



The Honeybee (*Apis mellifera*) Detects Bilateral Symmetry and Discriminates its Axis

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Honeybees were trained and tested with a choice between a black and white pattern composed of two pairs of equal orthogonal bars with bilateral symmetry and the same or a similar pattern with a different symmetry. The targets subtended $<50^\circ$ at the point of choice. Earlier results with the chevron pattern revealed that discrimination of rotation is improved when one of the patterns is bilaterally symmetrical about a vertical axis. Bees were trained on 7 different pairs of 4-bar patterns at the same time, taken successively to prevent the bees from learning any one pattern. The bees learned to discriminate a pattern with bilateral symmetry from one without symmetry, irrespective of the orientation of the axis of symmetry. They also discriminate between a pattern with one axis of bilateral symmetry and the same pattern rotated by 90° , irrespective of the actual pattern. Although the patterns are regularly changed during the training, the bees distinguish the axis of bilateral symmetry. When trained on one set of patterns, the bees also discriminate the axis in the same or other patterns rotated through 180° , when all bars have moved over to the other side, showing that they have not remembered one side of the pattern with each eye. For one pattern, the angular tuning curve for the discrimination of the axis of symmetry falls from a score of 80% correct on-axis to near 67% at 15° off-axis and 50% (random) at 30° off-axis. Copyright © 1996 Elsevier Science Ltd

Vision Honeybee Symmetry Pattern

INTRODUCTION

Bumble bees settle more frequently on flowers that are more perfectly symmetrical about a vertical axis than on their less symmetrical neighbours. This recent observation is the latest in a long history of the study of the bees' vision of shape. The biological significance is that flowers of the same species that are more symmetrical produce more nectar (Møller, 1995). Since the pioneering work of von Frisch (1914), efforts to train bees to discriminate simple closed shapes of similar size with differently oriented edges have been disappointing, and distributions of spontaneous choices also show no differences between simple shapes of similar outline (Zerrahn, 1933). Almost 70 years ago, working with black patterns on white paper to avoid the complexities of colour and odour, Hertz (1929, 1933) found that honeybees can discriminate one family of radially symmetrical circular patterns from another of star-shaped pat-

terns and also from groups of blobs on a horizontal table. She used a technical term from Gestalt psychology, 'Prägnanz', which means an ordered and balanced image with cohesion and simplicity, to describe the proposed special appearance to bees of radial symmetry about a point. The topic was reviewed by Wehner (1981) who concluded that "what the shape of the flowers contributes to the visual signal is largely unknown".

A wide variety of observations, however, have shown that bees somehow detect radial symmetry (Free, 1970). Recently, we have found that bees spontaneously prefer arbitrary patterns of bars that are presented vertically in flower-like combinations that subtend $<50^\circ$ at the choice point (Lehrer *et al.*, 1995). Other experiments show that bees can be easily trained with randomly selected patterns of radial sectors versus randomly selected concentric circles, both of which have no predominant orientation. They then generalize to other patterns containing either mainly radial or mainly circular features (Horridge and Zhang, 1995). More significantly for the present study, in the same apparatus as used here, when the targets subtend $<50^\circ$ at the point of choice, honeybees usually cannot discriminate when the choice is between a

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black and white pattern composed of two pairs of equal orthogonal bars and the same pattern rotated by any angle. Extensive results show that the bees do not remember either the orientations or the locations of the individual bars (Horridge, 1995). If they did, they would be able to discriminate them. There is no average global orientation in any of these patterns of 2 pairs of orthogonal bars and the bees take no account of rotation of radii or tangents. When two patterns of the same 4 bars differ in average global amount of radial or tangential edges, however, they are now discriminated irrespective of rotation, showing that the bees certainly remember something about the structure of the pattern, but it is not the relative positions of the bars.

All of these observations relate to the performance of the whole animal, and show that the parts of the pattern are not discriminated separately, with no concern about how both eyes are participating in the responses in forward vision. It has been realized only recently, however, that in fixed large targets, subtending 100° or more, the locations of black areas are used as local cues as if they are landmarks (Horridge, 1996) and it is important to rule them out by controlling the pattern subtense at the point of choice. For example, a stationary pattern of 4 black bars forming a right-angled cross must subtend more than 64° if the bees are to discriminate its rotation by 45° (Horridge, 1996). One way to prevent the locations of black areas being used as cues is to work with 4-bar patterns subtending $<50^\circ$ in forward vision, the other way is to shuffle the locations of black areas in the training patterns. From a wealth of data on patterns of 2 pairs of orthogonal bars, and from the spontaneous preferences, these methods led to the conclusion that bees have separate innate detectors for global radial and tangential features in the targets as a whole, subtending $<50^\circ$ at the eye (Horridge, 1994).

Comparable observations have indicated that bees have detectors of bilateral symmetry. For example, when landing on a flower with bilateral symmetry about a tilted axis, native bees align their body axes with that of the flower (Jones and Buchmann, 1974). This observation reminds us that in the most general case, normal flight between two obstacles or steering directly towards a target necessarily involves distinguishing and centring (but not necessarily remembering) the target. This is an important general point that re-appears in the discussion. In a recent series of tests we found a spontaneous preference for a vertical axis of bilateral symmetry among arbitrary unfamiliar flower-like patterns of black bars (Lehrer *et al.*, 1995, Fig. 8), a result which shows that there is some kind of intrinsic detector of this kind of symmetry. Then, training with various patterns of four bars revealed a special property of the chevron pattern, with 2 orthogonal radii and 2 tangents, when it has a vertical axis of bilateral symmetry (Horridge, 1995). Again, all of these observations related to the performance of the whole animal, with no concern about whether both eyes in forward vision are participating in the responses. The following

experiments are designed to define further this detector of bilateral symmetry. The first step is to repeat the standard procedure by training simultaneously on a number of different arbitrary patterns to see whether bees can detect bilateral symmetry irrespective of pattern, and training other bees to discriminate one axis of bilateral symmetry from another axis, irrespective of pattern.

