



Vision of the Honeybee *Apis mellifera* for Patterns with One Pair of Equal Orthogonal Bars

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The visual discrimination of patterns of two equal orthogonal black bars by honeybees has been studied in a Y-choice apparatus with the patterns presented vertically at a fixed range. Previous work shows that bees can discriminate the locations of one, or possibly more, contrasts in targets that are in the same position throughout the training. Therefore, in critical experiments, the locations of areas of black were regularly shuffled to make them useless as cues. The bees discriminate consistent radial and tangential cues irrespective of their location on the target during learning and testing. Orientation cues, to be discriminated, must be presented on corresponding sides of the two targets. When orientation, radial and tangential cues are omitted or made useless by alternating them, discrimination is impossible, although the patterns may look quite different to us. The shape or the layout of local cues is not re-assembled from the locations of the bars, even when there are only two bars in the pattern, as if the bees cannot locate the individual bars within the large spatial fields of their global filters. © 1997 Published by Elsevier Science Ltd

Pattern vision Honeybee Radial cues Tangential cues

INTRODUCTION

The story that led to these experiments began with the discovery that honeybees discriminate between some flower-like patterns presented on a vertical surface but not between some unnatural geometrical patterns (Von Frisch, 1914). Subsequently, Hertz (1933) found that bees discriminate between a class of patterns with concentric edges and a class of star-like patterns irrespective of the length of edge, when presented horizontally. Many others, e.g. Gould (1986), have found the bees discriminate very well when offered flower-like patterns. In the work referred to, the criterion for a correct choice was the landing of the bee on the target, so the angular size of the pattern was indeterminate at the time of the choice. Also the patterns were fixed, so on a vertical surface (Von Frisch, 1914) the bees could learn the location of any of the local features, and edge orientation was the only generalized cue that was inferred from work with fixed targets. On a horizontal surface (Hertz, 1933) the

bees could not relate the orientations of edges with the directions of their own flight lines, so orientation was not a useful cue and there was a good deal of confusion in the interpretations of the varied results.

Recently it was also discovered that bees cannot discriminate a cross of two bars at right angles from the same pattern rotated by 45° although similar rotation of a single bar is easily discriminated irrespective of reversal of contrast (Srinivasan *et al.*, 1994). These results led to the proposal that orientation is detected and discriminated by a family of filters, broadly tuned for orientation, that have relatively large fields. As in the transmission of light or information, a filter is defined as a component in the visual system which accepts and lets through a part of the signal. The output of a filter reveals no information about the origin or number of the stimuli in its input, so that two cues of the same kind that fall within one field cannot be separated without further information.

Recently, we found that bees trained to come to a check pattern and then presented with a varied choice avoid concentric patterns and prefer patterns with a radial structure rather than other patterns when seen from a distance, as if the visual system contains innate global filters for radial and tangential cues (Lehrer *et al.*, 1995). Later it was shown that bees can be trained to discriminate

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circular from radial patterns although areas of black, numbers of sectors and sizes of circles are all randomized during the training, showing that bees learn radial and tangential cues (Horridge and Zhang, 1995). Filters with large fields were proposed for the radial and tangential cues (Horridge, 1994). The present paper tests some of the implications of this theory of radial and tangential cues.

Supporting evidence also came from the persistent failure to discriminate two patterns of similar size composed of two pairs of equal orthogonal bars unless they differ in radial or tangential cues or in average orientation (Horridge, 1996a). An exception was found when two otherwise similar patterns differ in the angle of the axis of bilateral symmetry about a line (Horridge, 1996c). In these experiments there was no indication that the bees can reconstruct the spatial layout of four bars even in a pattern that was stationary during the training. It was concluded that "neither orientation of edges nor spatial layout of black areas is used as a cue. The processing of the image is not achieved by assembly from local features" (Horridge, 1996a). This is the key to the problem of designing suitable experiments. The bees appear to discriminate with the outputs of large-field, global filters that detect bilateral symmetry, orientation and radial/tangential cues (Horridge, 1997). The present paper continues the analysis with one pair of orthogonal bars.

MATERIALS AND METHODS

The bees came from a local hive within 50 m of the experimental apparatus so they could return to it for another reward within 5 min.

