Visual discrimination of radial cues by the honeybee (*Apis mellifera*)

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Abstract

This is a systematic study of the discrimination of black radially symmetrical patterns presented on a white vertical background and subtending 45° or 50° at the point of choice in a Y-maze apparatus. Before discrimination can occur, the ability to fixate is promoted by any radial pattern irrespective of the number of symmetry axes. A ring of spots can also stabilize the eye before the positions of the spots are discriminated.

Cues for discrimination are of two main types. First, with fixed patterns of sectors or spots, the cue is the location of an area of black relative to the fixation point, and the particular number of axes is less important than the size of the individual areas. Secondly, evidence is presented for a family of filters with large fields and coarse tuning that detect patterns of radially symmetrical edges. These filters become more evident when the patterns are made of thin black radial bars or when they are rotated at random during the training. An angular shift of one radial pattern relative to the other, or a difference between numbers of bars, is best discriminated when one of the patterns but not the other has angles of 30°, 60°, or 120° between radial edges, and least when the angles are 90°. Baffles in the apparatus make the bees pause and fixate so that discrimination is improved. When targets are rotated during the learning process, radial cues for discriminations must be presented as edges, not as spots or areas. Besides detecting and fixating flowers, this system could be useful to estimate the perfection of their symmetry. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

This is a systematic study of radially symmetrical black patterns on a white background. For many decades experimenters have found that symmetrical patterns containing radial edges are favourable for the study of visual discrimination by honeybees. There is clearly some relation between the bees' visual system and the forms of flowers. In one early example, bees discriminated well between different blue and yellow sector patterns (von Frisch, 1914); in another, bees apparently discriminated between fixed flower-like patterns with three, four, five or six blue petals by whether there was a petal below the central reward hole (Baumgärtner, 1928). In another example, bees learned to discriminate between a yellow square and cross, and were then tested successfully although the shapes were rotated or moved to other locations relative to the geometry of the apparatus (Friedlaender, 1931). Alternatively, when a variety of patterns of similar size were presented on a flat table, those with radial arms could be discriminated from the others, although the locations were shuffled and the orientations of edges were useless as cues (Hertz, 1933). By 1931 Friedlaender had concluded from the literature and her own work that bees could find and fixate upon patterns, irrespective of their orientation or location, if they were radially symmetrical.

At that time the emphasis was on the abilities of the bees, and for the following reasons it was difficult for the experimenter to identify the cues that the bees used, so the resulting theories were summaries of the performance rather than analyses of mechanisms. When the patterns were fixed during training, the cues could have been particular corners or edges, and different for different bees. When the criterion was the landing of the bee on the pattern, the bee's choice was made at an unknown

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range and target size. In successful discriminations of patterns that are fixed during training, it is impossible to know how the visual processing is divided among several mechanisms acting in parallel. At that time, the well-known patterns that cannot be discriminated were not used in the inference of mechanisms.

There are four ways to avoid the above problems. First, the apparatus is designed to force the bees to discriminate between two targets at a fixed range. Second, all features except the one of interest are randomized so the bees are obliged to find the relevant cue. Third, the pairs of patterns are designed to train or test only one difference at a time. Fourthly, pairs of simple patterns that differ but are not discriminated by the bees reveal when no cue is available. These pairs had enabled even the earliest workers to exclude some models of the visual system, such as the crude idea that bees simply form an internal copy of the image.

The mechanism with which bees first detect patterns from a distance, before they learn to discriminate between them, has scarcely been considered. The preferences of untrained bees might be relevant to this problem. In recent work, untrained bees were presented with a variety of patterns in the vertical plane and had to make a choice from a distance. Radial sectors or black radial bars on a white background were the most preferred, and concentric circles the least preferred. Symmetry was preferred over asymmetry, and six equally spaced radial bars were preferred over four, eight or 12 bars, as if there are innate detectors for certain radial patterns (Lehrer et al., 1995). Since the bees were not trained, the preferences could reflect features that promote fixation, and are not necessarily related to pattern discrimination. Similar arguments apply to targets presented horizontally (Hertz, 1933; Free, 1970).

In vertically presented targets at a fixed range, when the orientations of edges, locations of areas of black, and numbers of sectors, are all randomized by rotation during training, bees fixate on circular and radial patterns and discriminate very well between them, irrespective of the number of axes of symmetry. The trained bees then discriminate between patterns containing these cues and neutral patterns such as a checkerboard, so they use radial and tangential cues separately (Horridge and Zhang, 1995). When bees are trained on fixed patterns of several bars, they detect radial cues, even when the bars are at 90° to each other, but they respond in tests as if they do not distinguish between the individual orientations or spatial relations of the bars (Horridge, 1996a). In these experiments, they generalize the cues as if they have a set of wide-field coarsely tuned filters that distinguish any radial edge from other kinds of edges. Such filters would not necessarily discriminate between different numbers of axes.

There have been no systematic studies of discriminations between radial patterns with different numbers

of axes in vertical presentation, except that mentioned above from Baumgärtner (1928) and a brief reference by Horridge (1997; figure 4.8). Even in those examples, the patterns were fixed during training and the actual cue was unknown. Others with vertical presentation had used fixed crosses with four arms (Friedlaender, 1931; Wehner and Lindauer, 1966). With black bars on a white background, the bees use cues mainly from edges not areas of black, even though the targets are fixed, and edges at right angles on thick single bars reduce the orientation cue (Wehner, 1971).

Later, a substantial theory was built upon the single case that, unlike the orientation of a single bar, a 4-arm cross cannot be discriminated from the same cross that is rotated by 45° (Srinivasan et al., 1994). This theory assumes that each filter is 90° wide and sums the orientations of edges within its own field. The theory predicts that only one average orientation at each eye can pass the filters into the discrimination system, and therefore could not account for the discriminations of radial or tangential edges. A theory based only on orientation discrimination cannot account for any of the positive results with patterns that are rotated, or virtually rotated by being presented on a horizontal surface. The earlier positive results with square crosses were not explained until it was realized that for a large fixed square cross the cue was the location of the ends of the arms, and not the orientation at all (Horridge, 1996b), that fixed thin black bars are detected as edges not areas (Horridge, 1996a), and that bees discriminate between some pairs of radial patterns but not others (Horridge, 1997). Later, black or coloured areas as cues for location were separated from edges with green contrast as cues for fixation (Horridge, 1999d).

In fact, it is an intriguing problem how one would demonstrate the number and kind of filters for oriented edges when there are an unknown number of mechanisms in parallel. A distinction must be made between discrimination of radial versus other patterns, discrimination of a radial pattern from the same pattern rotated, and discrimination between radial patterns with different numbers of arms. The following experiments systematically investigate these questions with different sets of pairs of similar patterns with radial cues and different numbers of axes of symmetry.

