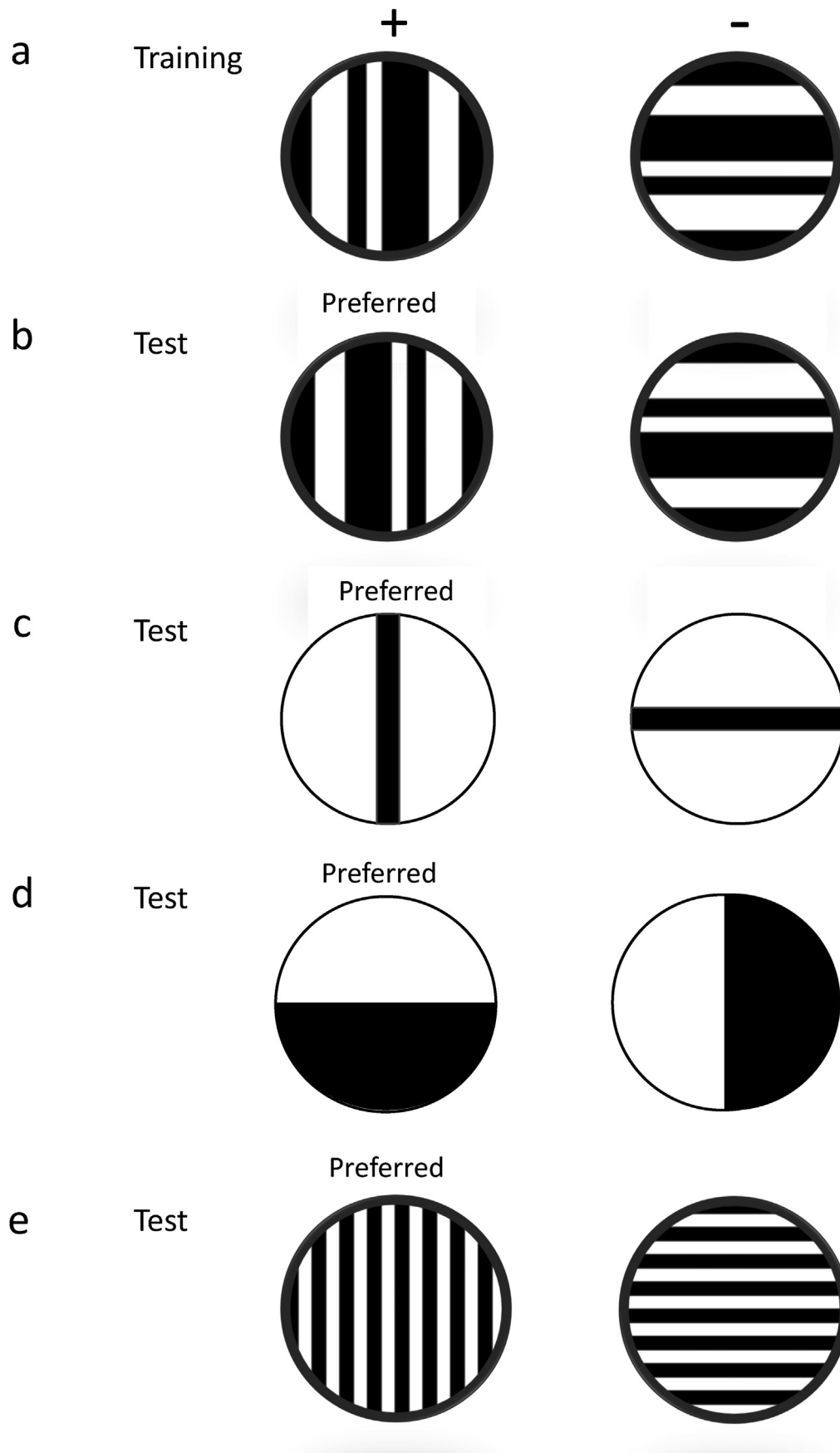


Fig. 5. Generalized learning of orientation as an abstract parameter. Bees, trained to discriminate between vertically-oriented and horizontally-oriented random gratings (a) by associating a reward with the vertical gratings (+), are tested on novel random gratings (b), single stripes (c), semicircles (d) and periodic gratings (e). In each test, the trained bees prefer the pattern with the vertically oriented contours.

investigations at the electrophysiological level. Subsequent recordings from insect optic lobes have indeed revealed the existence of broadly tuned orientation-sensitive neurons in the honeybee [59] as well as the dragonfly [60]. The evidence so far therefore suggests that the visual pathways of primates and insects analyse pattern orientation in similar ways.