The experiments were done in the Y-choice apparatus (Srinivasan and Lehrer, 1988), modified by the addition of the baffles and a circular entrance hole 5 cm dia. that helps to keep out newly recruited bees (Fig. 1). The apparatus was placed outside under a roof with an open front 3 m wide and 3 m high, with the targets facing bright daylight. The walls of the apparatus are of white card, the top is of clear Perspex. The baffles, of transparent 'Artistcare Drawfilm', 0.13 mm thick, are set in a cardboard frame 1 cm wide. They control the angle subtended by the target at the bees' decision point, and allow the observer to make a sharp decision about the success or failure of each choice. The hole at the centre of each baffle is 5 cm dia. and is surrounded by a black annulus 0.5 cm wide. The bees can also exit by walking under or over the baffle. They do not enter this way, but fly in through the central opening without landing on it. The patterns are printed in black on white copying paper of constant quality. The targets have a hole 2 cm dia. at the centre, in positive ones for access to the reward and in negative ones leading to a blind tube.

The bees are individually marked with a code of two colours. The reward is a fresh aqueous solution of sucrose sufficiently concentrated to keep the marked bees

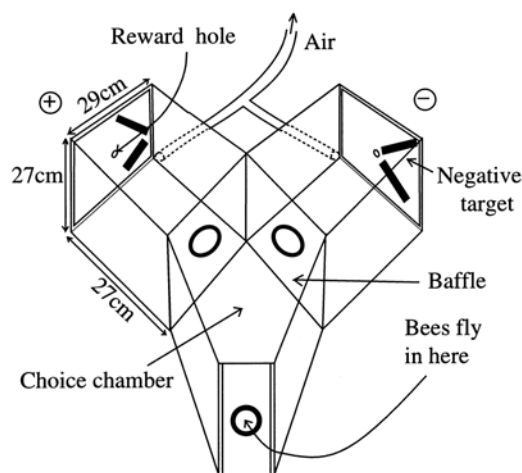


FIGURE 1. The modified Y-choice apparatus, which stands outside on a table under a roof. The bees that come regularly enter through a hole 5 cm dia. in the front to a choice chamber from which they can see both targets. They decide to enter through one of the baffle orifices 5 cm wide. The targets and the reward change sides every 5 or 10 min to prevent the bees from learning which side to go. The air pipes extract odours.

making regular visits without recruiting too many unmarked bees. During training the side of the positive target and of the reward with it are changed every 5 or 10 min to prevent the bees from learning which arm of the apparatus to choose, but in the figures the rewarded pattern (labelled + in the illustrations) is always shown in the left column. The bees were trained on one pair of patterns at a time, but in most of the experiments the patterns were exchanged for a different pair every 5 or 10 min. Usually this was done to shuffle the locations of the black areas to make the locations of black areas useless as cues. The bees had to ignore those features that were not constant and find a consistent feature of the positive patterns as opposed to the negative ones.

Honeybees from a local hive select one of the two targets while in flight in the central chamber (Fig. 1). They usually spend some time looking through the baffles. Each bee that enters is identified by its colour code, and the criterion for a score is when the bee passes through the hole in one baffle or the other. With the baffle at a distance of 27 cm, the targets of 25 cm dia. subtend an angle of about 50° at the point of choice. The bees require 20 or so visits to build up a memory of a single pattern. After an initial training period, the bees' choices were counted in each period of 5 min while training continued. These results are labelled 'train and test'. In other experiments, labelled 'test', a different pair of patterns was substituted for those in the training, and the bees' choices recorded. In tests it is essential to give a reward, which can be at random, otherwise the bees continue to search for it and confuse the arriving bees.

In most experiments the patterns are rotated or shuffled every 5 min to make the bar location useless as a cue. When possible, instead of interchanging the positive and negative patterns after 10 min on one side, they were both rotated and the reward was moved to the other arm

of the apparatus. This strategy means that the bees have less chance of using cues, such as differences in disruption or brightness of the pattern, regional layout of the pattern, differences in area of black regions, differences in odour, particular details in one pattern and not in the other, brightness or unexpected differences such as ultra-violet contrast on the targets, that are not relevant to the experiment.

Performance with difficult pairs of patterns is improved if training is continued for several days and large numbers of counts give a greater statistical significance, but training usually began in the morning and the experiment was usually completed within the same day and counts of choices were usually 100–250. As the intention was to analyse the discrimination system, not to realize the utmost capabilities of the bees, it was considered that short experiments are more ecologically realistic. By watching the bees in the choice chamber, one can frequently see whether they decide quickly or spend a long time examining first one target and then the other. If answers are forthcoming, they should not depend on the fine points of statistical analysis.

