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Small Brains, Smart Minds: Vision, Perception and 'Cognition' in honeybees

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Recent work is beginning to reveal that insects may not be the simple, reflexive creatures that they were once assumed to be. Honeybees, for example, can learn rather general features of flowers and landmarks, such as colour, orientation and symmetry, and apply them to distinguish between objects that they have never previously encountered. Bees exhibit "top-down" processing: that is, they are capable of using prior knowledge to detect poorly visible or camouflaged objects. Furthermore, bees can learn to navigate through labyrinths, to form complex associations and to acquire abstract concepts such as "sameness" and "difference". All of these observations suggest that there is no hard dichotomy between invertebrates and vertebrates in the context of perception, learning and 'cognition'; and that brain size is not necessarily a reliable predictor of perceptual capacity.

Indexing terms: Honeybee, Vision, Perception, Cognition, Pattern recognition, Associative recall, Delayed match to sample, Concept formation.

1. INTRODUCTION

UNTIL relatively recently, small creatures with tiny brains have been considered to be just that: small creatures with tiny brains. That is, their behaviour 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. This article reviews recent work in our laboratory where we have challenged the perceptual capacities of honeybees in several ways. Some of the questions that we have been pursuing are: Can bees learn abstract concepts? Can they 'generalize' these concepts? Can bees learn to look at objects in new ways? Can they learn complex associations? And how flexible is the capacity to learn?

The worker honeybee, by virtue of its lifestyle, is a spectacularly suitable organism for studying principles of pattern recognition and navigation, as well as of learning in a more general sense [1]. Gathering nectar and pollen is the *raison d' être* of a forager's existence. To forage successfully, a bee has to learn and remember not only the colour and shape of flowers that are bountiful in these nutrients, but also how to get to them. Since the species of flowers that are in bloom, say, this week are likely to be replaced by a different species at a different location the next week the bee needs, and indeed possesses, an impressive ability to learn colours, odours, shapes and routes quickly and accurately. A bee can learn a new colour in about half an hour (after it has made about five visits to collect a food reward) and a new pattern in about half a day (after 20-30 rewarded visits), and a new route to a food source in about 3-4 visits (provided the route is not through a complex labyrinth). The biology of the honeybee thus offers a tailor-made opportunity for studying the processes that underlie the recognition of patterns, the formation of complex associations and the learning of concepts. This review presents examples of studies in our laboratory that have addressed some of these questions.

2. PATTERN RECOGNITION: DISCRIMINATION OF PATTERN ORIENTATION

Can bees learn the orientation of a pattern in an abstract sense, and use this knowledge to distinguish between other patterns that they have never previously encountered? An early paper by Wehner [2] hinted that bees could indeed abstract pattern orientation in this way. This question was pursued further by van Hateren *et al* [3], who trained bees in a Y-maze to distinguish between patterns that carried vertical or horizontal stripes (Fig 1*a*). The two stimuli were presented in the vertical plane, each at the end wall of one of the tunnels of the maze. The stimulus representing one of the orientations was associated with a reward of sugar water. The stimulus representing the other orientation carried no reward. During training, the positions of the stimuli were interchanged frequently, and the reward was moved along with the positive stimulus, to prevent the bees from simply learning to fly to a specific tunnel. 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 (Fig 1*b-d*). Furthermore, bees trained to distinguish between two

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mutually perpendicular orientations were able to discriminate the orientations of other patterns that they had never encountered previously (Fig 2). Thus, bees are able to extract orientation information from patterns on which they are trained, and to use this information to evaluate novel patterns. Quantitative models suggesting the way in which orientation analysis may be implemented in the honeybee's visual pathway are described in [4]. Indeed, there is some evidence that the visual pathway of the bee possesses orientation-tuned channels [4-6], and that it may operate as a rudimentary version of the mammalian visual cortex.