MATERIALS AND METHODS

The experiments were done in the Y-choice chamber (Srinivasan and Lehrer, 1988), modified by the addition of the baffles and a circular entrance hole 5 cm in diameter (Fig. 1). The apparatus was placed in an open shed outside with the targets facing bright daylight. The walls of this apparatus are of white card, the top is of clear Perspex. The baffles, of transparent 'Artiscare Drawfilm' 0.13 mm thick set in a cardboard frame 1 cm wide, control the angle subtended by the target at the decision point, and allow a sharp decision about the success or failure of the bees' choices. The hole at the centre of the baffle is 5 cm in diameter and the bees can also exit by walking under or over the baffle. They never learn to enter this way, but always fly through the central opening without touching it. The experiments shown in Fig. 2 were done in 1993 before the baffles were introduced. In general the baffles improve the discrimination because they make the bees stop and look at the targets.

Honeybees from a local hive select one of the two targets while in flight in the central chamber. Each bee that enters is identified by its colour marking, and the criterion for a score is when the bee first passes a hole in a baffle. With the baffles at a distance of 27 cm (Fig. 1) the targets, of 25 cm diameter, subtend an angle of about 50° at the bee's eye when the bee is about to pass through. The targets have a hole 2 cm in diameter at the centre, in positive ones for access to the reward and in negative ones leading to a blind tube. The reward is a fresh aqueous solution of sucrose sufficiently concentrated to just keep the bees making regular visits without

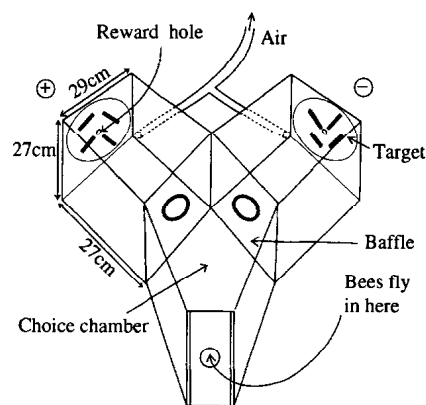


FIGURE 1. The Y-choice apparatus modified by the addition of an opening at the entrance, a transparent baffle in each arm with a hole 8 cm in diameter, and with odours extracted from the chambers adjacent to the targets. The decisions of the bees are scored when they pass the baffles, which are 27 cm from the targets.

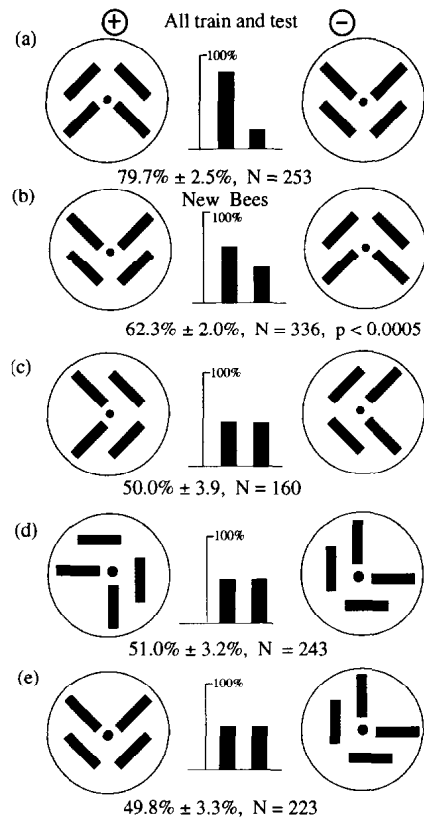


FIGURE 2. Evidence that a vertical axis of bilateral symmetry assists discrimination. The pattern is the same in all choices, except that one of the pair is rotated relative to the other. (a) and (b) When both patterns have a vertical axis, performance is excellent. (c-e) Without the vertical axis, the bees cannot discriminate (with no baffles). (e) The detector of symmetry has a broad angular tuning curve, as shown by the failure when one pattern is rotated by 45° . See also Figs 7(e) and 8(e), where this pattern is rotated by 90° relative to itself and (with baffles in the apparatus) discrimination is possible.

recruiting too many others. During training the side of the positive target and the reward with it are changed regularly to prevent the bees from learning which side to visit, but in the figures the rewarded pattern (+) is shown in the left column. The bees were shown one pair of patterns at a time; in the earlier experiments with a change of pattern pair every 20 min (Expts 1, 6, 7 and 8) and a change of side in the apparatus every 10 min. In the later experiments (Expts 2, 3, 4, 5 and 9) there was a change of the pattern pair every 5 min and a change of side every 10 min. The bees had to find a general property of the set of positive patterns as opposed to the negative ones.

After an initial training period, the performance was measured on each pair of patterns while training continued. These results are labelled 'Train and test' in the illustrations. In some experiments the trained bees were then repeatedly tested for periods of only 5 min on each side, with a pair of patterns that they had not seen before, first with the positive pattern on one side and then with the sides reversed. These results are labelled 'Test' in Figs 5, 8, 9 and 10. The patterns for these tests were introduced at random between longer periods of continued training. Previous studies have shown that the tests

have a negligible effect on the performance as long as the training continues, because the test periods are very short compared to the time required to train bees with patterns. The bees have time to make only one rewarded visit in any one test period, whereas they require 20 or so visits to build up a memory of a single pattern. Bees tested on a pattern they have not previously seen perform as well as before when they are returned to the training schedule. The positive target was rewarded in the tests because otherwise the bees fly around in the apparatus between targets as they search for a reward and they attract the attention of incoming bees.