Previous work has shown that bees can resolve the gratings and bars used here (Srinivasan and Lehrer, 1988). The resolution of the bee's eye for the equal black and white stripes of a parallel grating is equal for vertical and horizontal gratings, and is adequate to give at least 65% correct choice at a period of 4° per stripe period, which falls to 50% at 3° per period, measured with the same Y-choice apparatus with no baffles. In the following experiments the bars are all 2 cm wide, which subtends 4.2° from the point of choice at the hole in the baffle, and single bars are more easily resolved than gratings of the same bar width.

The bees are individually marked with one of five colours on the thorax and on the abdomen, and a record is kept of the choices of each bee. The group of bees makes a total of 5–15 visits in each period of 5 min. The number of correct choices, and the total number of choices, are counted in each period. The fractions of correct choices for 12–40 periods of 5 min each, together with the standard deviation and the numbers of periods and choices, are tested by a χ^2 test for a difference from a chance probability (0.5) and then converted to percentages. Each pair of patterns is illustrated in the figures with the percentage choice and their statistical significance, if this is in doubt.

RESULTS

With two bars at right angles to each other on the target, the orientation cue is reduced, as if the orthogonal orientations sum within the large spatial fields of the orientation detectors (Srinivasan *et al.*, 1994), but the radial and tangential cues of the same bars are still available. Two bars can also be used to make patterns for which the discrimination could depend on the spatial re-assembly of features as well as the other cues already

investigated. By isolating and eliminating the known cues of location and bar orientation, and radial/tangential cues, we can test whether bees can use any other feature such as the spatial arrangement that looks obviously different to us.

Fixed target, vertical axis of bilateral symmetry

With the two orthogonal bars in the upper halves of both targets [Fig. 2(a)], a group of bees was trained to discriminate a pair of stationary patterns. The positive target had two tangential bars, the negative target two radial bars. This arrangement was selected to overcome the known spontaneous preference for a radial cue (Lehrer *et al.*, 1995). The result after 2 h of training was $74.7 \pm 2.6\%$, $n = 229$, $P < 0.0001$, which is a remarkably good performance but tells us little about the possible cues used by the bees.

During periods of continued training, the trained bees were tested with the bars moved to the lower halves of the targets, but retaining their relations to each other, and forming the same upwardly or downwardly pointing arrowheads as in the training [Fig. 2(b)]. The result was $64.7 \pm 2.9\%$, $n = 93$, $P < 0.0001$, in favour of the former

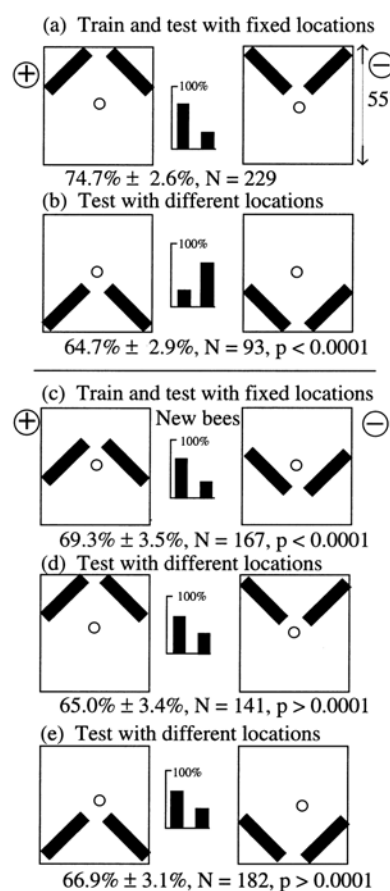


FIGURE 2. Training with fixed locations of two orthogonal bars. (a) Tangential bars (positive) on left, radial bars (negative) on right. (b) A test at another location shows that the bees prefer the target with the tangential cues. (c) With new bees, the bars are neither tangential or radial. (d) and (e) Tests at other locations now show that the bees have learned either the bar orientations or the directions of the arrowheads.

negative target. The bees have used the tangential and radial cues and ignored the bar orientations or the directions of the arrowheads. Of all the cues available, the bees choose the one least obvious to the human eye. This conclusion is not altered if the bees have learned to avoid the negative pattern in the training.