2. Materials and methods

The experiments were done in the Y-choice apparatus (Fig. 1). There is a circular entrance hole 5 cm in diameter that helps to keep out newly recruited bees. Some experiments (labelled n.b.) were done without baffles so that the bees made their choice in flight without stopping. In other experiments (w.b. or not labelled), the baffles made them pause in flight in the choice chamber
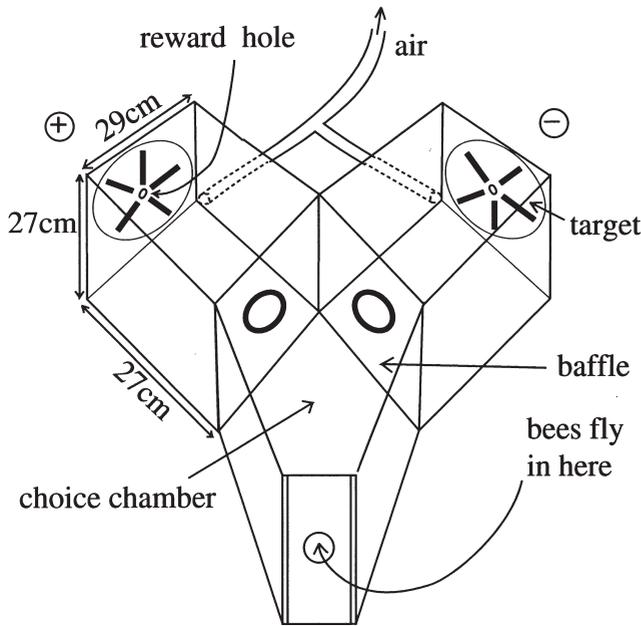
Fig. 1. The Y-choice apparatus modified with addition of baffles. The bees enter through the hole 5 cm in diameter at the front. They normally look at the targets through the transparent baffles until they decide to pass through. To prevent the bees from learning which side to go, the targets and the reward change sides every 5 or 10 min. Odours are extracted by the air pipe. As in all the figures, (+) and (−) indicate the rewarded and unrewarded targets.

and look at the targets. 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 in diameter and is surrounded by a black annulus 0.5 cm wide. The patterns are printed by computer or made by pasting pieces of black paper on white copying paper of constant quality. 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 apparatus was placed outside under a roof with an open front 3 m wide and 3 m high, with the targets facing bright daylight but in indirect sunlight. The luminance of the standard white paper that was used in all the experiments was regularly measured, and was near 20,000 cd/m^2, which is approximately 8×10^{15} green (550 nm) photons/s/m^2/sr. This is the luminance of green grass in sunlight near the experiments, measured with the same instrument (Spotmeter).

A new group of bees was used for each experiment. The reward is a fresh aqueous solution of sucrose, just strong enough to keep the marked bees coming without attracting unmarked bees. During training the side of the positive target and of the reward with it are changed every 5 min to prevent the bees from learning which

side to choose, but in the figures the rewarded pattern (labelled + in the illustrations) is always shown on the left. In all cases there was a central reward hole. In some of the experiments the patterns were held in one position relative to the geometry of the arm of the apparatus during the learning process. In others, the locations of the bars were randomized by rotation of the target every 5 min.

Honeybees from a local hive look through the baffles and select one of the two targets while in flight in the central chamber (Fig. 1). Each bee is identified by its colour code, and unmarked bees are removed. The marked bees were allowed 20 or so visits to learn the discrimination. After this initial training period, usually 2 h in the early morning, the bees' first choices were counted at the first entry at the first arrival in each period of 5 min. With the baffle at a distance of 27 cm, the targets subtend an angle of 50–55° at the point of choice.

Most of the results are performances after training for a few hours. In other experiments, labelled 'test', the first choices of the trained bees were recorded for another pair of patterns that differ from those in the training. In tests it is essential to give a reward, otherwise the bees continue to search for it, remain in the apparatus, and confuse the arriving bees. When targets are fixed during training, it is especially important to take precautions against learning during the tests. In a test, the reward was given with one pattern for a period of 5 min and later to the other pattern for 5 min. There were periods of 15 min further training between tests. In the tests the bees get a reward after they have made their only choice in that 5 min period, and when they return the patterns have been changed or moved to the other arm. Where possible, tests were interleaved with other tests so that the bees do not see any consistent cue during the tests, whereas they require 20 or so visits to build up a discrimination. When bees are tested by this standard procedure on patterns they have not previously seen, they perform as well as before when they are returned to the training schedule (Horridge and Zhang, 1995). By watching the bees in the choice chamber, one can frequently see whether they spend a long time examining both targets, or whether they move forward when they identify the rewarded pattern. Further details are given in previous studies (Srinivasan et al., 1994; Horridge, 1996a,b).

The choices made by the bees are independent because the sides are changed every 5 min, before the bees can return. Only marked bees are counted. Care is taken to avoid the situation where one bee follows another, but this is not serious because the leading bee is also an average bee. Two estimates of the variance have been made. In the first, the choices are taken in blocks of 20 in the order of recording them. The average score and its standard deviation between blocks are calculated and converted to percentages. The percentages

of correct choices for up to 30 of these blocks are given, with the standard deviation between blocks, and the total numbers of choices. This value of SD is given without brackets. The method is arbitrary because the result depends on the size of the blocks. If the bees have a preference for one side of the apparatus, the percentage of correct choices is unaffected but the SD is too large. An improvement by learning during the count also makes the SD too large, so interpretation leans on the cautious side.

In the second method (Friedlaender, 1931), an estimate of the SD is the value of $\sqrt{[p(1-p)/N]}$ where p is the fraction of correct choices and N is the total number of choices. This method assumes that the individual choices are independent and have a binomial distribution in a single group about the mean, as they should because the two sides are alternated and the bees make only one visit each 5 min. The (SD) estimated from this formula is given in brackets after each score. By this method a score of 60% based on 200 choices is more than three times the estimated standard deviation away from the null (random) hypothesis of 50%. The second method usually gives smaller values of the SD than the first method; the difference is a measure of the hazards of real experiments. A performance of two SD's or three estimated (SD's) away from 50% is accepted as significant. Many of the significant results are demonstrations that the bees cannot discriminate certain patterns, in which case statistics are unnecessary.

3. Results

3.1. Two positions of the same fixed radial bars, no baffles

Let us first consider the case with no baffles and thin bars that are fixed during the training. Some of these experiments were done in 1995 and have been briefly reported (Horridge, 1997). Without baffles, the bees make their decision in flight through the choice chamber, often without slowing down or fixating. The patterns subtend about 40° at the point of choice. At this size, with black bars, cues from edges predominate. The result is quite different if the targets are very large, in which case area locations predominate (Horridge, 1996b).

With 40° targets, the bees discriminate a pattern of three bars at 120° to each other from a similar pattern rotated through 30° or 60°, no matter how the patterns are oriented [Fig. 2(a–d)]. Examples of discrimination of mirror images and upside-down images are included in this group.

With four bars at 90° to each other, discrimination from a similar cross rotated through 45° is not possible, no matter whether the patterns are symmetrical about a vertical axis [Fig. 2(e)] or inclined at 22.5° to the vertical
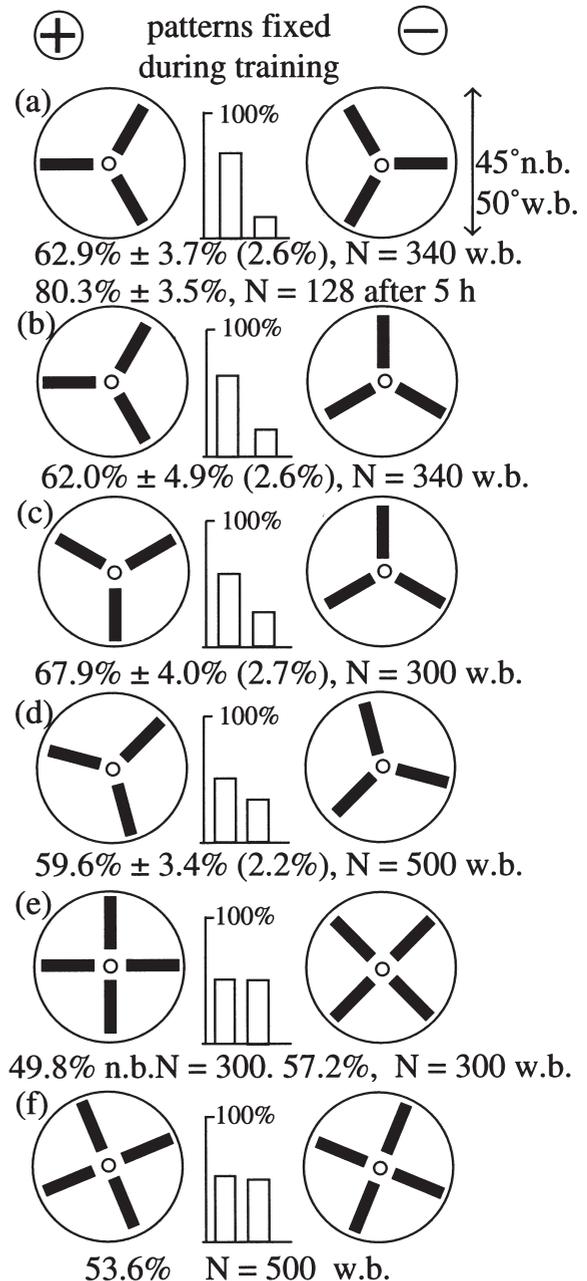
Fig. 2. Fixed patterns of three and four equally spaced bars, with baffles (w.b.) or no baffles (n.b.). (a–d) Patterns of three bars are well discriminated from identical patterns rotated by 30° or 60°, irrespective of their relative positions. (e–f) Patterns of four bars are not discriminated. In all illustrations, the angular size of the target is given, as seen from the point of choice at the baffle. The numbers indicate the frequencies of correct choices; the bar charts indicate the choice frequencies.