Except in Fig. 9(f), the patterns of a pair are identical but the negative pattern is rotated relative to the positive one. This strategy means that the size, area of black, average orientation, length of edge, degree of disruption, average orientation and amount of radial and tangential features in the pattern is unchanged and also the bees have less chance of using cues, such as differences in disruption or brightness of the pattern, regional lay-out of the pattern, differences in area of black regions, or the existence of particular detail in one pattern and not in the other, that are not relevant to the experiment. These pattern pairs allow a further powerful control to be made. Instead of interchanging the positive and negative patterns after ten minutes on one side, they were both rotated and the reward was moved to the other side. This strategy acted as a control against differences in odour, brightness or unexpected differences such as ultraviolet contrast on the targets, but the result was the same as interchanging the targets.

The patterns are printed in black on white copying paper of constant quality. 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. Gratings of period 4° are drawn to scale in the figures, and single bars are more easily resolved than gratings of the same bar width.

The bees are individually marked and a separate record is kept of the performance of each. The group of bees make a total of 10–20 visits in each period of 10 min. The results from each pair of patterns are kept separate. The number of correct choices, and the total number of choices, are counted in each period. The fractions of correct choices for 6 to 20 periods of 10 min each, together with the standard deviation and the total numbers of periods and choices, are tested by the χ^2 test for a difference from 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 in doubt. Performance is defined as the percentage of correct choices.

RESULTS

Experiment 1

In a preliminary series of tests done in 1994 before the baffles were introduced, bees were trained to discriminate a chevron pattern of 4 bars with a vertical axis of bilateral symmetry from itself turned through 180° [Fig. 2(a)]. The performance, after only 2h of training, was $79.7\% \pm 2.5\%$, $N = 253$. This is a remarkable result for a pattern consisting of two pairs of equal bars at right angles, which has no predominant orientation. A new group of bees discriminated the same patterns the other way up [Fig. 2(b)], but the bees were unable to learn the discrimination with the axes turned in other combinations of orientations [Fig. 2(c–e)]. Without further evidence, all that can be said is that a vertical axis of bilateral symmetry of one of the patterns assists discrimination. In Fig. 2(e), the pattern with a vertical axis cannot be discriminated from itself rotated by 45° , but, in experiments done in 1995 with baffles in place, a difference of 90° in the axes of symmetry could be discriminated, as in Figs 7(e) and 8(e). These results showed that there is something interesting about bilateral symmetry, and the feature that assists discrimination, whatever it is, has an angular tuning curve.

Experiments in which the pattern is randomized. With patterns subtending less than 40° at the choice point, flying bees have previously been trained to discriminate orientation of a grating irrespective of the spacing of the bars (van Hateren *et al.*, 1990) and to discriminate radial and tangential contours irrespective of spatial frequency or rotation (Horridge and Zhang, 1995). The method was to randomize the patterns with reference to one feature so the bees learn to ignore that feature, while they learn some other cue which is consistently different between the two targets. Similarly the method adopted here is to train bees to discriminate the symmetry or the axis of bilateral symmetry irrespective of the pattern by repeatedly changing the pattern. At this point, however there are several possible experiments, some of which involve different axes of symmetry, and there is also a decision required as to which shall be the positive and which the negative target. The following experiments are only a selection of all possible experiments along these lines.

The 7 bilaterally symmetrical patterns [Fig. 3(a–g)] and the 5 patterns with no axis of symmetry were each composed of 4 identical bars arranged in various ways. The patterns are all composed of 2 pairs of bars at right angles to each other, so all have the same area of black, the same amount of edge, and no pattern contains a predominant orientation. The known cues that bees might use from a range of 27 cm are thereby reduced to a minimum. It has already been found with patterns of this type that the bees remember neither the orientations nor the locations of individual bars (Horridge, 1995). The patterns differ among themselves in the amount of radial and circular (tangential) edge. In presenting all the pattern pairs in succession, we are teaching the bees to

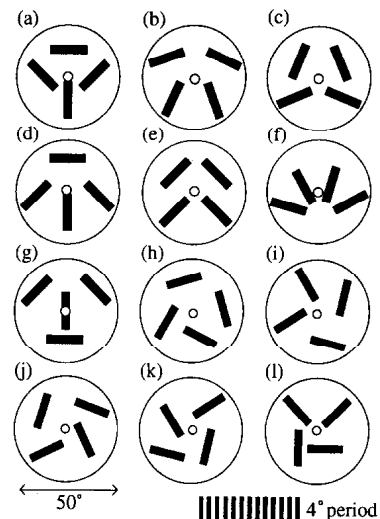


FIGURE 3. The patterns of 2 pairs of orthogonal bars with no average orientation in the pattern as a whole. (a–g) With a vertical axis of bilateral symmetry. (h–l) With no axis of symmetry. The grid of period 4° shows the lower limit of useful spatial resolution of the bees' eye, measured in the same apparatus.

ignore the unique properties of any one pattern. As each pattern is now compared with itself or with another from this group, the pair of targets to be discriminated at any one time do not differ in most of the possible cues known to be useful to bees.

Experiment 2. A horizontal axis of symmetry versus no axis

A group of bees was trained with the 7 bilaterally symmetrical patterns of 4 bars [Fig. 3(a–g)] in succession on the positive target for a period of 10 min each and with one of the five irregular patterns of 4 bars [Fig. 3(h–l)] also changed every 10 min on the negative target. The positive and negative targets changed sides every 5 min. The positive patterns were all presented with their axis of bilateral symmetry horizontal, with the same side at the top each time. The negative targets were presented in order but with no particular orientation. As a result, the positions and orientations of the bars changed in both patterns every 10 min. The only feature that was constant was the horizontal axis of bilateral symmetry in the positive targets.