1.3.3. Visual acuity

The ease with which honeybees can be trained to discriminate pattern orientation has also been used to measure the spatial acuity of their visual system. Bees are trained to distinguish between horizontal and vertical periodic gratings of the same spatial frequency. The spatial frequency is then progressively increased to determine the point beyond which the bees are no longer able to distinguish the two orientations, because the gratings can no longer be resolved [47]. This cutoff spatial frequency, which provides a measure of the spatial acuity of the honeybee's visual system, is about 0.25 cycles/deg. This figure is consistent with that expected from measurements of the optical properties of the honeybee's compound eye, namely, the angular size of the visual fields of individual ommatidia, and the interommatidial angle [47]. The spatial acuity of the honeybee is a factor of 240 poorer than that of humans, who have a cutoff spatial frequency of about 60 cycles/deg [61]. However, the spatial acuity of bees is adequate for resolving the details of objects that are of relevance to them.

1.3.4. Detection of pattern symmetry

Bees can be trained to learn other general properties of objects, such as 'symmetry', in a general way: they can be trained to distinguish between patterns that have left-right symmetry, and patterns that are asymmetrical. The trained bees are then able to distinguish between novel symmetrical and asymmetrical patterns that they have never previously encountered [62]. The ability to learn and recognise symmetry in an object may also be important in enhancing foraging success. Bees seem to have a spontaneous preference for symmetrically shaped objects [63], possibly because an asymmetrical flower may have lost a petal and is not as healthy and nectar-bearing as a symmetrical one. There is also evidence that bees group together complex patterns that are mirror transformations or left-right transformations of each other [64]. There has likely been a co-evolution between flowers and their pollinators, with the flowers signalling health and food-bearing capacity through their symmetry, and bees preferring to visit symmetrical flowers.

1.3.5. Detection and discrimination of camouflaged objects

Bees can be trained to detect and perceive camouflaged objects [65,66]. Many of us would be familiar with the famous photograph of a Dalmatian standing against a spotted background (see Fig. 1 in [65]): first-time viewers usually do not spot the Dalmatian until they are told to 'look for a dog' in the picture. Evidently, prior knowledge, also known as 'top-down processing' in neuroscience, plays a key role in aiding our perceptions. We asked whether bees also possess top-down processing, by conducting the following experiment [65]. Fig. 9 shows two camouflaged objects: one is a textured ring, positioned about 6 cm in front of a similarly textured background, and the other is a textured disc presented against a similarly textured background. In the experiment the textures of the objects and the backgrounds have the same contrast, but in this illustration the object textures are shown with a lower contrast in order to make them visible against the background. The only way that a bee can detect each of these camouflaged objects is to sense the motion parallax - the motion of the object's image relative to the background - caused by the fact that the background is farther away. When we attempted to directly train bees to distinguish