[Fig. 2(f)]. Similarly, a pattern with five bars at 72° to each other cannot be discriminated from a similar pattern rotated by 36°. Two possible variations were tried [Fig. 3(a,b)]. With four or five bars, the presence of a vertical bar below the reward hole makes no difference, with targets of this angular size.

Six bars at 60° to each other, however, are discrimi-

patterns fixed during training

(a)

⌐100%

45°n.b.
50°w.b.

52.3%, N = 200 n.b.   56.3%, N = 400 w.b.

(b)

⌐100%

48.3%, N = 400 w.b.   51.2%, N = 154 n.b.

(c)

⌐100%

79.3% ± 2.9% (3.2%), N = 160 n.b.

(d)

⌐100%

61.5% ± 4.4% (2.8%), N = 300 w.b.

(e)

⌐100%

63.7% ± 5.0% (2.8%), N = 300 w.b.

(f)

⌐100%

47.1%, N = 340 w.b.
with 65% black on 35% black
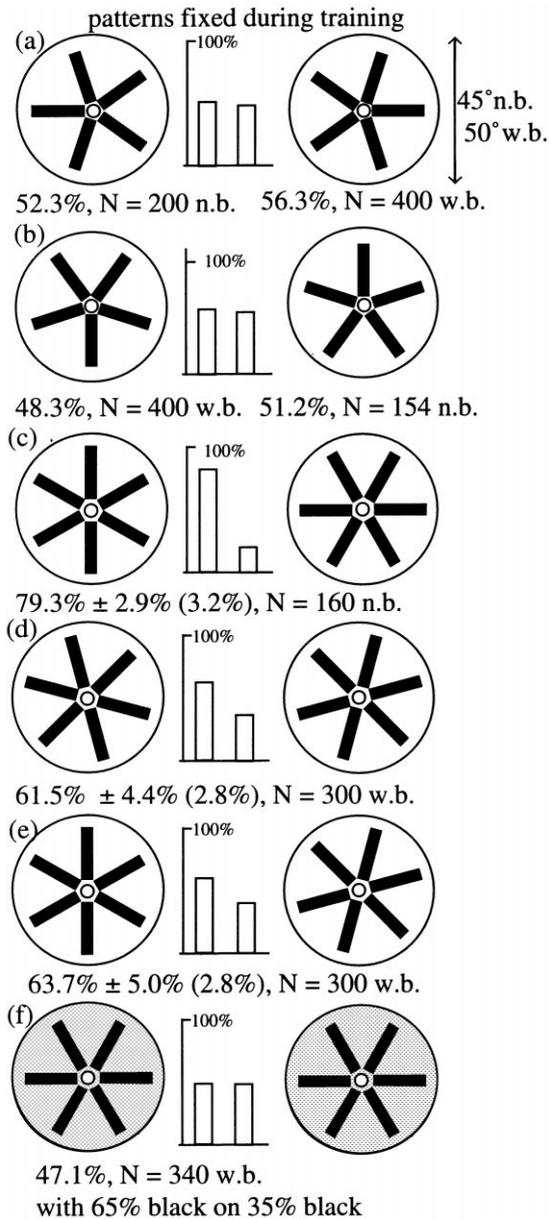
Fig. 3. Fixed patterns of five and six equally spaced bars, with baffles (w.b.) or no baffles (n.b.). (a–b) Patterns of five bars are not discriminated. (c–e) Patterns of six bars are well discriminated irrespective of their relative positions, except (f) when contrast is reduced to 30%. The numbers indicate the frequencies of correct choices; the bar charts indicate the choice frequencies. As in all the figures, (+) and (−) indicate the rewarded and unrewarded targets.

patterns fixed
during training

(+)   (−)

(a)

⌐100%

45°

56.4% ± 3.4% (3.9%), N = 154 n.b.

(b)

⌐100%

49.5%, N = 221 n.b.

(c)

⌐100%

52.5%   N = 240   w.b.

Fig. 4. Fixed patterns of seven and eight equally spaced bars are not discriminated from the same pattern rotated. In all illustrations, the angular size of the target is given, as seen from the point of choice at the baffle. The numbers indicate the frequencies of correct choices; the bar charts indicate the choice frequencies.

from a similar pattern rotated through half the angle between the bars is not possible.

In summary, with patterns subtending 40°, and without baffles, the bees perform well only when there are three or six bars, with patterns of this critical size, without baffles, so they are certainly not using locations of areas of black. There is no evidence that the bees require a vertical bar below the reward hole as a cue, although the patterns are fixed in orientation during the learning process. This result is in contrast to Baumgärtner (1928) who used oval blue petals, not black bars. A variety of experiments show that with fixed black bars on a white background, the bees use cues from edges in preference to locations of areas (Wehner, 1971; Horridge, 1996a).

3.2. Two positions of the same fixed radial bars, with baffles

The baffles in the Y-choice apparatus (Fig. 1) force the bees to pause in flight before they choose one side or the other. The baffles improve the performance, perhaps because the bees spend time looking at the patterns. As seen from the point of choice, the patterns are fixed in orientation and in relation to the reward hole during the learning period. Many of the experiments above, with various numbers of bars, were repeated with baffles (w.b.) or with no baffles (n.b.), as labelled on the figures (Figs. 2–4). The performance is poor for four, five, seven

nated from a similar pattern rotated by 30° [Fig. 3(c–f)], even when neither pattern has a vertical bar [Fig. 3(d)]. A rotation of 15° is discriminated [Fig. 3(e)]. As described in a different context (Horridge, 1999c), this discrimination requires more than 30% contrast [Fig. 3(f)] but when the cue is the orientation of a coarse grating of period 20°, a contrast of 20% is sufficient (Giger and Srinivasan, 1996). With seven black bars [Fig. 4(a,b)], and with eight bars [Fig. 4(c)], discrimination

or eight bars. Because the patterns are fixed, the bees could use any number of cues, such as the position or orientation of a particular bar. The results show that they do not do so. The differences between the results for different numbers of arms cannot be explained by filters which each sum the edge orientations within their own large field (Srinivasan et al., 1994). To account for these results, and all positive results with randomly rotated patterns, there must be a family of filters that detect radial edges. Recent work shows that these filters are colour blind and not concerned with areas of colour or black (Horridge, 1999c).