The bees learn this task in 90–150 min and appear not to notice the changes in pattern. The average percentage of correct choices for each period of 50 min, starting at 100 min after the start of training, is plotted with standard deviations, in Fig. 4(a), showing progressive improvement to a high level.

Experiment 3. A vertical axis of bilateral symmetry versus no axis

A new group of bees was trained with the same 7 bilaterally symmetrical patterns of 4 bars [Fig. 3(a–g)] in succession on the positive target for a period of 10 min each and with one of the five irregular patterns of 4 bars [Fig. 3(h–l)] as the negative target. The positive and negative

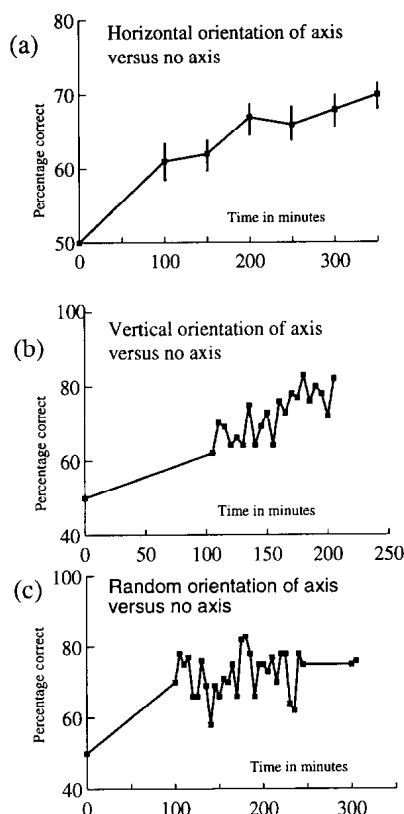


FIGURE 4. Results of discriminations of the symmetrical patterns [Fig. 3(a–g)] taken together versus the asymmetrical ones [Fig. 3(h–l)] also taken together. Note the excellent performances. (a) With a horizontal orientation of axis versus no axis. These are averages with standard deviations over periods of 50 min, showing steady improvement. (b) With a vertical orientation of axis versus no axis. These are raw data for each 5 min over a shorter period. (c) With a random orientation of axis versus no axis, also raw data for 5 min periods.

targets changed sides every 5 min. The positive patterns were all presented with the axis of bilateral symmetry vertical, the same way up each time. As before, the negative targets were presented in order but with no particular orientation. As a result, the positions and orientations of the bars in both patterns of a pair changed every 10 min. The only feature that was constant was the vertical axis of bilateral symmetry in the positive targets.

The bees also learn this task in 90–150 min, as before. The average percentage of correct choices in one experiment, for each period of 5 min starting at 100 min after the start of training, is plotted in Fig. 4(b), showing improvement to nearly 80%.

Experiment 4. Random orientation of the axis of bilateral symmetry versus no axis

A new group of bees was trained with the same 7 bilaterally symmetrical patterns of 4 bars [Fig. 3(a–g)] on the positive target in succession for a period of 10 min each and the same five irregular patterns of 4 bars [Fig. 3(h–l)] as the negative target. The positive and negative targets changed sides every 5 min. The symmetrical patterns were all presented with the axis of bilateral symmetry in any orientation. As before, the negative targets were presented also with no particular orientation. The pos-

itions and orientations of the bars changed in both patterns of a pair every 10 min. The only feature that was constant was the existence of an axis of bilateral symmetry at some angle in the positive targets.

The bees also learn this task in 90–120 min, as before. The average percentage of correct choices for each period of 5 min, starting at 100 min after the start of training, is plotted in Fig. 4(c), showing improvement to nearly 80%. The average performance over this period was $73.9\% \pm 3.5\%$, $N = 157$, in the first hour of tests and $72.85 \pm 3.6\%$, $N = 148$, in the second hour.

Experiment 5. Discrimination between two oblique axes irrespective of the bar positions or orientations

A new group of bees were trained to discriminate between one of the patterns of 2 pairs of orthogonal bars, (a) in Fig. 3, with oblique axis, and the same pattern rotated by 90° [Fig. 5(a)]. This pattern has an obvious (to us) axis of bilateral symmetry. The result after 90 min of training was $75.3\% \pm 2.3\%$, $N = 175$, $P < 0.0001$. The trained bees were then tested for periods of 5 min at intervals during continued training with both patterns turned through 180° , so that all the bars keep their orientations but move to the other side of the targets. The

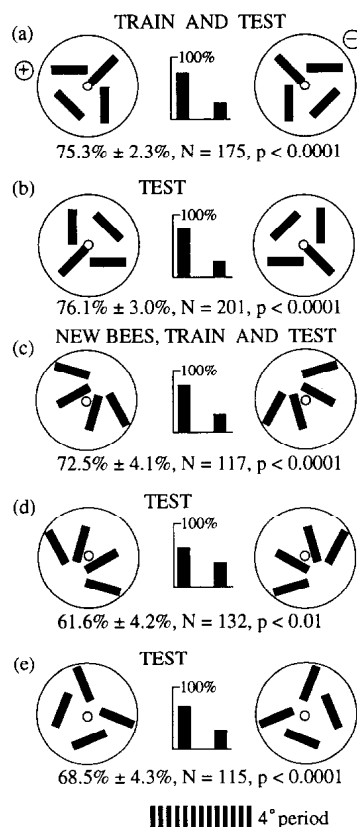


FIGURE 5. Discrimination of a pattern of 2 pairs of orthogonal bars with oblique axis of symmetry from the same pattern rotated by 90° . (a) Train and test with a pair of fixed patterns. (b) Test with both patterns rotated by 180° so that all bars are in new positions on the opposite sides of the targets. (c, d) A new group of bees with a different pattern, and (e) tested on an unfamiliar pattern. Experiments of this type show that the axis is discriminated irrespective of pattern, but fixed patterns differ in tolerance to rotation and in acceptability of transfer from one to another.