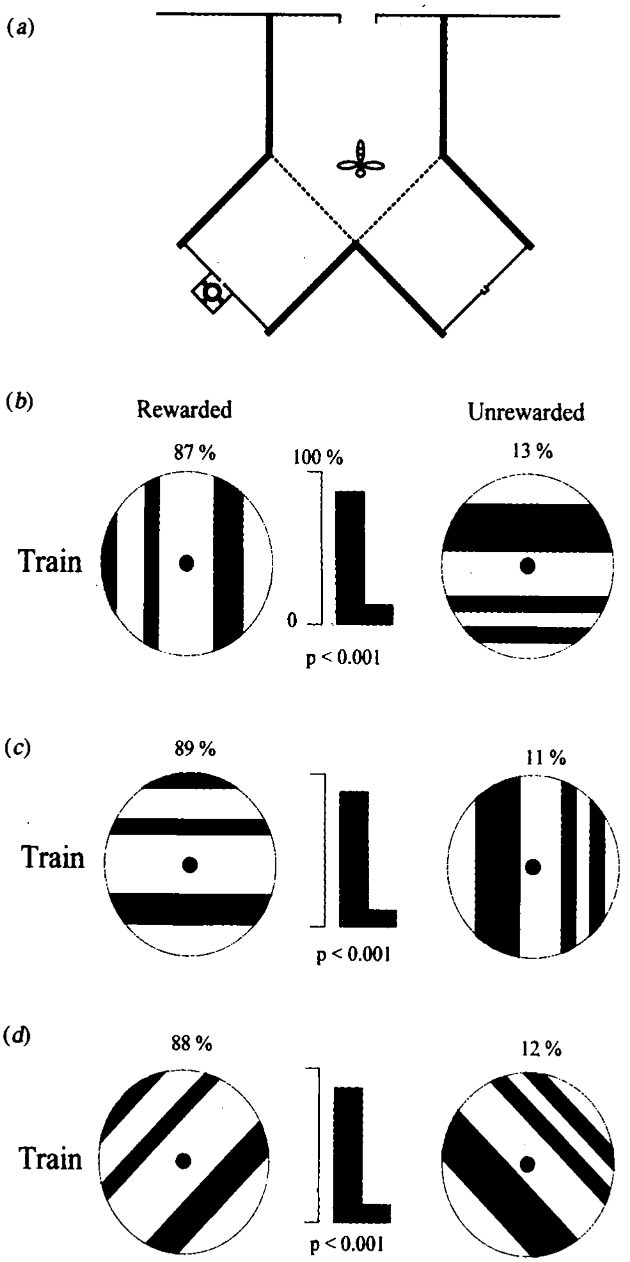

Fig 1 (*a*) Y-maze apparatus for training and testing bees in pattern discrimination tasks. Bees can be trained in the Y-maze to distinguish between vertically and horizontally oriented random stripes irrespective of whether they are rewarded on the vertical orientation (*b*) or the horizontal orientation (*c*) Bees can also learn to distinguish between stripes that are oriented at + 45° and – 45° (*d*) The numbers and bars denote the relative frequencies of choices in favour of the two stimuli, *n* denotes the number of choices analysed, and *P* is the value associated with a chi-squared test for significant differences from random-choice behaviour. (*b* – *d*) adapted from [3].

Recent work has revealed that bees can learn other abstract properties of patterns, such as bilateral symmetry [7,8]. Bees can also distinguish between radially- and circulary-symmetrical patterns in a rather general way [9,10].

2.1. "Top-down" processing in pattern recognition

Many of us who view the scene in Fig 3*a* for the first time would not see a familiar object, especially if we are unaware of the picture's content. Once the camouflaged Dalmatian has been discovered, however, it is detected and recognised instantly every time the picture is re-encountered. Evidently, prior experience or knowledge aids the visual system significantly in the task of uncovering objects [11-13].