3.2.1. Two positions of the same fixed sectors, with baffles

In this series of targets, the rewarded one presents a pattern of alternating black and white sectors and the unrewarded one the same pattern rotated by one sector. The targets differ, therefore, in the locations of areas of black and white and in the sign of the contrasts at edges, but the locations of the edges coincide in the two targets. This strategy appears to force the bees to use the locations of areas in the vertical plane as their cues because they do not discriminate the sign of the contrasts (Horridge, 1999d). Bees discriminate between patterns of this type, but most previous workers have used only patterns with a multiple of four radial axes with bilateral symmetry about a vertical midline (von Frisch, 1914; Wehner, 1981; Srinivasan and Lehrer, 1988).

Results of training for 3 h with different numbers of sectors at constant range are shown in Fig. 5. The data has been collected, using the same apparatus, with baffles, at various times over a period of 4 years. In general, the greater the number of sectors, the poorer the performance. The new results show that bilateral symmetry is not important for patterns of areas, as it would be for patterns of edges [Figs 2(c, d); 3(c, d)]. The limit of discrimination is at about 18 periods (36 sectors) for targets that subtend 50° at the point of choice. This is similar to the earlier result with enormous targets subtending 130° at the point of choice (Wehner, 1981; figure 59 therein).

These results contrast with those from patterns of radial bars (Figs. 2–4) in that performances are in general better, but not specifically better for three or six periods of sectors. The distinction between the two types of pattern is that black bars on a white background have very strong green contrast at their edges, their edges lie in directions that differ between the pair of patterns, and these directions are detected by filters, whereas the difference between two sector patterns is in the locations of areas of black, not edge directions. Location is the cue for the sector patterns, as confirmed by making sector patterns from two coloured papers that give no contrast to the green receptors where they meet. Unlike orientation cues without green contrast, these sector pat-
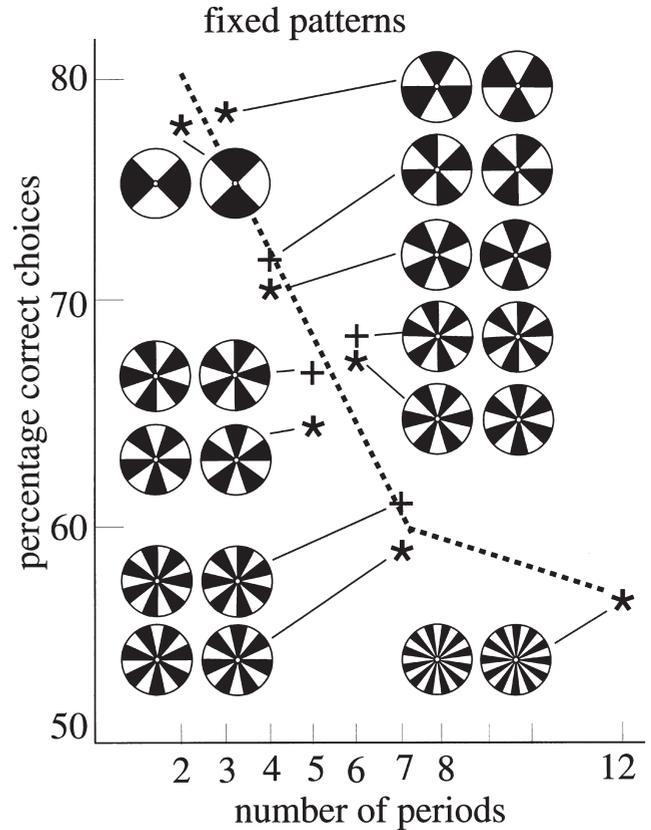
Fig. 5. Fixed patterns of equally spaced alternately black and white sectors, all subtending the same angle at the point of choice. In each pair, one is rotated by one sector relative to the other. In general, the greater the number of sectors, the poorer is the discrimination, with a resolution limit near 18 periods. The bees respond similarly to patterns with or without bilateral symmetry about a vertical axis. (★) bilaterally symetrical, (+) not symmetrical.

terns are as well resolved as those with contrast to the green receptors (Srinivasan and Lehrer, 1988; Horridge, 1999d). With location as a cue, pairs of mirror images or upside-down images are discriminated, and lack of a vertical axis of symmetry makes no difference (Fig. 5).

3.2.2. Two positions of a centred ring of spots, with baffles

In this series, the positive target was an equally spaced ring of large black spots with radial symmetry on a white background, and the negative target an identical pattern rotated by half of the angle between the spots (Fig. 6). Different groups of bees were trained with pairs of targets with 2–8 spots. The diameters of the spots were adjusted to make the total area of black the same on all the targets. In general, discrimination is good, showing that the bees stabilize the image well enough to localize at least one spot. The performance falls off as the number of spots is increased, and depends on spot size or spot separation. There is no obvious advantage of two, three or six spots over other numbers of spots, as if the performance is not related to the previously identified
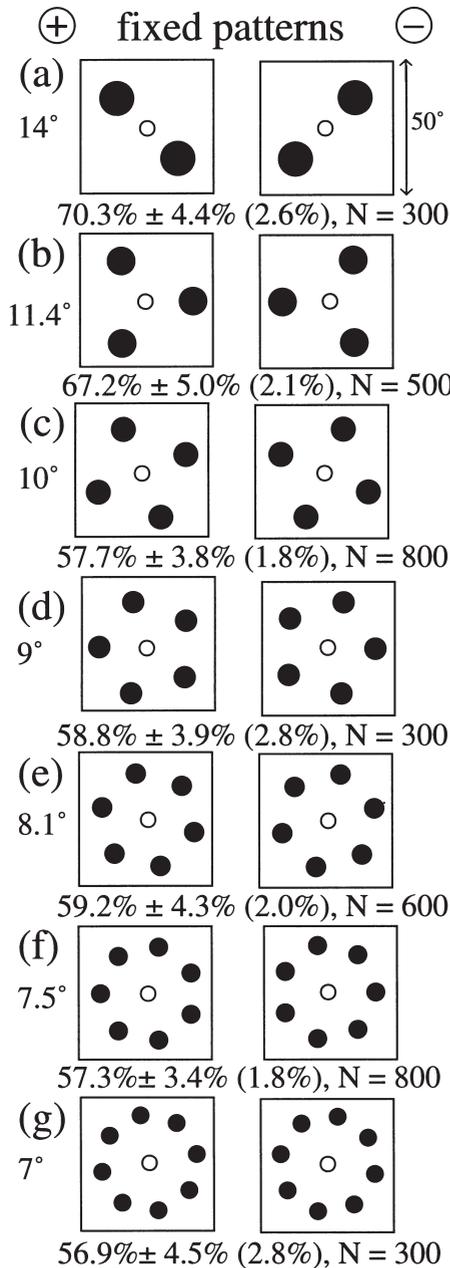
Fig. 6.   Fixed patterns of spots. The total area of black is constant. Discrimination falls off with decreasing spot size and increasing spot number. The angular size of the spots, as seen from the point of choice, is shown on the left.

radial filters for edges. The pairs of patterns with an odd number of spots are mirror images, but this brings no obvious advantage. The results resemble those with fixed sectors but are in marked contrast to those with fixed radial bars (Figs. 2–4).

3.3. Discriminations with baffles and rotation

In the following series, the targets were randomly rotated to a new position every 5 or 10 min to preserve the relations between radial edges but to make locations

of areas and edges useless as cues. With random rotation, questions of mirror images, or upside-down images, are irrelevant.

3.3.1. Discrimination of the number of spots, with random rotation

In these experiments, the positive target was a radially symmetrical pattern of black spots on a white background and the negative target a similar pattern with an additional spot (Fig. 7). The total area of black was the same for each pattern. Both targets are rotated at random every 5 or 10 min. In contrast to the experiments with fixed black spots (Fig. 6), the bees are unable to discriminate the difference even between two and three spots.