result of the tests was $76.1\% \pm 3.0\%$, $N = 201$, $P < 0.0001$. With another pattern, (f) in Fig. 3, the same procedure was followed, with a similar positive result [Fig. 5(c and d)]. In this case, a further test was made with an entirely different pattern [Fig. 5(e)] with the result $68.5\% \pm 4.3\%$, $N = 115$, $P < 0.0001$. The bees discriminate the axes of bilateral symmetry very well when the patterns are turned over and are not disturbed by the change in pattern. Clearly they are not learning one side of the pattern with one eye and the other side with the other eye.

Experiment 6. Discrimination between two axes of symmetry, vertical positive, irrespective of pattern

In this experiment, the same seven different bilaterally symmetrical patterns were used in succession as the positive target, but the axis of symmetry was vertical in each. The unrewarded target in each pair was the same pattern turned on its side. Four of the patterns were turned clockwise and three anticlockwise. As the training proceeds, the bees' choices of the positive show a steady rise from near 50% to about 70% over a period of 6h at the end of the day (Fig. 6). On the next day the performance reaches 80%, so there is no doubt that the bees learn to discriminate all the patterns simultaneously in favour of the vertical axis.

The long training time suggests that it is difficult for the bees to ignore the differences between the patterns while discriminating the general features of two different axes of symmetry. At any rate, the learning process takes longer than learning a single discrimination between two fixed patterns, which usually takes less than 2h. The progressive learning process shows that the bees are not simply expressing their known innate tendency to choose a vertical axis of bilateral symmetry (Lehrer *et al.*, 1995), although that earlier result showed that untrained bees must have innate detectors for a vertical axis of bilateral symmetry. The next experiment was designed to avoid the innate preference.

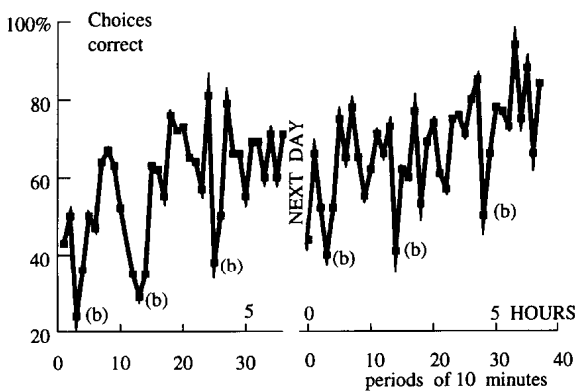


FIGURE 6. The simultaneous learning to discriminate the vertical axis of symmetry of all 7 patterns in Fig. 3(a-g) from the same pattern (in each pair) with the axis horizontal. The percentage of correct choices of the positive (vertical axis) target is plotted for each period of 10 min over two periods of training on successive days on the 7 pairs of patterns, taken in approximately the order shown in Fig. 3. The poor performance with pattern (b), as indicated, shows that the patterns differ in ease of discrimination of the axis.

Experiment 7. Discrimination between two axes of symmetry, horizontal positive, irrespective of pattern, keeping each pattern separate

With the same seven pairs of patterns [Fig. 3(a-g)], the one with vertical axis of symmetry now became the negative target while the same pattern turned through 90° became the positive one in each pair. The innate preference for a vertical axis of symmetry must therefore be reversed by the training. In the training procedure, a new group of individually marked bees were trained for the first day in periods of 10 min on each side with each pair of patterns. The 7 patterns were selected approximately in the order shown. The separate results for each pattern in 12 repeated 'Train and Test' periods of 10 min each (6 on each side for each pattern) tested on the second day are shown in Fig. 7. The bees clearly learn to discriminate the 2 axes of symmetry even though there are 7 patterns.

The training was then continued on the third day, when, after more training, the 'Test' periods were started. In these tests the positive and the negative patterns of each pair were both turned through 180° , so that the bees made a forced choice between two patterns that they had

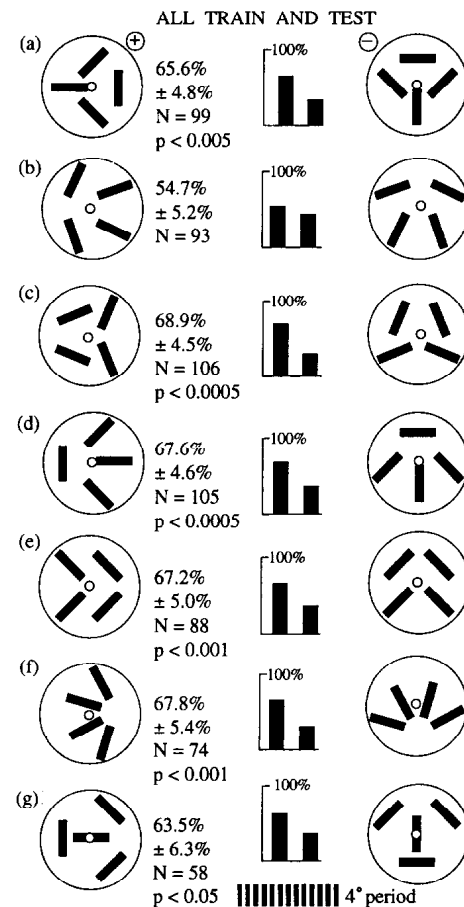


FIGURE 7. The results of training with the 7 pairs of patterns. In this experiment the positive pattern of each pair had its axis of symmetry horizontal. The result on each pair of patterns is kept separate, although the pairs of patterns were taken in turn during the training. The limit of useful spatial resolution of the eye is shown by the grating of period 4° , drawn to the same scale.