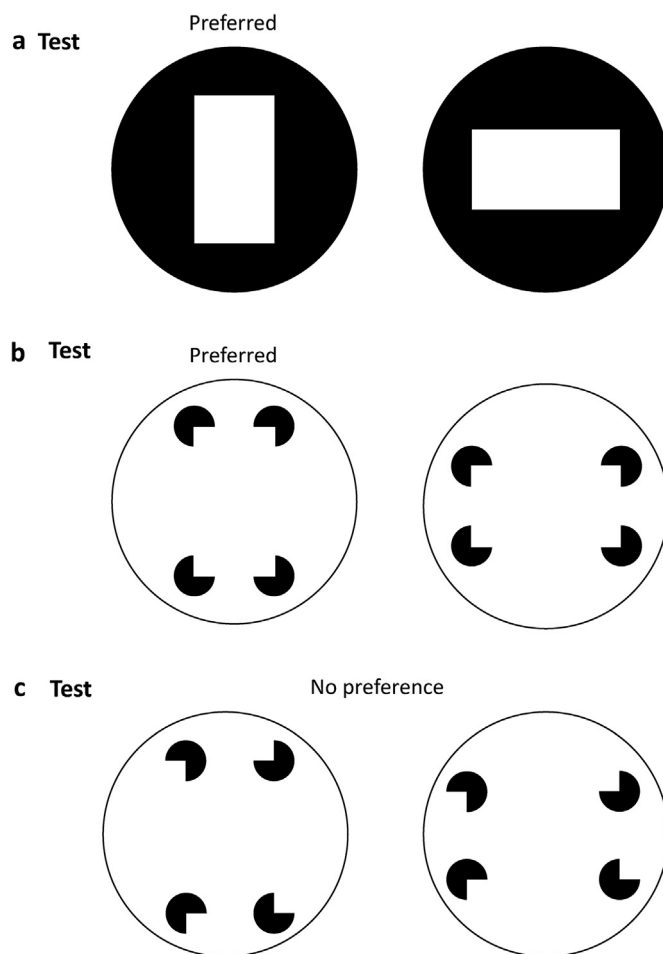


Fig. 6. Perception of illusory contours. Bees, trained to distinguish between random vertical and horizontal gratings (as in Fig. 5a) show a preference for the vertically oriented rectangle (a), and for vertically oriented Illusory contours (b), but this preference disappears when the illusory contours are eliminated by rotating the Pacman figures (c).

between the two stimuli, we had no success: Bees never learned to distinguish the stimuli, despite five days of training (Fig. 9a). However, if one begins by training bees to distinguish between *uncamouflaged* versions of the same shapes (Fig. 9b) - which they learn well - and then tests them with the camouflaged shapes (Fig. 9c), they choose the corresponding camouflaged shape immediately, without requiring any training on the camouflaged shapes [65]. Furthermore, these bees can then be further trained to discriminate new camouflaged shapes - such as a horizontal rectangle and a vertical rectangle - *without* pre-training them on uncamouflaged versions of these novel shapes (Fig. 9d). Evidently, the bees are able to learn the cue for breaking the camouflage (sensing motion parallax) from the first training, and apply this cue to detect and recognise new camouflaged objects [65,66]. Thus, bees can be trained to perceive scenes in novel ways.

1.3.6. Maze learning

Bees can learn to navigate through complex mazes and labyrinths (Fig. 10). We trained bees by initially attracting them to a feeder and then moving the feeder slowly, step by step, along the correct route through the labyrinth to the goal, where the feeder was finally positioned. Bees required about five days' training (about 150 visits) to learn this task [67]. However, their task can be simplified, and the learning process accelerated, if they are