Is top-down perception of this nature a sophistication that is restricted to primates and higher mammals? To examine this question, Zhang and Srinivasan [14] attempted to train bees to distinguish between two shapes — a ring and a disc — when each shape was presented in a camouflaged fashion as a textured figure 6 cm in front of a similarly textured background (Fig 3*b*). It turned out that bees were unable to learn to make the discrimination, despite lengthy training spanning over 100 rewards per bee (Fig 3*b*). Next, Zhang and Srinivasan examined whether bees could learn to distinguish the camouflaged stimuli if they were first trained on a related, but simpler discrimination: that of distinguishing between a black ring and a black circle, each presented 6 cm in front of a white background. The ring and the circle were of the same size and shape as their textured counterparts, and their spatial configuration in relation to the background was identical to that in the previous experiment. The bees were able to learn this new task (Fig 3*c*). When these pre-trained bees were tested on the task of Fig 3*b*, they could distinguish between the stimuli immediately (Fig 3*d*). Clearly, the bees were using knowledge acquired from the black-and-white stimuli of Fig 3*c* to discern the camouflaged objects. Moreover, bees trained in this step-by-step fashion could go on to learn to distinguish between other camouflaged objects that they had never previously encountered, such as two differently oriented bars (Fig 3*e*), without any pre-training on black-and-white versions of the new shapes.

Although the figures in Fig 3*b* are camouflaged, they can be detected by virtue of the apparent relative motion between the figure and the more distant background, as the

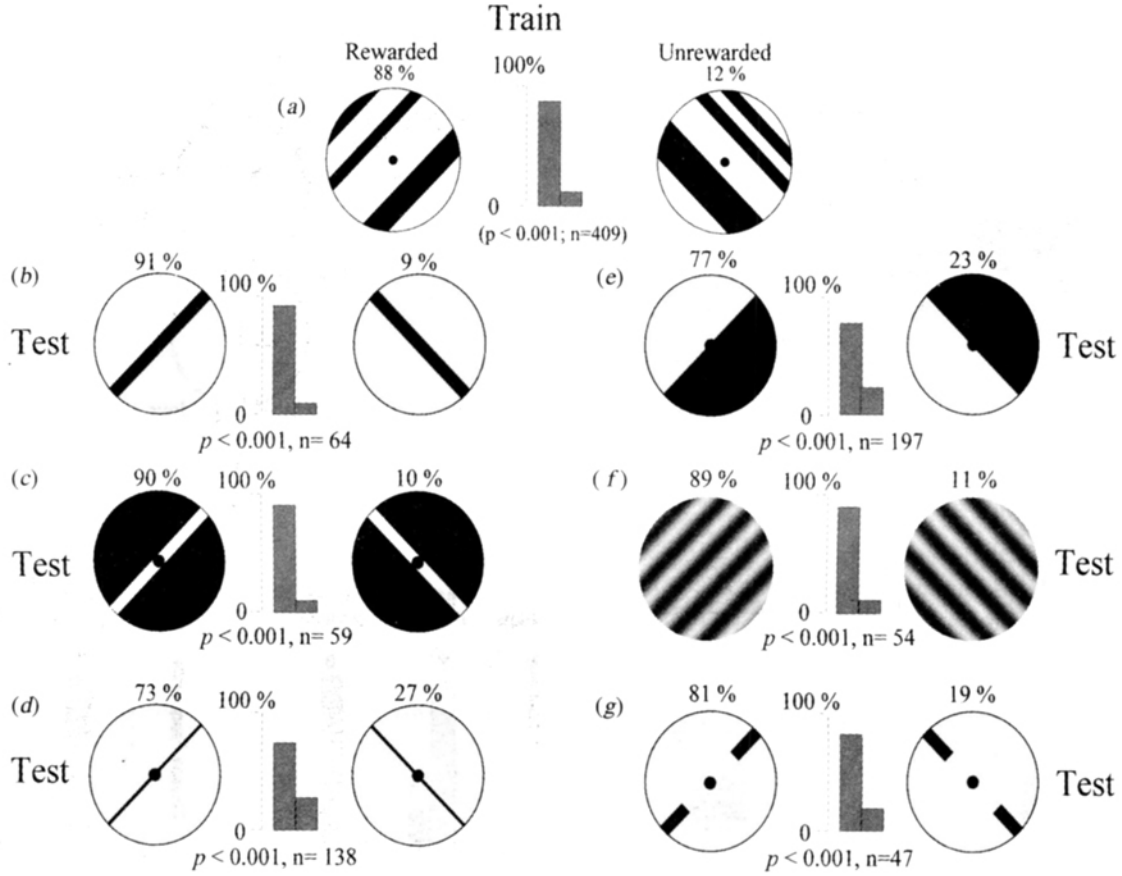

Fig 2 Bees, trained to distinguish between random stripes oriented at + 45° and – 45°, as in (*a*) are able to extract the orientation information in these patterns and use it to discriminate the orientations of other patterns (*b* – *g*) which they have never previously encountered. Other details as in Fig 1 Adapted from [3].