With a new group of bees, the same bars are placed across the middle of the fixed targets, so they are neither radial nor tangential relative to the central reward hole [Fig. 2(c)]. There are several potential cues of location of fixed black areas, fixed and corresponding orientation differences on both sides of the targets, and one of the arrowheads formed by the two bars points upwards while the other points downwards. Not surprisingly, the bees discriminate, with a result of $69.3 \pm 3.5\%$, $n = 167$, $P < 0.0001$, but more experiments are required before this result can be interpreted.

These trained bees were tested with the bars in the upper half [Fig. 2(d)] or the lower half of the targets [Fig. 2(e)]. In each case the bees prefer the former orientations of the bars, irrespective of their new position on the target. This time there was no radial or tangential cue to learn, and the bees use another cue, either the orientations of the bars separately on the two sides or the direction of pointing of the arrowheads formed by the bars. In view of the other results presented here, the latter is unlikely. In previous work it has been found that when the pattern has a vertical axis of bilateral symmetry, the separate average orientations of bars on the two sides of the target can be discriminated if there is no other cue available (Horridge, 1996a).

Alternating patterns, vertical axis of bilateral symmetry

A new group of bees was trained with three targets alternating between being radii and tangents and neither radius or tangent on the positive and negative patterns every 5 min [Fig. 3(a)]. The positive and negative targets changed sides every 10 or occasionally 5 min, and the orientation cues are not at fixed locations. The tangents and radii are made useless as cues by alternating them. In the positive pattern the arrowhead formed by the two bars points upwards: in the negative pattern it points downwards. Despite this consistent difference, the performance after 3 h of training was $46.9 \pm 2.5\%$, $n = 389$. The failure to discriminate the obvious (to us) difference in pattern shows that there are no cues available to the bees from the spatial relations between the bars.

On a different day and with a new group of bees, the positive cue was two consistently tangential bars while the negative cue was consistently radial but the global arrowheads alternate in their directions of pointing [Fig. 3(b)]. The bees discriminate well. The result was $70.9 \pm 2.9\%$, $n = 119$, $P < 0.0001$. When the trained bees were tested on unfamiliar patterns [Fig. 3(c)], the result was $66.5 \pm 3.5\%$, $n = 109$, $P < 0.0001$. The bees discriminate the tangential or the radial cues with little loss of performance although in the test the orientations of all the bars are changed by 45° .

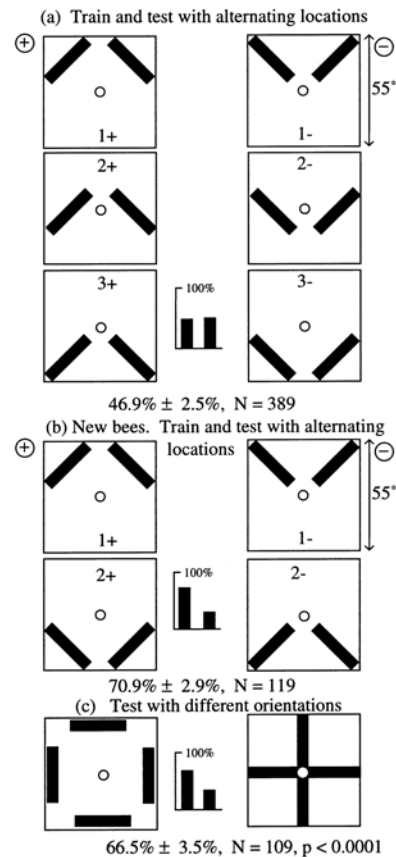


FIGURE 3. Failure to discriminate a difference in the relations between two bars. (a) In the positive pattern the bars form an arrowhead that points upwards; in the negative pattern it points downward, but the bees fail to discriminate this shape. The location and radial/tangential cues are all made useless by changing between targets 1, 2 and 3. (b) With new bees and consistent positive tangential cues, and negative radial cues, but orientations on both sides alternated, discrimination is good. (c) The trained bees also discriminate radial or tangential cues although they are rotated and re-arranged.

Fixed target, horizontal axis of bilateral symmetry

With the bars both presented on the left sides of both targets [Fig. 4(a)], a new group of bees was trained to discriminate a pair of fixed patterns. To overcome any possible spontaneous preference for a radial cue, the positive target had the tangential bars and the negative target the radial bars. The result after 2 h of training was $71.1 \pm 2.3\%$, $n = 113$, $P < 0.0001$, which is a remarkably good performance but tells us little about the possible cues used by the bees.