not seen before; the positive with a horizontal axis of bilateral symmetry and the other with a vertical one (Fig. 8). The tests were for 5 min on each side, separated by periods of at least 10 min of further training, and were repeated 6 or 8 times on each side. The results of these tests all show that each pattern with a vertical axis of bilateral symmetry is correctly avoided, although all are unfamiliar and the left and right sides of the targets have been interchanged. The results reveal three details. First, as also shown in Fig. 6, pattern pair (b) for some unknown reason appears to be the hardest to learn and also the hardest to discriminate from itself when rotated through 180° [Fig. 7(b)]. Secondly, the standard deviation is almost 8% of the mean, which is more than double the value found (as in Fig. 2), in straight discriminations of two fixed patterns without the randomization of form. Thirdly, the bees have a higher success rate in the tests than they did in the original training, which is easily explained in that the results of the 'Tests' all come from the later part of the training, and the bees steadily improve as in Fig. 5, while most of the 'Train and Test' results come from the second day.

Experiment 8. Tests on quite different patterns

Next, on the fourth day, tests with the same trained bees were extended to unfamiliar and quite different tar-

gets in pairs, also presented for 5 min on each side at each presentation. Four of the targets are designed to test whether the bees still discriminate against the vertical axis of bilateral symmetry on patterns with more than 4 bars [Fig. 9(a, b)] or fewer than 4 bars [Fig. 9(c, d)]. The other two tests were designed to discover whether the bees had acquired a preference for an average orientation or radial co-ordinates as cues. The results with unfamiliar patterns [Fig. 9(a–d)] confirm that the vertical axis of bilateral symmetry is still avoided irrespective of pattern. The other tests may reveal a little of what lies in the memory of the bees. The trained bees have some preference for horizontal over vertical edge orientation [Fig. 9(d, e)], and radial over circular edges [Fig. 9(f)], which is in agreement with the idea that an axis of bilateral symmetry is detected by an orientation filter acting on the image that has passed through a radial filter. The radial preference could also be attributed to spontaneous preferences (Lehrer *et al.*, 1995), but in previous work (but with targets subtending 130° at the eye), Wehner (1968) found no spontaneous preference for the orientation of single bars.

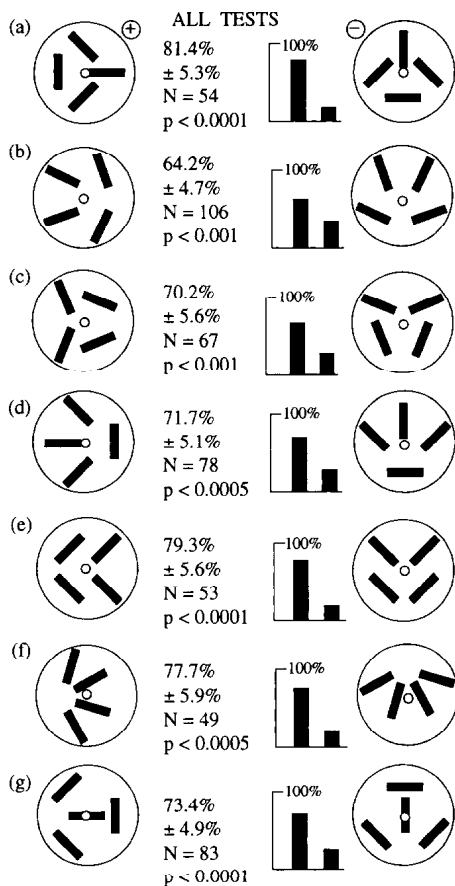


FIGURE 8. The results of briefly testing the trained bees (Fig. 7) with all the pattern pairs turned through 180°. The bees still select the member of each pair with the horizontal axis of symmetry, although the patterns are reversed top-bottom and side-to-side.

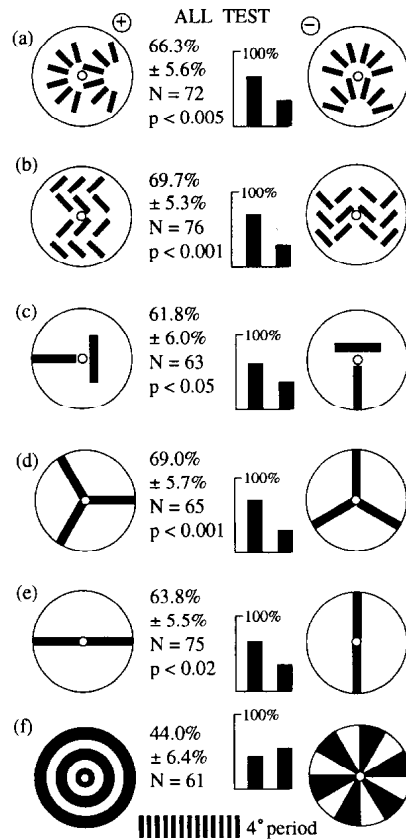


FIGURE 9. The results of testing the trained bees with different patterns, (a, b) with more bars, (c, d) with fewer bars. (e) A test of preference for horizontal or vertical. (f) A test of preference for radial or circular components. If anything, the latter results suggest that the bees are relying on filters for global radial and horizontal components to detect a horizontal axis. The limit of useful spatial resolution of the eye is shown by the grating of period 4°, drawn to the same scale.