bee approaches the figure. Evidently, the bees had learnt to use motion parallax as a cue to break the camouflage and thereby discern the otherwise invisible figures. Quite apart from learning to use previously acquired information about specific shapes, the bees had learnt to use an entirely new cue, which they normally did not use for pattern discrimination. In other words, they had learnt to change the way in which they looked at the stimuli. This phenomenon of "top-down" processing is strikingly reminiscent of learning processes in human visual perception.

2.2. Maze learning

The ability to learn mazes has been investigated extensively in a number of vertebrates, notably rats, mice, pigeons and fish [15-18]. Relatively few studies, however, have explored the capacity of invertebrates to learn complex mazes. Two recent studies have investigated the ability of bees to learn mazes. One study showed that bees could readily learn to navigate through a labyrinth, composed of a number of interconnected chambers, if the correct exit in each chamber was labelled by a small mark next to it [19]. Bees were also able to learn more abstract cues to navigate through such a labyrinth. In a variant of the above experiment, it was shown that bees could learn to link the direction of the turn within each chamber to the colour of the chambers' back wall. They learned to turn to the left, for example, if the wall was green and to the right if it was blue. Surprisingly, bees were able to learn this abstract rule just as well as the rule of simply following a mark [19]. In another recent study it was shown that bees could negotiate certain types of mazes by detecting and learning regularities their structure [20]. For example, they could learn rules such as "always turn right" or "alternate left and right turns". Once they had learnt the rule (which required about half a day, or ca.15 rewarded visits), they could negotiate a similarly-structured maze of any size [20].

2.3. Associative recall

It is a common experience that a smell or a sound can trigger a vivid recollection of an associated event in the past — even if it involves a different sensory modality, and even if the episode occurred a long time ago [21,22]. Clearly, the human brain displays impressive cross-modal associative recall — a faculty that has obvious survival value.