This result is in marked contrast to their ability to dis-
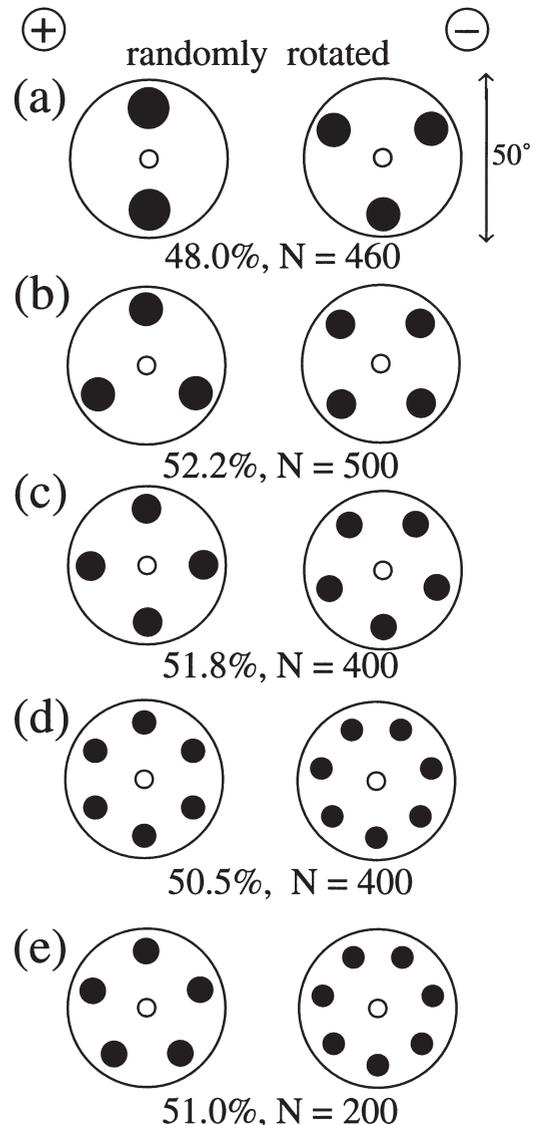
Fig. 7.   Randomly rotated patterns of spots, all with the same total area of black. The bees are unable to discriminate even two from three spots, although the results in Fig. 6 show that they see the targets.

criminate radial edges in randomly rotated targets, but is in agreement with the general finding that they must first be able to fixate upon the patterns and then radial filters are revealed when the bees detect radial edges. With a small number of spots on each target, the conditions are unfavourable for fixation on a consistent centre, differences in total size and length of edge are weak cues, the areas of black, the global orientation and the locations are not cues, and there are no radial edges. Obviously, they do not count the spots. The bees found no cue, which means that the radial filters do not operate with areas, and the spots provide no edges that are radial with reference to the pattern centre. This is an example of a significant negative result. The bees see something and make a choice; they just cannot remember the correct pattern.

3.3.2. Different numbers of radial bars, with random rotation

The next five strategies with random rotation (Figs. 8–11) are efforts to identify the filters for particular numbers of axes of radial symmetry by selection of pattern pairs that would not be discriminated by non-specific filters for any radial edge.

In the first, the positive target is a pattern of (n) black radial bars on a white background and the negative target a similar pattern of (n+1) bars (Fig. 8). Both targets were randomly rotated every 5 min. The bees must not be given the opportunity to learn the difference between the total areas of black or the differing widths of individual bars. Therefore the widths of the bars were changed every 5 or 10 min during training so that either the total areas or the bar widths were equal on the two targets. This precaution is an example of the randomization technique that teaches the bees to ignore unwanted cues.

The results are given in Fig. 8. The bees are able to discriminate the number of axes of symmetry when one of the pair has three or six bars. They remember the number irrespective of rotation, but fail to discriminate between five and seven bars. They also fail to discriminate between four and five bars, as found by Baumgärtner (1928) when patterns of four and five flower petals were presented vertically and randomly rotated.

3.3.3. Equal numbers of bars at different angles, with random rotation

In the following experiments, the strategy is to try to isolate the radial filters by using as cues the angles between the radial edges. The bees were trained to discriminate between a (positive) pattern of (n+1) similar bars with one bar missing from the ring and a (negative) pattern of (n) equally spaced bars. The two targets have an equal number of similar bars (Fig. 9). They were randomly rotated every 5 min during the training, so that the gap in the ring continually changed its position. The
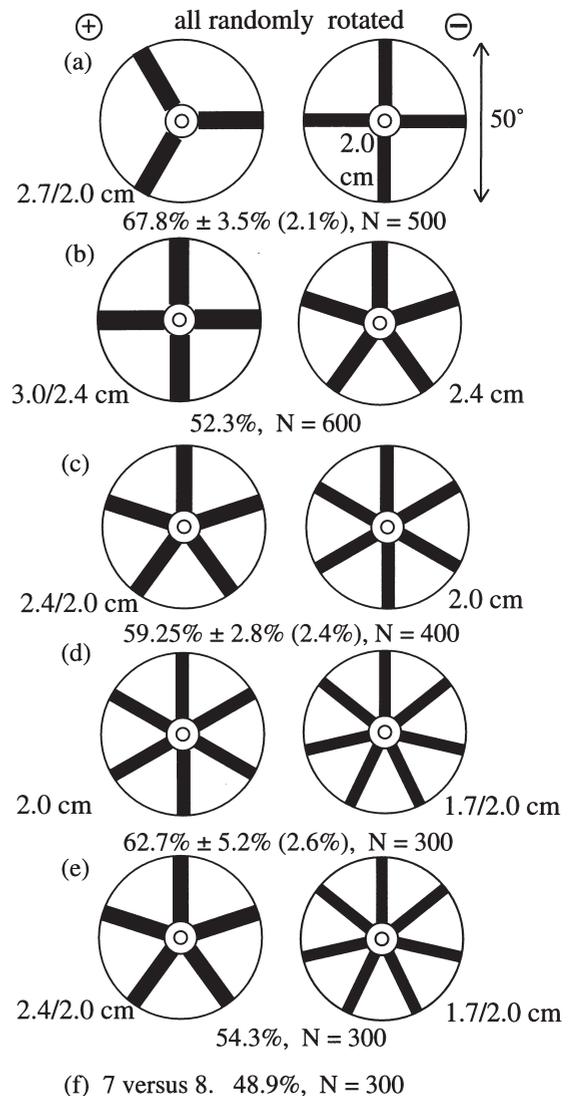
Fig. 8.　Randomly rotated patterns of (n+1) and (n) regularly spaced radial bars are discriminated when one pattern has angles of 120° or 60° between bars. The bar widths (given next to each pattern in cm) are alternated between the angular widths shown, to teach the bees to ignore differences in areas of black.

bees are able to discriminate between 4-minus-1 and 3 bars, between 6-minus-1 and 5 bars, and between 7-minus-1 and 6 bars. Each of these pairs includes one pattern with angles of 60° or 120° in one of the targets. The bees were not able to discriminate between 4 and 5-minus-1 bars or between 8-minus-1 and 7 bars. These pairs provide no cue for filters with three or six axes of radial symmetry.