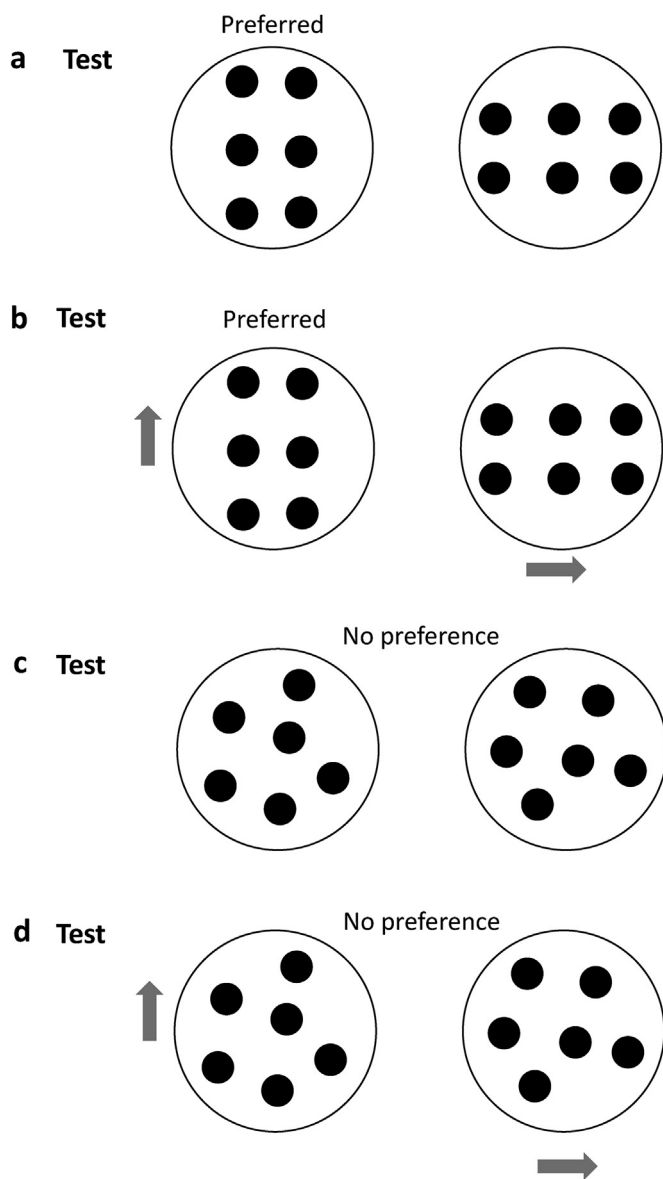


Fig. 7. Evidence that image motion cues do not play a role in the discrimination of pattern orientation. Bees, trained to discriminate vertically and horizontally oriented gratings (as in Fig. 5a), show a preference for vertically oriented rows of dots over horizontally oriented rows, regardless of whether these dot patterns are stationary (a) or moving in the directions indicated in (b). On the other hand, these trained bees do not discriminate between patterns of randomly arranged dots, regardless of whether they are stationary (c) or moving (d).

provided with navigational signals.

For example, if the training feeder carries a green label – and each chamber in the maze carries a similar green label that indicates the correct exit – the bees associate the label with ‘food’ and learn rapidly (in about 4 h) to follow this indicator to the goal (Fig. 10a) [67]. The signal can also be provided in a different way. For example, each chamber in the maze could have a front wall carrying a colour, and two side walls, each with an unmarked exit (Fig. 10b). The bee would have to learn to take the right-hand exit if the front wall is blue, and the left-hand exit if the front wall is yellow. Bees can learn this task relatively rapidly, too – within about 6 h, even though the signal is more complex and symbolic in this case [67]. Interestingly, bees that have been trained to use signals (of either type) are able to blaze a trail through the maze,

reaching the goal in about 15 s and making relatively few errors – whereas bees that are trained on a signal-free maze move more slowly and make more errors, as one might expect. However, it is only in the case of the signal-free maze that the bees actually *learn* the route through the maze. Bees that are trained with the signals find it difficult to navigate the maze if the indicators are removed after the training [67]. Evidently, these bees rely primarily on the signals for their navigation. This is very analogous to the human experience of driving a car. The driver does not learn the route well when the guidance is provided by a passenger or a GPS device.

Bees are also adept at learning patterns of regularity in mazes, if such patterns exist [68]. For example, constant-turn mazes in which the correct turn in each chamber is always a left turn, or always a right turn, are learned quickly and accurately. Bees can also learn to navigate zig-zag mazes (where the correct turn alternates between left and right in successive chambers), although not as well as the constant-turn mazes. Bees that have been trained on a zig-zag maze can use this learned pattern to navigate a longer zig-zag maze, without further training [68].

1.3.7. Delayed match-to-sample tasks

A typical delayed match-to-sample task (hereafter referred to as a DMTS task) is one in which a subject is briefly shown a ‘sample’ stimulus (say, a blue disc). After a short period of time, the subject is presented with two ‘test’ stimuli (a blue disc and a yellow disc), only one of which matches the previously seen sample. The subject’s task is to select the test stimulus that matches the sample: i.e. to choose the blue test stimulus if the sample was blue, and the yellow test stimulus if the sample was yellow. The DMTS task is primarily an investigation of working memory, as the sample needs to be retained in memory only for a short period of time. The long-term ‘learning’ component of the task is that of learning the nature of the task *per se*, i.e. the concept of ‘matching’.

It has been known for a considerable period of time that humans and other primates, and pigeons can perform DMTS tasks. In 2001, we set out to examine whether this capacity extends to invertebrates (in particular, honeybees), by using a modified version of the Y-maze experimental paradigm [69]. Bees encountered a sample stimulus at the front of the entrance to the Y-maze. They then had to choose between two test stimuli, one at the end of each arm (as in Fig. 4). The choice was made in the decision chamber (where the sample stimulus was no longer visible), and therefore required the bees to retain the sample stimulus in short-term memory in order to select the matching test stimulus. We found that bees performed the DMTS task very well, irrespective of whether they were required to match colors, patterns or even scents [69]. In addition, bees could also be trained to select the ‘non-matching’ test stimulus, rather than the matching one [69]. We were also able to measure the duration for which bees could retain the memory of the sample stimulus [70]. This was done by placing the sample stimulus at the entrance to a long tunnel through which the bees had to fly to reach the Y-maze, and manipulating the flight distance (and therefore the flight time) between the sample stimulus and the decision chamber. These experiments revealed a working memory that lasted for about 5 s for visual patterns [70], which is not very different from the duration for which a person can remember a phone number before dialing it. Interestingly, bees that have been trained to match colors are immediately able to match patterns, without having to be trained on the patterns [69]. Thus, the concept of ‘matching’ is learned in a general way. Even more interestingly, bees that have been trained to match scents can immediately match colors, indicating that the learned concept of matching can also be transferred across sensory modalities [69].