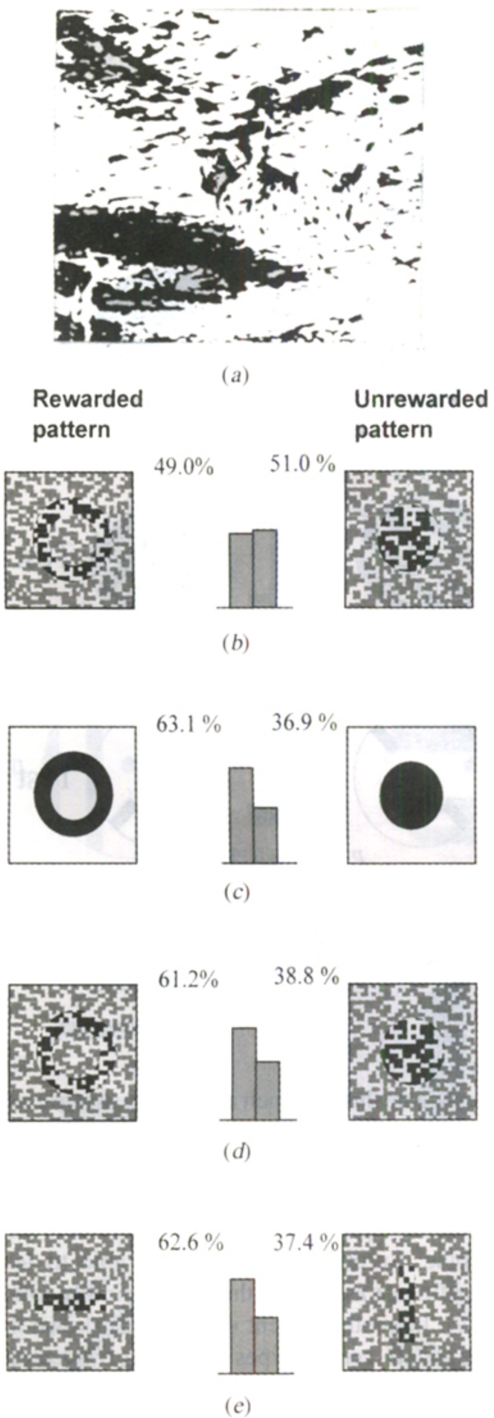

Fig 3 Top panel: A familiar, but camouflaged object (readers experiencing difficulty in recognising the Dalmatian dog may wish to view the picture upside-down). Photo courtesy RC James (*a*)-(*e*): Investigation of "top-down" processing in insects. Bees are unable to learn to distinguish between a camouflaged ring and a disc (*a*) However, they can be trained to discriminate black-and-white versions of these shapes (*b*) Bees pre-trained on the black-and-white shapes can immediately discriminate the camouflaged versions (*c*) They can also learn to distinguish new camouflaged shapes (*d*) They could distinguish between the stimuli (*e*) without having to be pre-trained on black-and-white versions of these shapes. Other details as in Fig 1. Adapted from [14].

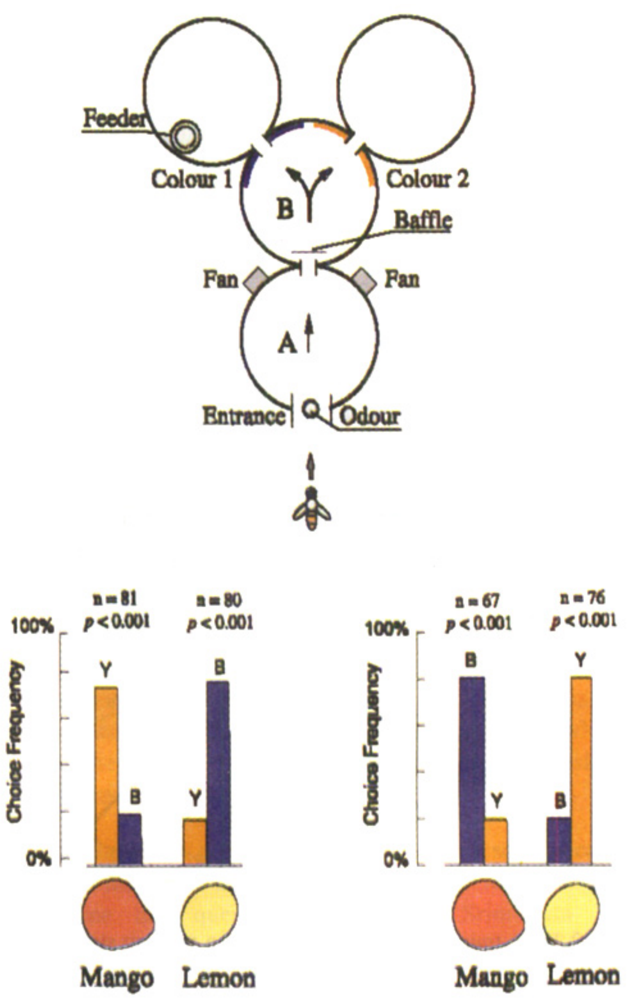

Fig 4 Cross-modal associative recall (*a*) Experimental setup. Bees have to learn to choose the appropriate colour in chamber B (blue or yellow) according to the scent (lemon or mango) that they experience from a vial at the entrance to chamber A. The fans create a slight positive pressure in chamber A, ensuring that the bees encounter the scent only as they enter that chamber, and not in chamber B. The baffle ensures that the bees do not see the colours until they enter chamber B. (*b*) Results of tests. After [23].

Srinivasan *et al* [23] examined whether this capacity extends to insects.