3.3.4. Equal numbers of bars at different angles, with random rotation

With random rotation of the target every 5 min, the processing mechanism functions better when one target has angles of 60° or 120° between bars. Bees performed poorly in discriminations between three radial bars
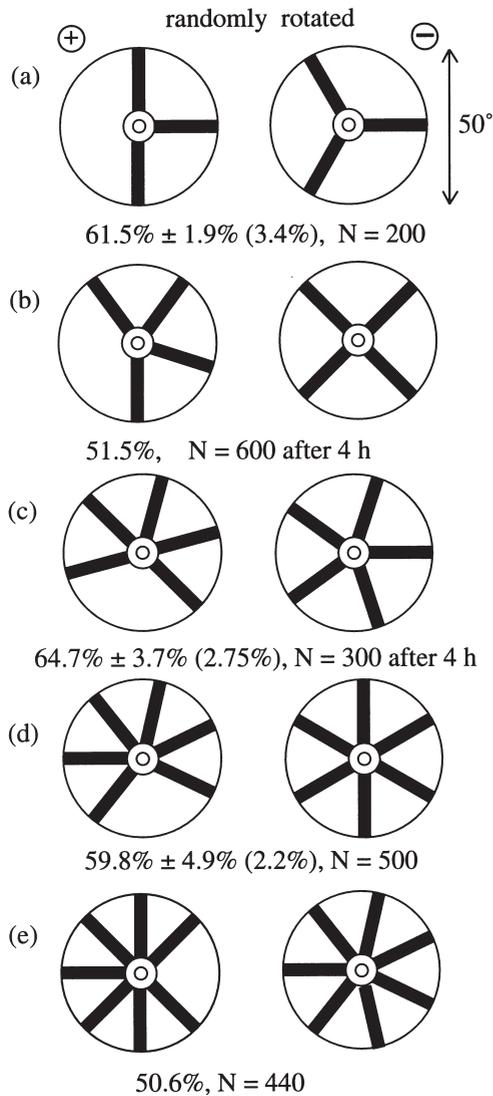
Fig. 9. Discrimination between patterns of (n+1) regularly spaced bars with one bar missing versus (n) regularly spaced bars of the same size, with random rotation every 5 min. All pairs were trained for 3 h (check) on separate groups of bees. The bees discriminate better when one pattern of the pair has angles of 120° or 60° between bars.

Fig. 10. Randomly rotated patterns with equal numbers of regularly spaced radial bars are discriminated when one pattern has angles of 120° or 60°. In (f) both targets have two sets of three bars at 120°, but are discriminated because only one of them has bars at 60°.

(positive) at 72° versus three similar bars (negative) at 90° to each other [Fig. 10(a)]. With three bars at 90° and 135° (positive) versus three at 120° (negative), they discriminate well [Fig. 10(b)]. With four bars at 72° (positive) versus four similar bars at 60°, and with four bars at 51.4° (360°/7) versus four similar bars at 60°, they also discriminate. With six bars at 45° (positive) versus six similar bars at 51.4°, they fail [Fig. 10(e)]. With six bars at 45° and 135° (positive) versus six similar bars at 60° they discriminate very well [Fig. 10(f)]. In this final example, both patterns have two sets of three bars at 120°, so the discrimination is not based on a 120° filter. Therefore the 120° filter is separate from the 60° filter, as previously inferred (Horridge, 1999a).

3.3.5. Discrimination of a particular angle between radial bars, with random rotation

In this series of experiments, the task for the bees is to learn to discriminate a target with a given number of radial bars from a target with one more or one less similar bars. The positive target had (n) equally spaced radial bars (all 10×2 cm) where n=3 to 7. The negative target alternated every 5 or 10 min between (n+1) and (n−1) bars (Fig. 11). The alternation of the negative targets is

all randomly rotated
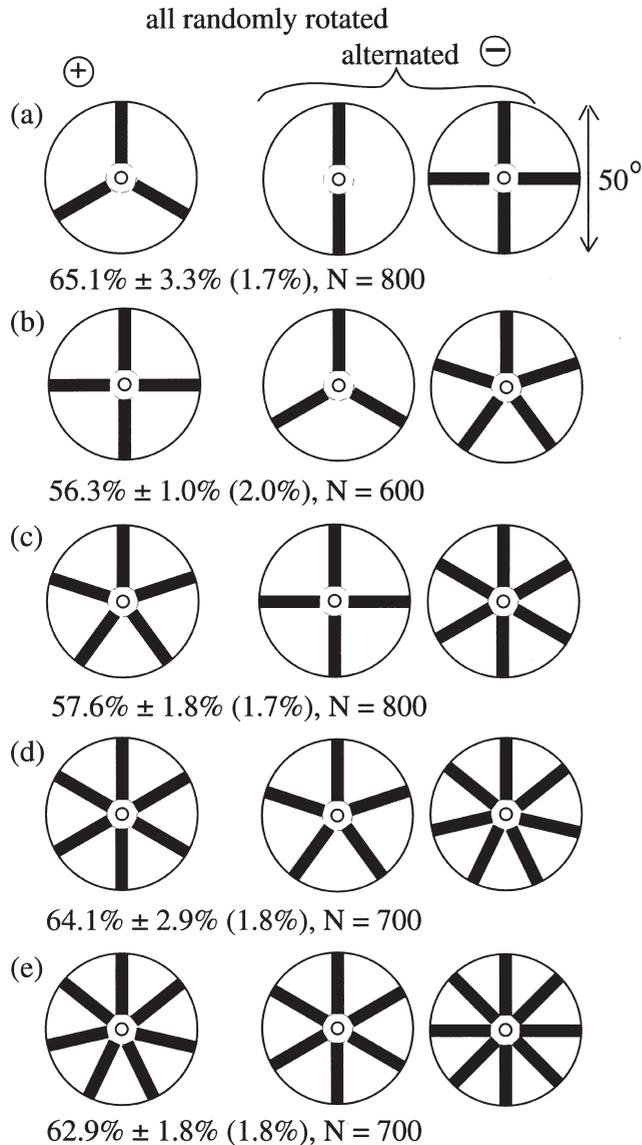
Fig. 11. Discrimination between patterns of (*n*) equally spaced bars (positive) versus (*n*−1) and (*n*+1) similar bars, with random rotation every 5 min. The best performance is with a positive pattern of three or six bars.

intended to teach the bees to ignore the total area of black or length of edge. All targets were rotated at random every 5 or 10 min so the locations or orientations of the bars cannot be used as cues.

With three equally spaced bars in the positive target, the result after 3 h training was 61.1% *N*=800 over the next 4 h [Fig. 11(a)], with the bees still improving at the end of that time. For other numbers of bars, the best results are obtained when six bars are discriminated from five or seven bars. Discrimination is surprisingly good with the other numbers of bars, probably because one of the patterns has three or six bars in every case.

3.3.6. Radial and oblique bars, with random rotation

When the equally spaced radial bars are turned though 45° about their mid-points, a family of spiral patterns are generated (Fig. 12). The oblique bars are neither radial nor tangential, so this discrimination is not between two radial patterns. The task of the bees is to discriminate a pattern with oblique bars (positive) from a pattern of the same number of radial bars (negative), both randomly rotated every 5 min.

With these targets the bees do not discriminate the patterns of three bars [Fig. 12(a)]. This was a surprising result and was therefore repeated. The result is compatible with coarse angular tuning of the filters with three arms. With four bars, the result was a little better [Fig. 12(b)]. However, 5, 6, 7, or 8 oblique bars are discriminated from the same number of radial bars [Fig. 12(c–f)] with no particular improvement at 6 bars. This response would be expected if there is an efficient generalized discrimination of radial edges from other kinds of edges, irrespective of pattern or number of axes, as already inferred from a variety of experiments (Horridge and Zhang, 1995; Horridge, 1996a).

The trained bees are unable to discriminate the pattern of oblique bars, on which they were successfully trained, from its mirror image [Fig. 12(i–l)], and so the original discriminations cannot be explained by the different orientations of bars at the two sides of the pattern. The bees behave as if they have no filter for the oblique bars, but they can discriminate the radial cues and avoid them.

The bees cannot be trained to discriminate equally spaced oblique bars from the mirror image of the same pattern [Fig. 12(g,h)], showing that, as found previously (Horridge 1996a, 1998), they do not identify the orientations of the individual bars.