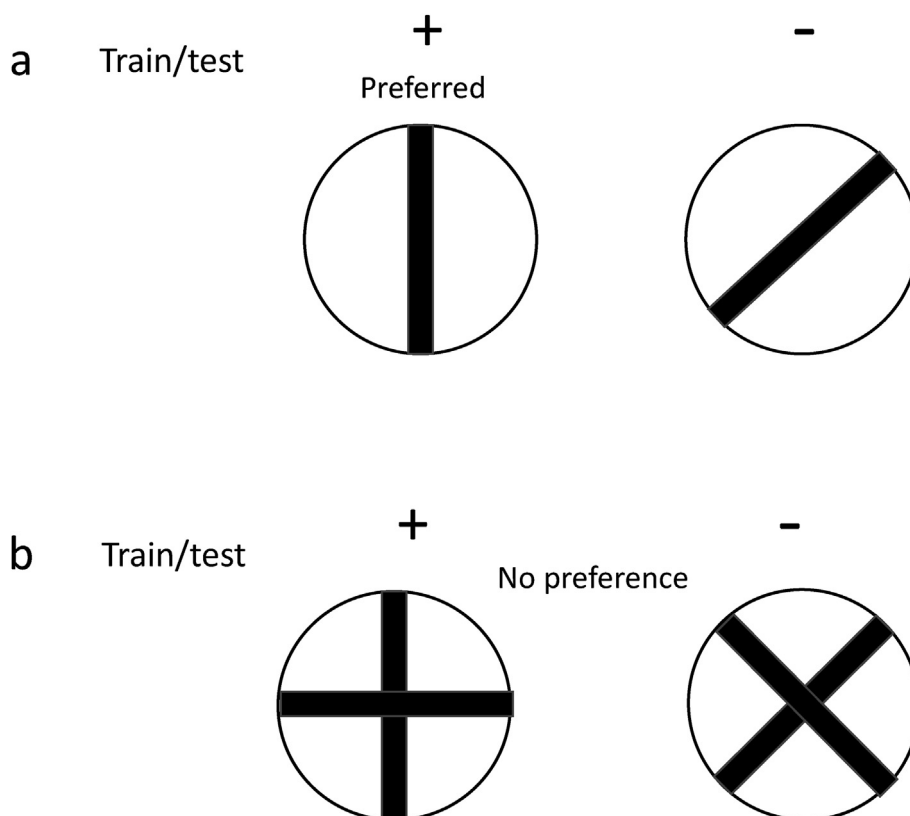


Fig. 8. Experiments investigating tuning properties of putative orientation-sensitive channels in the honeybee's visual pathway. Bees can learn to discriminate an orientation difference of 45 deg in a single stripe (a), but not in a cross (b).

1.3.8. Delayed symbolic-match-to-sample tasks

The Delayed Symbolic-Match-to-Sample Task (DSTMS) is a more complex version of the DMTS task which involves learning associations between symbols, rather than simply matching symbols. For example, a bee, confronted with a choice between a horizontal grating and a vertical grating at the decision chamber, has to learn to choose the horizontal grating or the vertical grating according to whether the sample stimulus at the entrance is a blue disc, or a yellow disc. Bees are able to learn this task well [71]. This experimental paradigm has also been used to show that bees can also learn to associate specific scents with specific colors [72]. Furthermore, bees can learn an extended version of the DSTMS task which involves establishing two successive associations in an apparatus comprising a concatenation of Y-mazes [71]. When the apparatus presents a blue disc at the entrance, the bee has to learn to choose a horizontal grating over a vertical grating in the first decision chamber, and a pattern comprising concentric black-and white rings over one comprising radial black-and white sectors in the second decision chamber. When the apparatus presents a yellow disc at the entrance, the bee has to learn to make the opposite set of choices. Bees are quite adept at this task of learning second-order associations, as well as conceptually grouping the six stimuli into two groups of related stimuli: (i) blue disc, horizontal grating, and rings; and (ii) yellow disc, vertical grating, and radial sectors [71].