To investigate whether recall of a colour can be triggered by exposure to a scent, the two kinds of stimuli should be presented sequentially. Furthermore, the colour should not be present when the scent is encountered, and vice versa. These requirements were met by using the apparatus shown in Fig 4*a*. As the bees entered chamber A, they received an olfactory stimulus from a vial placed at the entrance. They then had to fly to chamber B, which had two exits, one labelled with the colour blue and the other with yellow. Here the bees had to learn to choose the "yellow" exit if they had encountered the scent of "mango" at the entrance to chamber A, and the "blue" exit if they had encountered "lemon". The positions of the blue and yellow labels in chamber B were interchanged every 10 min, and the reward moved with the appropriate colour, to ensure that the bees learned to find the reward by associating each scent at the entrance with the appropriate colour, and not with a particular exit in chamber B (left or right).

After one day's training, the associative recall of the bees was tested by admitting them into the apparatus one at a time, and recording their choice behaviour. When the bees encountered the scent of mango at the entrance, they showed a strong and significant preference for the yellow exit. When the entrance was lemon-scented, they clearly preferred the blue exit (Fig 4*b*). Evidently, the scent of mango evoked recall of the colour yellow, and lemon recall of blue. Bees could also be trained to establish the opposite associations, namely, yellow with lemon and blue with mango (Fig 4*b*).

Thus, bees can learn to recall specific colours when they experience particular scents. Intriguingly, bees trained on this task sometimes hesitate to choose a colour in chamber B, then return to the entrance of chamber A and hover in front of the scented vial with extended antennae, as if to sample the scent once more, before returning to chamber B to make their choice. Bees can also be trained in the direction opposite to that shown in Fig 4: that is, they can learn to recall a specific scent when they see a particular colour [23].

For a foraging honeybee, associative recall of this nature can facilitate the search for a food source. For example, detecting the scent of lavender can initiate a search for purple flowers. Indeed, one might surmise that the nectar samples that a potential foraging recruit receives from a dancing bee would stimulate the recruit into recalling some of the host flower's other attributes, such as its colour, shape and texture, and perhaps even the route to the flower patch, if the recruit had visited the patch previously.

Bees can group more than two stimuli together in an associative manner. In an extension of the above study, Zhang *et al* [24] were able to show that bees could be trained to group 6 different visual stimuli into two sets, each comprising 3 of the stimuli. The experimental apparatus was a more elaborate version of the maze shown in Fig 4. This maze displayed an "indicator" stimulus at the entrance and contained two successive decision chambers. The indicator was a grating that was oriented either horizontally or vertically. Decision Chamber 1 presented two coloured discs: one blue, and the other green. Decision Chamber 2 offered two visual patterns: one composed of concentric black-and-white rings, and the other comprising radial black-and-white sectors. When the indicator was a horizontal grating, the bees had to learn to choose the blue disk in Decision Chamber 1, and the sectors in Decision Chamber 2. On the other hand, when the indicator was a vertical grating, the bees had to choose the green disk in Chamber 1, and the rings in Chamber 2. Bees learned this task well. Thus, they could remember the indicator stimulus (which was no longer visible, once they had entered the maze) and use this information to choose the appropriate stimulus in each chamber [24]. Evidently the bees were able to conceptually group the 6 stimuli in the experiment into 2 sets: one consisting of the horizontal grating, the blue disk and the sectors, and the other comprising the horizontal grating, the green disk and the rings. Exposure to the horizontal grating triggered recall of the blue disk and the sectors, whereas exposure to the vertical grating triggered recall of the green disk and the rings.

3. LEARNING THE CONCEPTS OF "SAMENESS" AND "DIFFERENCE"

A related question is whether honeybees are able to group stimuli according to certain rules, or concepts, such as 'sameness' or 'difference'. In vertebrates, the capacity to acquire such concepts has been studied using two experimental procedures, the Delayed match-to-sample task (DMTS) and the Delayed non-match-to-sample task (DNMTS) [25,26]. In either task, the subject (animal or human) is initially presented with a "sample" stimulus (A). This is followed by two test stimuli, A and B, one of which matches the indicator. In the DMTS task, the subject has to learn to choose the matching test stimulus: that is, to choose A when the sample is A, and B when it is B. In the DNMTS task, the subject is required to learn to choose the non-matching stimulus: B when the sample is A, and vice versa.