The idea of a family of filters, which as a group detect radial edges from other types of edges, irrespective of the number of axes, is compatible with these results.

3.4. Random sizes of bars

3.4.1. Two positions of six bars

To avoid the unknown cues that are provided by the locations of areas and edges in fixed patterns, a useful technique is to randomize the sizes of the bars while retaining the essential feature, which in this case is the number and directions of equally spaced bars. This strategy is demonstrated with two patterns of six bars (Fig. 13). The patterns change sides in the apparatus every 5 min, and they are changed in the sequence 1, 2, 3, 4 every 10 min. The consistent difference between the positive and negative pattern is a rotation of one relative to the other by 30°. The bees learn to ignore the differences in the lengths of the arms in successive presentations.

Performance is excellent. After training for 3 h, the result was 74.7±3.1% (2.5%), for the next 300 choices.

all pairs randomly rotated

(a) train — 49.0% N = 700
52.5%, N = 420

(g) train — 53.7%, N = 300

(b) train — 59.3% ± 3.9% (2.8%), N = 300

(h) train — 51.0%, N = 200

(c) train → test — 62.3% ± 5.8% (2.8%), N = 300

(i) 48.0%, N = 200

(d) train → test — 59.8% ± 2.3% (2.2%), N = 300

(k) 46.5%, N = 200

(e) train → test — 61.5% ± 5.1% (2.4%), N = 400

(l) 47.5% N = 200

(f) 8 bars   60.0% ± 4.4% (2.4%), N = 300
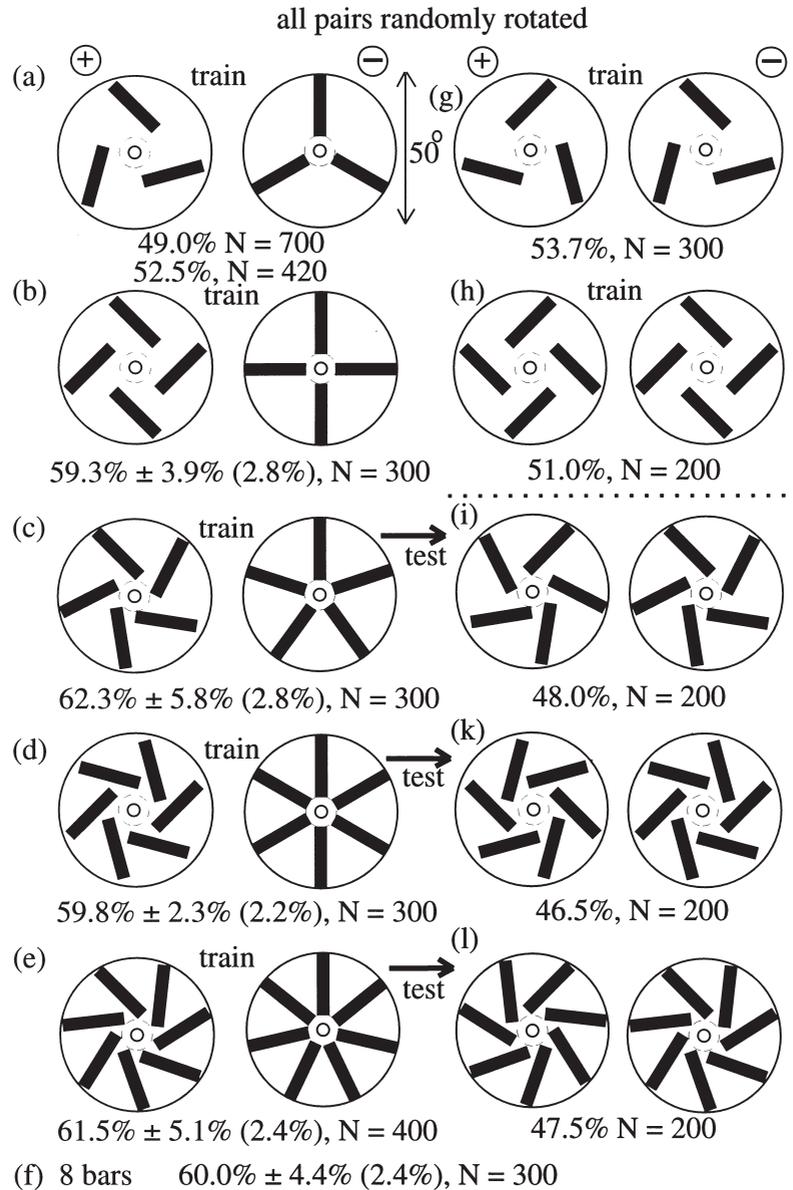
Fig. 12. A test for a generalized detector of radial edges. Discrimination between a pattern of equally spaced oblique bars (positive) and the same number of radial bars, with random rotation. (a) Patterns of three bars are poorly discriminated. (b–e) Performance improves with the number of bars. (g–l) The mirror images of the oblique bars are not discriminated when training bees or testing trained bees.

On the other hand, when the trained bees are tested with parts of the training patterns, they hesitate before making a forced decision and perform badly. In test 1 they were presented with the training patterns with the vertical and horizontal bars removed [Fig. 13(b)]. In test 2 they were presented with the vertical and horizontal bars alone [Fig. 13(c)]. The bees behave inflexibly towards the unfamiliar patterns, as if they rely on the whole pattern. Possibly the random lengths of the individual bars weaken the cues, and we know that the 6-arm radial/radial filters are not very sensitive [compare Fig. 3(f)], so even the whole pattern may be near the lower limit of detection.

3.4.2. Different numbers of bars of random size, fixed angles, no baffles

Preliminary experiments (not illustrated) showed that with fixed targets and no baffles, a pattern of (n) radial bars can be discriminated from a pattern of (n+1) bars when n=2, 3, 5, or 6, even when the positive and negative patterns both have a vertical bar below the reward hole. However, such results are open to the objection that the patterns differ in amounts of edge, area and locations of black, all of which are possible cues. Moreover the patterns are fixed, with the result that the cues used by the bees cannot be identified by the experimenter.

six fixed bars, random sizes
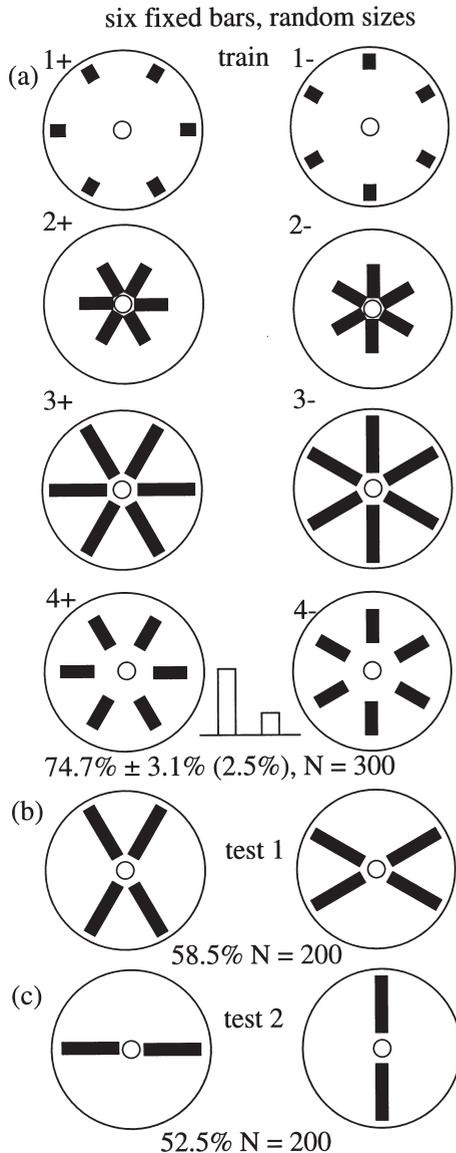
Fig. 13. Discrimination of rotation by 30° of six bars of (a–d) variable size and distance from the centre to prevent memory of location, but constant in angular position. (b–c) Tests with parts of the patterns in (a) show that the whole pattern is required, as if the filters are few with radial/radial discrimination and the cue is noisy with bars of variable lengths [see also Fig. 3(f)].