1.3.9. Learning complex associations

Bees can go one step further, and establish links between scents and complex behaviours. It is a common human experience that a smell, or a musical tune, can trigger recollection of a particular experience – pleasant or unpleasant – that occurred many years ago. This phenomenon of 'associative recall' – learning to associate

a sensory stimulus with an event – helps us avoid harmful or disagreeable situations, and seek pleasurable ones. Do bees possess associative recall? To examine this, we trained a group of marked bees to fly to a feeder that was placed at one of two locations, A or B, in a meadow [73]. When the feeder was placed at A, it was laced with the scent of rose. When it was placed at B, it carried the scent of lemon. The position of the feeder was switched every half an hour. This training was continued for 2 days. At the end of the training period, the feeder was removed. Early in the morning of day 3, we placed two 'dummy' feeders – one at A, and the other at B. Neither of these dummy feeders carried any sugar water or scent, but they had the same visual appearance as the training feeders. We then injected the scent of rose into the hive of the colony. The colony was quiet, because it was early and the bees had not commenced foraging. The injection of scent caused the marked bees – and only the marked (trained) bees – to emerge from the hive, and search for food at location A. Virtually none of these bees visited location B. Later, when we injected the scent of lemon into the hive, the same marked bees re-emerged, this time to search for food almost exclusively at location B. Since the dummy feeders carried no scent, we can be sure that the tested bees were not 'homing in' on a scent. Rather, the whiff of a familiar scent in the hive triggered a recall of the location of the food in the bees' minds, and motivated them to fly there. This simple experiment demonstrates clearly that bees can associate scents with locations of food [73,74]. Further studies have demonstrated that bees can also learn to associate scents in the hive with specific visual properties of feeding destinations, such as their colour [75]. Thus, bees, like humans, possess a capacity for complex associative recall. In honeybees, scent-triggered recall of locations deteriorates when the number of locations is increased to three, but this performance is