In collaboration with Martin Giurfa's laboratory in Berlin, we examined whether honeybees could learn the concepts of "sameness" and "difference" [27]. We began with the DMTS task. Bees were trained on sector and ring patterns, using the apparatus illustrated in Fig 5*a*. In the training the bees had to learn to choose the sector or the ring pattern in the decision chamber, according to the sample stimulus at the entrance. The bees learned this task well, showing a clear ability to chose the matching stimulus in each case (Fig. 5*b*, left-hand panel). The trained bees were then subjected to a transfer test in which the stimuli were two colours, blue and yellow. The bees were immediately able to transfer the matching task to the colours, despite the fact that they had never been trained on the colours (Fig 5*b*, right-hand panel). They were also able to transfer the matching ability to other novel stimuli, such as gratings oriented at + 45 deg and – 45 deg [27].

Bees could also be trained to match odours, as shown in the left-hand panel of Fig 5*c*. Furthermore, bees trained on odours were immediately able to transfer the learned matching ability to colours, as shown in the right-hand panel of Fig 5*c*. Thus, the concept of 'matching', once learned, can be transferred from one class of visual stimuli to another, or even across sensory modalities.

We then examined whether bees can learn the concept

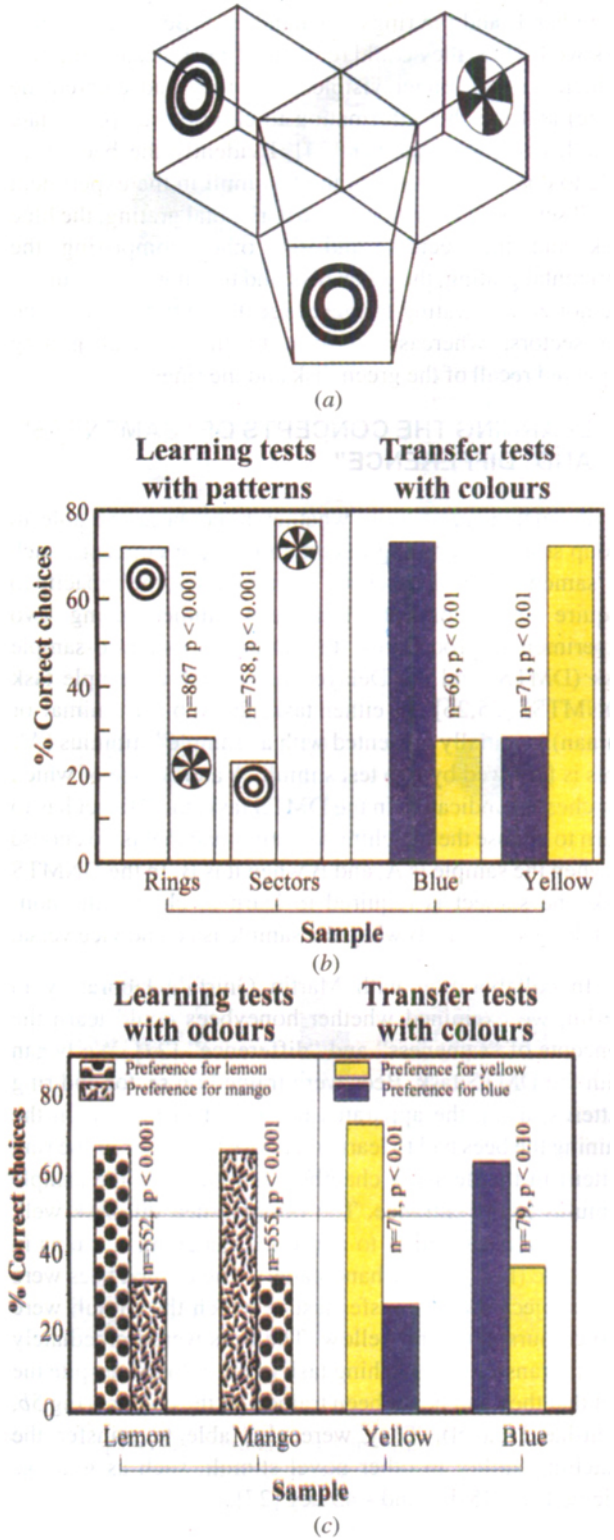

Fig 5 Learning the concept of 'sameness', and transferring it to novel stimuli in the same sensory modality, or in a different sensory modality (*a*) Results of learning tests with sectored and ring patterns (left panel) and transfer tests with colours (right panel) (*b*) Learning tests with odours (left panel) and transfer tests with colours (right panel) (*c*) Bees trained to match odours (left panel), transfer of learned matching ability to colours (right panel). Modified from [27]. Details in text.