During periods of continued training, the trained bees were tested with the bars in the same orientations but moved over to the right sides of the targets, which reverses the radial/tangential cue [Fig. 4(b)]. The result was $66.3 \pm 2.8\%$, $n = 103$, $P < 0.0001$, in favour of the tangential bars in their new positions. The bees use the tangential or the radial cues and ignore the consistent directions of the arrowheads. As in Fig. 2(b), the relation between the bars is ignored and of the cues available the bees choose the one least obvious to the human eye.

In the next experiment, all bars are tangential relative to the central reward hole but the arrowheads point in

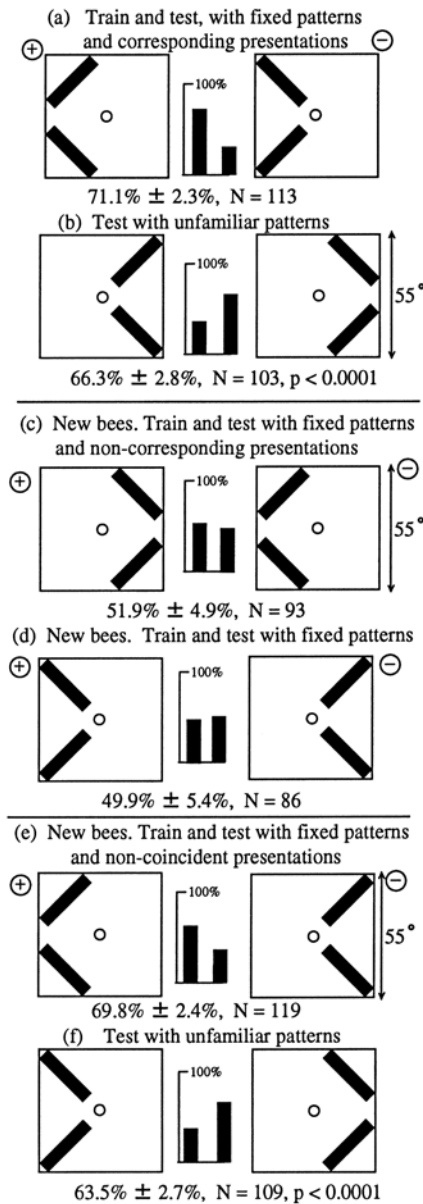


FIGURE 4. Training with fixed locations of two orthogonal bars. (a) Tangential bars (positive) on left, radial bars (negative) on right. (b) A test at another location shows that the bees prefer the tangential cues. (c) All bars are tangential, and the patterns are not discriminated despite the consistent differences in orientation and global pattern. (d) With new bees, all bars are radial and the patterns are not discriminated. (e) With new bees, as in (a) but with the bars on opposite sides of the targets at each presentation. (f) A test shows that the bees prefer the tangential cue, and ignore the orientations or the directions of the arrowheads.

opposite directions [Fig. 4(c)]. The bees fail to discriminate. In a similar experiment, all bars are radial relative to the central reward hole and the arrowheads again point in opposite directions [Fig. 4(d)]. The bees again fail to discriminate. There are potential cues of orientation and location of black areas in these fixed patterns but, unlike Fig. 2(c), the choice is presented only on one side at a time, the orientations to be compared are on opposite sides of the targets at each presentation, and the orientation cue is weakened by having the two bars on the

same side. These are important points not previously recognized.

Finally, a new group of bees was trained with the fixed patterns [Fig. 4(e)] with radial and tangential cues presented on opposite sides of the targets, unlike Fig. 4(a). The performance was $69.8 \pm 2.4\%$, $n = 119$, $P < 0.0001$. These trained bees were tested with the arrowheads pointing the other way [Fig. 4(f)]. The result was $63.5 \pm 2.7\%$, $n = 109$, $P < 0.0001$, in favour of the tangential cue. The bees had learned the radial/tangential cues although they were on opposite sides of the target at each presentation. In the test they ignore the orientations of the bars, the locations of areas of black and the directions of the arrowheads.