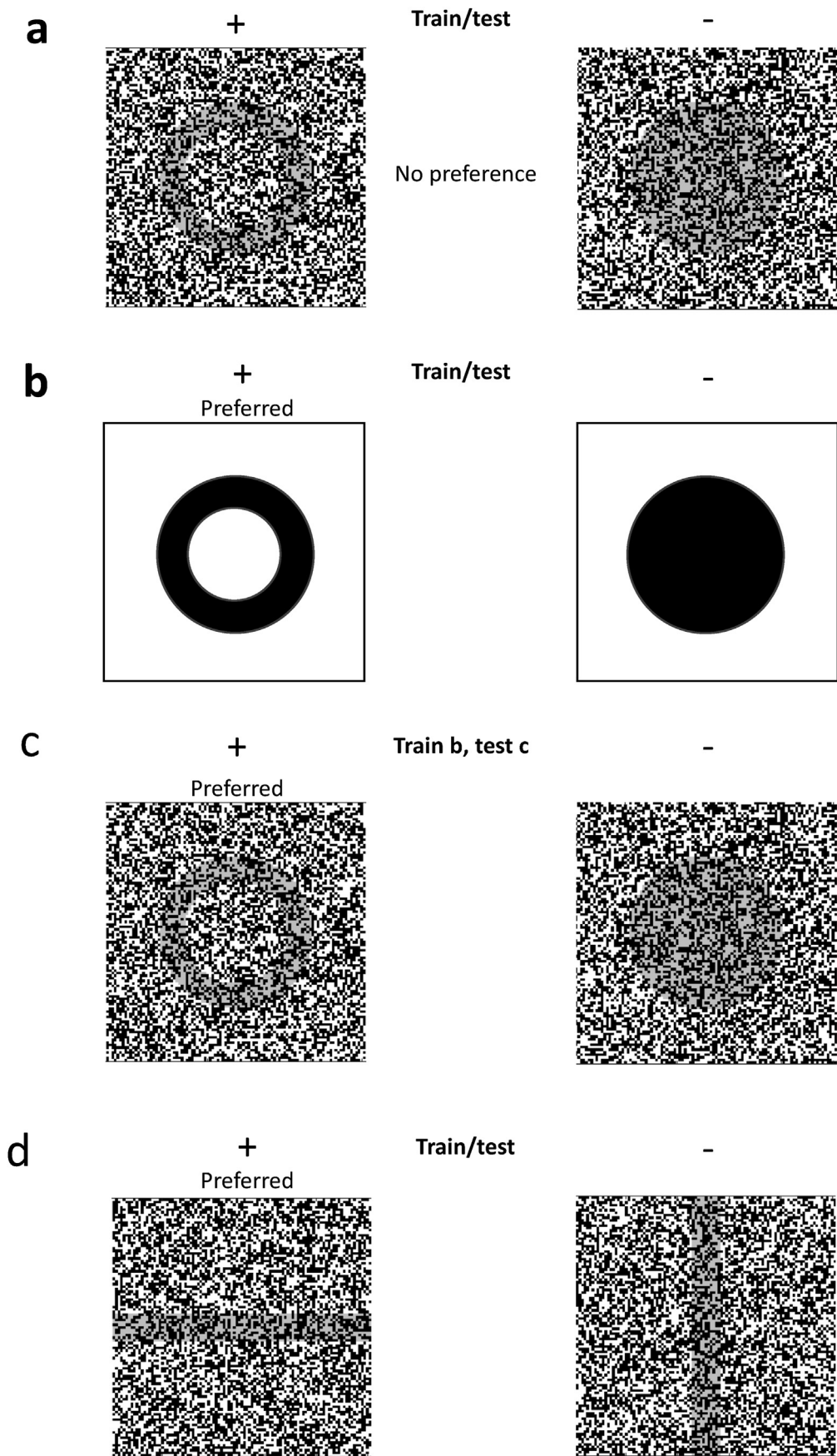


Fig. 9. Experiments to investigate whether honeybees can detect and discriminate between camouflaged objects. Details in text.

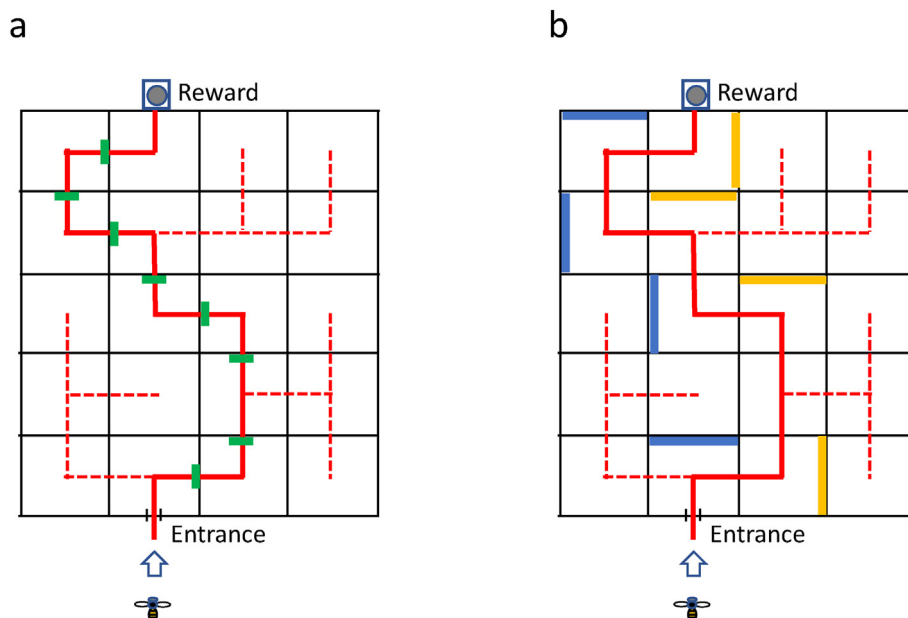


Fig. 10. Maze learning in honeybees (a) by following a mark; and (b) using colour as an abstract navigational signal. Details in text. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

partially restored when the feeders are labeled with distinct colors [76]. Thus, recall of locations can be strengthened when there is an opportunity to associate more than one sensory signal with each location.