of 'difference' (the DNMTS task), using the same apparatus. In one experiment, the training stimuli were colours (blue and yellow). Here, bees had to learn to choose yellow in the decision chamber when they encountered blue at the entrance, and vice versa. In another experiment, the training stimuli were linear gratings, oriented horizontally and vertically. There, bees had to learn to choose the vertical grating in the decision chamber when they encountered a horizontal grating at the entrance, and vice versa. Figure 6*a* shows learning curves obtained in these two experiments. It is evident that the bees learned both non-matching tasks well. Furthermore, in each case the trained bees were immediately able to transfer this non-matching concept to novel stimuli. Bees trained on the colours were able to perform non-matching on the gratings, and vice versa (Fig 6*b* & *c*).

These findings demonstrate that honeybees can indeed learn the concepts of "sameness" and "difference", and

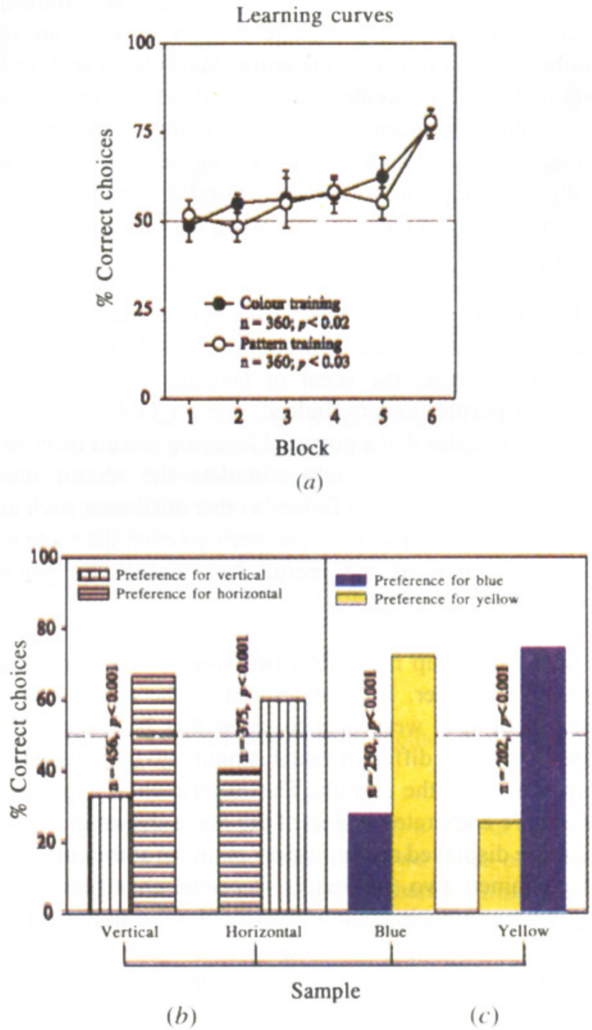

Fig 6 Learning the concept of 'difference', and transferring it to novel stimuli (*a*) Learning curves for bees trained on colours (filled circles) and on gratings (open circles) (*b*, *c*) Results of transfer tests. Modified from [27]. Details in text.

apply them to novel situations – situations on which they have not directly been trained.

CONCLUSIONS

Our work and that of other laboratories is beginning to suggest that learning and perception in insects is more intricate and flexible than was originally imagined. While these processes 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 [28]. The cognitive abilities of an animal seem to be governed largely by what it needs in order to pursue its lifestyle, rather than whether or not it possesses a backbone.

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