Alternating patterns, horizontal axis of bilateral symmetry

A new group of bees was trained with two alternating pairs of patterns. The positive targets have two bars forming an arrowhead that points consistently to the left: the negative targets have an arrowhead that points consistently to the right [Fig. 5(a)]. The bars on each target alternate every 5 min between being radial and being tangential so this cue is made useless. The positive and negative targets change sides every 10 min or sometimes 5 min. The bees clearly could not find any clue in this training situation and their performance after 2 h was $49.9 \pm 5.4\%$, $n = 86$. They spend a long time looking at first one pattern then the other through the baffles. They do not discriminate the directions of the global arrowheads. They do not even remember the separate orientations of the individual upper or lower bars which are preserved when the patterns are changed every 5 min. The form of the pattern as a whole apparently does not contain any feature that the bees' visual system can use, whereas for the human eye the discrimination of the shape as a whole is obvious.

As previously found (Horridge, 1996a), the sums of the patterns in Fig. 5(a) are not discriminated either. The result was $50.0 \pm 3.9\%$, $n = 160$ [Fig. 5(b)]. These patterns as a whole have the same average orientation, horizontal axis of bilateral symmetry and average radial/tangential cues. The difference to us lies in the direction of the arrowheads, but we have abundant evidence that the bees cannot re-assemble the bars to make a pattern.

If we alternate the orientations of the bars and the directions of the global arrowheads but preserve the radial and tangential features in a new experiment which is the converse of that in Fig. 5(a), the bees now have a cue they can use. A new group of bees was trained with the patterns in Fig. 5(c). The bars in the positive pattern are consistently tangential while in the negative pattern they are consistently radial. The performance after only an hour of training was $67.6 \pm 4.0\%$, $n = 134$, $P < 0.0001$. Once again, we find that learning is rapid with a tangential/radial cue although the cues are presented on opposite sides of the targets. As shown also in a pre-

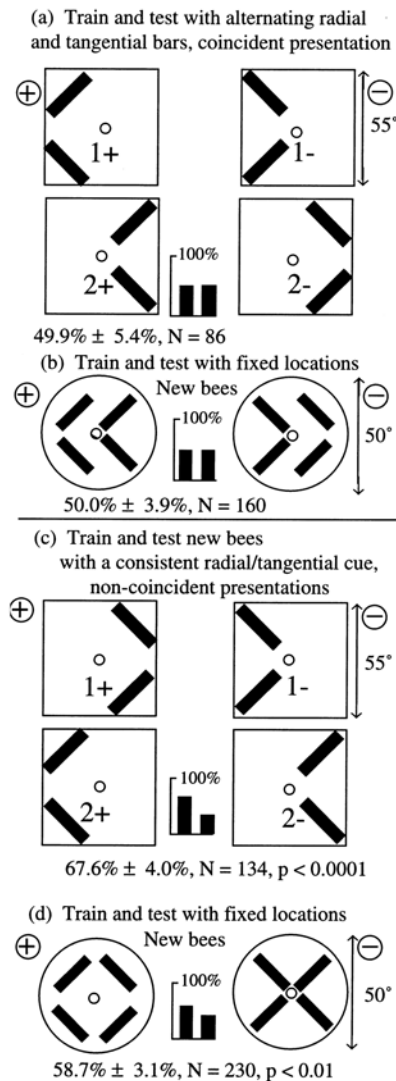


FIGURE 5. Failure to discriminate the consistent relation between two bars. (a) The bars on the positive targets form an arrow head pointing to the left, while the negative targets point to the right. Despite this obvious difference to us, the bees fail to discriminate. Note that the bars are presented on the same side of the targets at any one time, but the bees do not use bar orientations. The bars alternate between being tangents and radii. (b) The sums of the targets presented in (a) are not discriminated. (c) With new bees, the positive tangential and negative radial features are consistently useful cues although the bars are on opposite sides of the targets at each choice. (d) A new group of bees discriminates two patterns that are the sums of 1 and 2 in (c).

viously published result (Horridge, 1996a), they can discriminate a diagonal cross from a diamond shape [Fig. 5(d)].

These experiments again show that when there are two bars at right angles to reduce the global orientation cue, and location is excluded as a cue, the local orientations of the bars and their relation to each other contribute nothing to pattern discrimination, but radial/tangential cues are easily discriminated.

Learning a different cue on each side of the target

The results so far agree with the idea that only the outputs and not the locations of the filter inputs are

remembered, and there are indications that the two sides of the target are processed separately. The orientation filters do not detect the individual orientations when there is more than one bar on one side of the target (Figs 4 and 5). The detectors of radial and tangential cues do not notice whether the pattern is rotated [Fig. 2(b), Fig. 3(c)]. The bees do not re-assemble a shape, even one formed by only two bars [Fig. 3(a), Fig. 5(a)].