1.3.10. Numerical competency

Several studies are beginning to demonstrate that bees can 'count'. An early investigation suggested that bees can perform sequential counting up to the number three [77]. This was done by showing that bees, trained to forage at a feeder in an open field, could pinpoint the location of the feeder by counting the number of prominent landmarks that they encountered *en route*. We repeated this investigation in a more rigorous fashion by eliminating the possible use of odometric cues [78]. In our study bees were trained to fly along a tunnel, lined with a series of landmarks, to a feeder that was positioned at the first landmark, or the second, or the third, etc. in different experiments. In each experiment, the flight distance to the feeder-bearing landmark was constantly varied, whilst keeping the number of intervening landmarks constant, in order to exclude the use of odometric cues. Furthermore, chicane partitions were interposed between landmarks, so that only one landmark was visible at any time during the flight to the feeder. This ensured that the counting (if existent) was truly sequential. This study revealed that bees can learn to count sequentially up to a maximum of four [78]. Larger numbers seem to be grouped into a single category: 'Greater than four'. Bees can also learn to distinguish between pictures that contain different numbers of objects, even if the objects are varied in size and shape [79]. In other words, bees can acquire a true concept of 'numerosity'. Recent work from other laboratories has shown that bees can even be trained to add and subtract – that is, to evaluate the sum of, or difference between, the numbers of objects in two different scenes [80] – as well as to learn and recognise the concept of 'zero' [81]. Another recent study has shown that bees can establish a subjective correspondence between the concepts of 'object number' and 'object size': bees that are trained to choose higher numerosities tend to prefer larger objects [82]. A DSTMS paradigm has been used to show that bees can be trained to associate abstract symbols with the numbers

of objects that they represent [83]. There is also evidence that bees can establish a correspondence between the size and the brightness of an object [84]. Numerical competency could help a foraging bee decide whether to abandon landing on a flower or a bush that already carries a large number of bees, and seek a different location where there is less competition.

2. Conclusions and outlook

The findings described here suggest that honeybees provide a very useful model in which to study basic principles of vision, perception, flight guidance, navigation and 'higher' cognition in creatures with brains weighing less than a milligram. Some of the simple, elegant principles of sensorimotor control unearthed by these studies have inspired the design of novel, biologically inspired algorithms for the guidance and navigation systems of autonomous aerial vehicles.

The more one studies bees, the more one realises that these creatures are not very different from humans, after all. The findings that bees not only possess remarkable skills with respect to flight guidance and navigation, but also display impressive cognitive faculties such as complex associative recall, the ability to abstract general properties of visual patterns, to break camouflage, to use symbolic signposts to navigate complex routes, to enumerate objects, and will even prevent their nestmates from visiting a perilous location [85], suggest the presence of some form of consciousness that we are only beginning to explore.

One of the unanswered questions is whether bees – and, indeed, many other invertebrates – experience the sensation of pain. There is little doubt that animals such as dogs or cats can feel pain. However, if an insect flinches when it is prodded with a pin, we surmise that this reaction is simply a 'reflex', because of our reluctance to attribute the sensation of pain to 'less intelligent' animals. A thoughtful discussion of this prevalent mind-set is provided in [86]. This attitude may change as we learn more about the cognitive capacities of animals with small brains and relatively simple nervous systems. It is noteworthy that some animals, such as fish, squids and octopuses, are now officially recognised to be

pain-sensitive and are included in the ethical guidelines for animal experimentation [87–89]. Experiments with honeybees in our laboratory so far have hinted at the ability to perceive pain, but they are not conclusive [90,91]. It is possible that we are yet to conduct the most appropriate experiments for probing the question. Clearly, more work needs to be done in this area.

While this article has focused on the behaviour and capacities of individual bees, there is much to be learned from the study of the colony as a whole. For example, our current knowledge of communication within the hive may be just the tip of a giant iceberg. Acoustic signaling is known to play an important role in the honeybee's waggle dance, as well as in many other behaviours. Stingless bees living in tall forests use acoustic signals to communicate information about the height of a food source when it is located atop a tall tree [92]. We do not yet know whether bees use sound to communicate additional attributes of a food source, such as the colour, size or shape of the flower. The sounds emanating from a hive could also provide a useful indication of the hive's condition. Microphones implanted in the hive, combined with automated sound analysis based on machine learning could aid beekeepers in monitoring a colony's foraging activity remotely, checking whether the queen is present, and detecting when the colony is preparing to swarm.

Declaration of competing interest

I declare that there is no conflict of interest in this submission.

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