Experiment 9. Angular tuning of detection of the axis of bilateral symmetry

In its design, which is derived from an unpublished analysis of the filters for radial and tangential features, this experiment differs from those already described. All targets carry a pattern of three equally spaced radially arranged bars [Fig. 10(a)]. This pattern was selected because it is a simple example of bilateral symmetry [see Fig. 9(d)] and it matches the radial filter. The two positive targets each have one horizontal bar and the pattern is turned through 180° (positions 1 and 2 in Fig. 10) every 5 min to shuffle the locations of the bars and make them individually useless as cues but preserve the horizontal axis of bilateral symmetry. The two negative targets [Fig. 10(b)] carry exactly the same pattern but with one bar vertical, also rotated through 180° every 5 min. The pattern with the vertical axis of symmetry was selected as the negative one to avoid a spontaneous preference for the vertical axis known from previous work (Lehrer *et al.*, 1995). The positive and negative patterns were

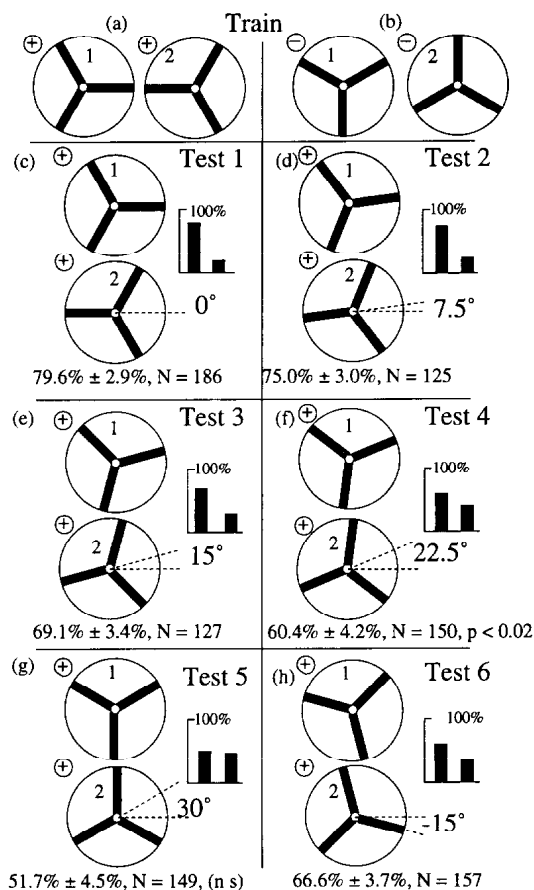


FIGURE 10. Estimation of the tuning curve of detection of a vertical axis of bilateral symmetry for one particular pattern. (a) The positive pattern, with one bar horizontal, alternated between positions 1 and 2 to make the positions of the bars useless as cues. (b) The negative pattern also alternated between the positions 1 and 2, with a vertical axis of symmetry in both. (c) Test of discrimination between (c) and (b) by the trained bees. (d-h) Results of the tests with the positive patterns 1 and 2 rotated by various angles as shown. At a rotation of 30° the positive patterns are identical with the negative patterns and cannot be discriminated.

interchanged every 10 min. As in experiment 7, the bees are therefore trained to avoid the pattern with the vertical axis irrespective of the location or orientation of the bars. The result, after 2h of training was $79.6\% \pm 2.9\%$, $N = 186$ [Fig. 10(c)], showing that the bees can certainly see the difference in the orientations of the symmetry axes irrespective of the bar positions, as would be expected from earlier experiments.

Starting after 3h of training, the trained bees were tested with the same pair of negative targets, but the pairs of positive targets were now rotated by an angle θ which is (d) 7.5° , (e) 15° , (f) 22.5° , (g) 30° , and (h) -15° , relative to their previous orientation during the training. The bees are therefore asked to discriminate between a familiar negative target and new positive targets that are rotated by the angle θ [Fig. 10(d-h)].

Rotation of the positive targets by 30° brings them back to the same targets as the negative pair, which acts as a convenient control, and also shows that the angular tuning curve must be quite narrow. The tests were carried out for 5 min on each side at intervals of 10 or 20 min during continued training, and the results at each angle of the positive target were kept separate. The results show that the performance is at a maximum when $\theta = 0^\circ$ falling to zero when $\theta = 30^\circ$, as expected. The tuning of the detector for bilateral symmetry, irrespective of its regular reversal by 180° , is about 30° in total width at 50% of the optimum performance. When the axis of symmetry of this pattern is not regularly reversed during the training and tests, the optimum is found when the patterns differ by 60° , and the tuning curve is wider, as already indicated in Fig. 2(e) for another pattern.

The rudiments of a theory of detection of the axis of bilateral symmetry

If the bee has several global radial filters with three segments, like the pattern in Fig. 10, and also large-field filters for average orientation over large areas, then in principle, bilateral symmetry can be detected without postulating a dedicated filter for it. In any case, any large-field spatial filter with two similar but separated pass regions can detect bilateral symmetry.

Let us suppose that the projection of the image on the retina is passed through a global radial filter which gives the best response and then through the large-field filter for average orientation of edges which also gives the best response. The product of the filters taken together can then detect bilateral symmetry of at least some patterns. The number of patterns that can be discriminated depends on the number of filters available, the filter properties, and how they interact. The difficulty with this theory is that we know very little, as yet, about the tuning of the orientation filters, or of the radial filters, in terms of angle or spatial frequency. The experiments are at the stage of demonstrating the phenomenon, not yet analysing its mechanism.