The next experiments explore the ability of the flying bee to discriminate a radial/tangential or an orientation cue on one side of the target while a different cue is presented on the other side when the location of black is rendered useless as a cue and the average orientation is reduced by using two orthogonal bars. Combinations of 2 bars at right angles to each other offer several possibilities. A new group of bees was trained with two alternating pairs of patterns. The positive target has a radius consistently on its left side and a tangent on its right by alternation between positions 1 and 2 every 5 min: the negative targets have these cues consistently on the other sides [Fig. 6(a)]. The result, after an hour of training, was $66.3 \pm 4.1\%$, $n = 131$, $P < 0.0005$. Clearly the two sides of the target are seen separately and do not cancel each other, although it is possible that the bees have learned to discriminate only one side.

In a second experiment, the left side of the positive target consistently showed a bar oriented NW–SE and the right side consistently showed a bar oriented NE–SW [Fig. 6(b)]. The orientations are reversed consistently on the negative target, so that, unlike Fig. 4(c, d) each choice of two orientations is available on each side of the target at each presentation. The locations of black and the radial and tangential cues are made useless because the bars are alternated between positions 1 and 2 every 5 min. The global orientation of the whole shape is also useless as a cue for the same reason. The bees are just able to discriminate with a different local orientation on each side of the target. The result was $59.5 \pm 3.0\%$, $n = 267$, $P < 0.002$ after 1 h of training. The performance is definite but not outstanding, as expected in a subtle discrimination of orientations, and would have improved with longer training. The bee must centre its attention on the centre of the target, and the orientation cues are compared on their own sides. The orthogonal orientations do not cancel out completely although they are both on the target at the same time, suggesting that the two sides are discriminated independently when the cue is bar orientation.

Thirdly, radial/tangential cues were all made useless by alternation of the patterns as in Fig. 6(c), and orientation cues are presented on opposite sides. On each side of each target all three cues alternate. The two patterns still look consistently different to human vision because the global orientations of the whole patterns are NW–SE on the positive target and SW–NE on the negative one. However, the bees search in vain for a useful cue, and the result after 3 h of training was $49.2 \pm 4.6\%$, $n = 197$. Again the conclusion is that the bees fail because the

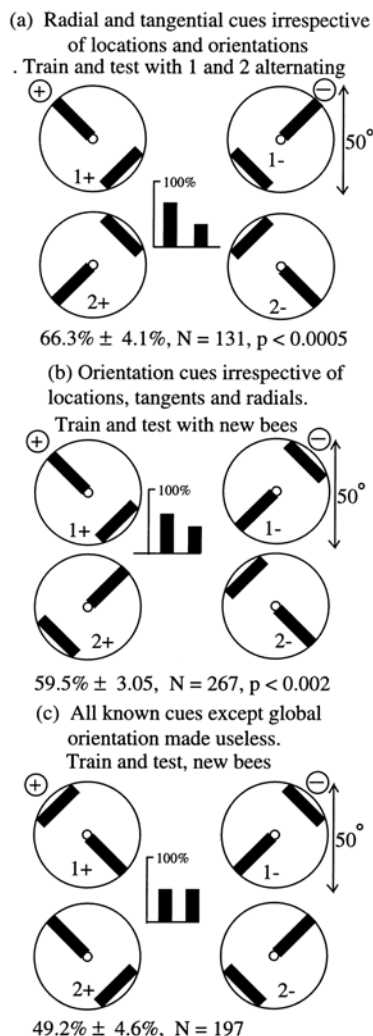


FIGURE 6. Different cues on the two sides of the target. (a) Discrimination with a radius consistently on the left side and a tangent on the right side when locations and both local and global orientations are made useless by alternation. (b) Discrimination of two different orientations on the two sides of the target when locations, tangents and radials are made useless by alternation, and each choice of orientations is presented on its own side. (c) Failure to discriminate the consistent global orientation difference when locations, tangents and radials are made useless as cues and each choice of orientations is presented on opposite sides of the targets.

only cues they can use are made useless, and they cannot discriminate the consistent orientation of the relation between the bars.

These results are consistent with the postulate of a limited variety of global filters. Whether mirror images are discriminated or not by bees depends on whether a filter detects a difference. The only peculiarity of mirror images is that the positive and negative cues are presented simultaneously on opposite sides of each target and the cues to be compared are on corresponding sides of the two targets. In mirror images, the best cue is an oblique global orientation.

DISCUSSION

Honeybees apparently see quite well as they forage or search for new resources, but their ability to remember and discriminate among the infinite variety of natural images must be limited by their relatively small and economical visual processing systems. To help matters, they have a limited number of dedicated tasks for which we suppose a limited variety of cues are adequate. To discover the cues that the bees use, we have to find tasks that defeat their discrimination ability, so that when they fail, we can infer that they have no available cue for that pair of patterns, although it may be obvious to us that the patterns are different. This method is the only one available where there are mechanisms acting in parallel. In contrast, the bees' successes in discriminating pairs of patterns with several possible cues tell us a little about performance or internal mechanisms. When locations of areas of black are shuffled in patterns of 1, 2, or 4 bars, seen from a distance, the critical cues can be isolated one by one, and turn out to be size, orientation, radial and tangential edges, and an axis of bilateral symmetry (Horridge, 1997). These cues are all generalized over the range of the controlled variety of presentations in the training programme. There may be other types of useful cues, as yet unknown, but the bees always fail to re-assemble a shape from the spatial relations between even two bars.

Visual systems generalize, and generalization is a property of broadly tuned filters with large fields. For example, these filters respond to a part of a suitable pattern as if it were the whole pattern. The large fields tolerate movement or small changes in the image, and the broad tuning accepts a range of cues.

The bees respond as if the learning and later discrimination of radial or tangential cues is independent of where they are presented on the target (Figs 2-5), but two cues on opposite sides of the target are not confused if presented during training and no other cue is available [Fig. 6(a), (b)]. They detect radial and tangential cues irrespective of rotation of the target [Fig. 2(b), Fig. 3(c)] as if they belong to a radially-symmetrical pattern that would fill the target but is partially obscured [Fig. 3(c), Fig. 5(d)].

When the orientation cues to be discriminated are presented on the corresponding sides of the two targets at each choice, the bees do not confuse two well-separated orthogonal bars on the two sides of the target [Fig. 6(b)]. When the radial and tangential cues were excluded, and bar location was alternated, the separate orientations of the two bars were not learned [Fig. 3(a)]. They discriminate orientation on each side of the target separately in fixed targets when radial or tangential cues are unavailable [Fig. 2(c)], but they prefer to use radial/tangential cues [Fig. 2(b)]. After all, when working for a reward of sugar, the bee visual discrimination is adapted to flower-like patterns.

The right angle between the two bars weakens the glo-

bal orientation cue, and orientation cues to be compared must be presented on corresponding sides of the positive and negative targets. In all the experiments, and in many others in previous work (Horridge, 1996a, b, c), when locations of black areas are made useless as cues, the bees behave as if they have in parallel several global filters with large fields that cannot separate two or more orientations, tangents or radial cues within their fields. Consequently, they cannot re-assemble a shape from the spatial relations between the bars.

These results are relevant to the understanding of the discrimination of mirror images and also of patterns with a vertical axis of bilateral symmetry by bees. Mirror images always present the difference to be detected in opposite ways on both sides of the target. We see that mirror images may or may not be discriminated, depending on whether there is a suitable global filter [Figs 4, 5(b), 6(a) and (c)]. In other patterns, a vertical axis of symmetry assists discrimination because the cues are similar on the two sides of each target.

A large part of the puzzle of bee pattern vision has been their failure to discriminate many simple shapes that look obviously different to us, although they discriminate certain other patterns very well. It is difficult for us to appreciate that bees discriminate patterns of two bars without remembering either the separate bars or the spatial relations between them. However, in our own vision we are familiar with our discrimination of colours without being able to identify their constituent wavelengths. We also appraise coffee aroma, wine or food without being aware of any individual chemoreceptor responses. In this respect, bee vision of form resembles our vision of colour or our chemosense, in that the cues that make possible the discrimination are not separately recoverable. Just as we fail to discriminate some green colours that have different component wavelengths, bees fail to

discriminate two patterns that offer them similar mixtures of spatial filter outputs. They separate the image into retinal elements and then detect some cues, but they cannot re-assemble the image. Understanding that re-assembly of the image is not essential for pattern discrimination is the key to the enigma of bee pattern vision.

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