DISCUSSION

The previously published spontaneous preferences for arbitrary patterns (Lehrer *et al.*, 1995, Fig. 8), show that untrained bees can detect the vertical axis of bilateral symmetry in patterns of orthogonal pairs of bars. This result alone showed that bees have some kind of innate mechanism that detects the vertical axis of bilateral symmetry irrespective of pattern. The next step was to show that flying bees can learn to associate this axis with a food source irrespective of pattern.

The bees were trained on a variety of patterns composed of identical bars in orthogonal pairs, with the whole target subtending less than 50° at the choice point. The patterns have no average global orientation in the pattern as a whole and are all similar in area of black, length of edge and degree of disruption. In earlier work it was shown that the bees cannot discriminate some of these 4-bar patterns that consist of radii and tangents from the same pattern rotated. The bees cannot be using the lay-out of the areas of black, locations of bars or orientations of individual bars, for if they could remember any of these they would be able to discriminate the patterns. Pairs of patterns of 4 bars, however, can be discriminated when the patterns differ in amount of radial or tangential contours, showing that the bees remember them (Horridge, 1995). From this previous work it was concluded that bees have innate global filters for radial and tangential contours in the pattern as a whole.

The experiments reported here show that the bees detect an axis of bilateral symmetry and discriminate a rotation of it. The possibility that the bees memorize all seven different patterns used in the training is ruled out by the failures in Fig. 2(c, d, and e), and by the tests with both patterns rotated through 180° (Fig. 8), and again by tests with quite different patterns that they have not seen before (Fig. 9). The results must be due to learning over the course of a few hours, as shown by the learning curve (Fig. 6). The bees learn to discriminate in favour of the pattern with the horizontal axis of symmetry, against the previously observed preference (Lehrer *et al.*, 1995). For several reasons it is also unlikely that the bees are learning a kind of sum or fusion of the locations of the bars on all the patterns. First, there is no evidence for the idea, and much against, that successive images are summed in bee vision. Such a summation would contradict the whole purpose of discrimination. Secondly, there is no evidence that bees remember the orientations or locations of individual bars in 4-bar patterns, as mentioned above. Thirdly, when bars are crossed or adjacent in a pattern, the discrimination of orientation is rapidly degraded by corners and crossings (Srinivasan *et al.*, 1994). Randomization of features in a group of patterns never results in the learning of a superimposed pattern. When gratings were randomized to demonstrate generalization of orientation, the orientation was not lost in solid black. When bees learned the range of a target of randomized size (Lehrer *et al.*, 1988), the apparent size was eliminated as

a variable and was not averaged in some way. Randomizing one set of features during the training shows the bees what aspects not to learn. Finally, rotation of the targets through 180° reverses the two sides of the targets, so the bees cannot be learning one side with one eye and the other side with the other.

The bees see both patterns of a pair before they choose one in the apparatus (Fig. 1), and after training they pick out the one with the appropriate axis of bilateral symmetry, even though they may not have seen the pattern before. The method relies on the randomization of the patterns presented in the training. When this is done, it is not necessary to show that the test patterns are all discriminated from the training patterns to show that the bees are using the axis of symmetry as a cue. If there is a filter in the visual system for black spots, for example, representing feeding bees, it does not matter whether different kinds of black spots can be discriminated from each other. Similarly, if there is a filter for vertical bars, it does not matter whether different kinds of vertical bars can be distinguished. With the group of patterns used here, a generalized detector of the axis of symmetry irrespective of pattern is demonstrated because the pattern can be randomized in the training procedure. Whether the patterns can be discriminated from each other depends on how much they differ in other ways, and has nothing to do with the direction of the symmetry axis.

In the environment that we share with the bees, the top and bottom of objects like trees or bushes are quite different, but the two sides are similar, and a rough bilateral symmetry about a vertical axis is common. We appreciate this unconsciously when we approach objects from either side. Similarly, we can move down the middle of a path or jump on the middle of a rock without thinking about the position of its axis of symmetry. We see the same object from either side without being confused by the appearance of it. This frequently encountered bilateral symmetry is a form of redundancy. In human vision, bilateral symmetry is most obvious and detected fastest when the axis is vertical (Palmer and Hemenway, 1978).

Møller (1995) has already found that flowers with more perfect symmetry produce more nectar, suggesting that the flowers have adapted themselves to the visual system of the insects, which evolved much earlier. The wider functional significance of bilateral symmetry could be that it indicates something associated with food, a predator, another bee, or a useful landmark.

Global filters of this degree of complexity perhaps work in the same way as the face detectors in human vision. If the bee has global detectors for radial symmetry and also for average orientation in large fields, these detectors could collaborate to respond to a bilaterally symmetrical structure, and they would act irrespective of pattern. After being passed through a radial filter, many bilaterally symmetrical patterns are left with some preferred orientation, which reveals the axis.

The present conclusion is that the bees have detectors

of the axis of symmetry, which is to us an abstract idea describing certain classes of patterns, even though they do not necessarily discriminate the forms of the patterns that carry it. It is difficult for us to appreciate that the bees are sensitive to the pattern as a whole and discriminate a global feature of it without remembering the locations or orientations of individual bars, but in our own vision we are familiar with our discrimination of colours without being able to identify their constituent wavelengths. In this respect, bee vision of form resembles our vision of colour; the components of it are not separately discriminated. Like the smile of the Cheshire cat in Lewis Carroll's *Alice through the Looking Glass*, the abstract feature, the smile, persists although the cat is no longer distinguished. Generalization of this type is the essence of vision, in that whole objects and complex relationships are recognized irrespective of local variables. These skills are hardly likely to be confined to humans. It is suggested that bees that move around in the same environment as ourselves have a similar capability because they also operate with large-field global filters.

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