To teach the bees to ignore all cues except the one of interest, the patterns were randomized by use of bars of different sizes and different distances from the centre, and by rotation of the targets every 5 min (Fig. 14). Despite the randomization of bar length, orientation and position, two patterns of different numbers of equally spaced bars can be discriminated when one of them contains three or six bars. After training for 4 h, a good performance of 66.6% was found with three bars versus four bars. Performance was poor for the discrimination between four and five bars, and between five and seven bars, but was good for discrimination between six bars and either five or seven bars (Fig. 14).

random rotation

(a) 3 versus 4.
   66.6% ± 3.8% (2.7%), N = 300
(b) 4 versus 5.   51.8%, N = 300

(c) 5 versus 6.
   80.1% ± 2.7% (2.3%), N = 220

(d) 7 versus 6.
   77.7% ± 4.0% (3.0%), N = 200
(e) 5 versus 7.   55.7%, N = 300
(f) 7 versus 8.   48.7%, N = 300
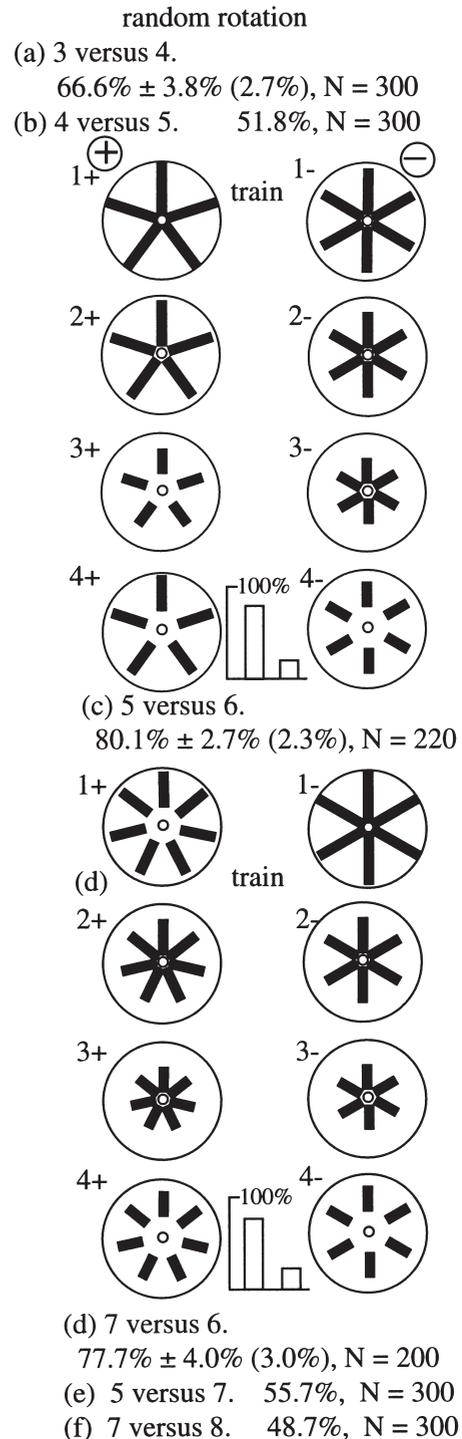
Fig. 14. (a) Discrimination between various numbers of bars of variable size and distance from the centre, with random rotation every 5 min. Only the examples with five versus six and six versus seven bars are illustrated. In general, discrimination occurs when one of the patterns contains three or six bars.

3.5. Off-centre rings of spots

In this series, the same number of spots are arranged in a ring on each target (Fig. 15). The spot sizes are as

(a) 66.0% ± 3.8% (2.2%), N = 500

(b) 55.5% ± 3.0% (2.5%), N = 400

(c) 50.2%, N = 500

(d) 48.4%, N = 700

(e) 64.0% ± 2.6% (2.8%), N = 300
62.9% ± 3.0% (3.5%), N = 240

(f) 60.25% ± 2.9% (2.4%), N = 400
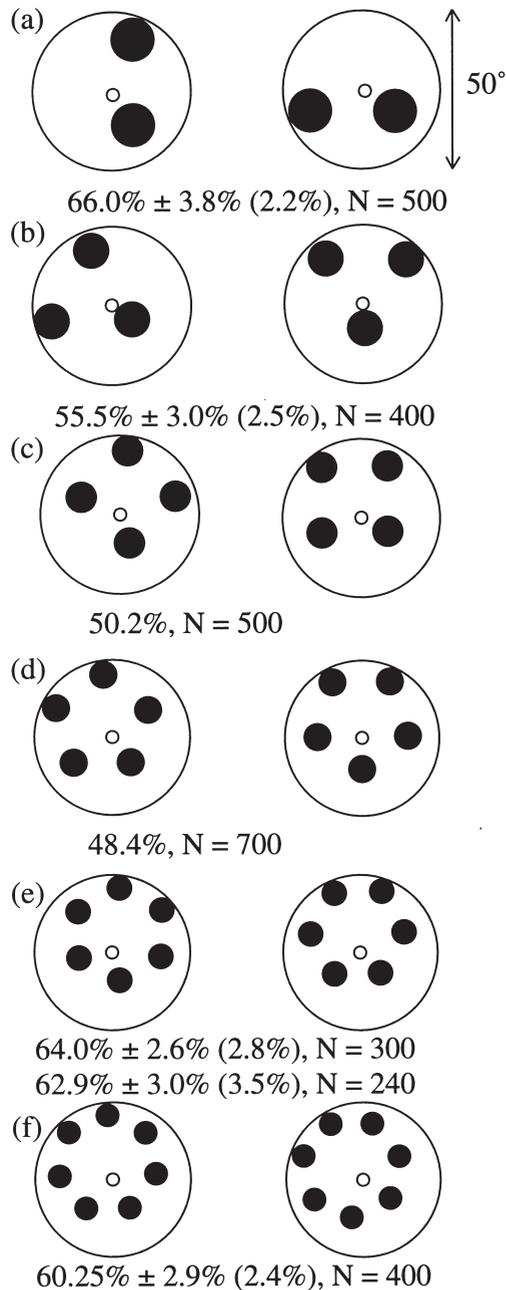
Fig. 15. Spots in an off-centre ring. The target is rotated every 5 or 10 min by an exact multiple of the angle between the spots. The positive target always has one spot at the top and the negative target always has two spots at the top. The rotation of the target moves all the spots relative to the reward hole, but the spots remain in their locations if the bee fixates its attention on the centre of the ring. Performance is poor with three, four or five spots, but with a ring of 6 or 7 spots the bees can fixate and discriminate better than in Fig. 6.

before (Fig. 6) so the total area of the black is the same for all targets. Unlike Fig. 6, the centre of the ring is off-set by 35 mm from the centre of the target, and the target is rotated every 5 or 10 min by an exact multiple of the angle between spots, so that the locations of all the spots change by up to 70 mm relative to the geometry of the apparatus. The positive target always has one spot

at the top above the other spots and the negative target always has two spots at the top (Fig. 15). There are no pairs of left/right mirror images, but the patterns with an odd number of spots present up/down mirror images. From data in Figs. 6 and 7 we know that edges and filters are irrelevant when discriminating between similar patterns of spots, which are discriminated by the location of at least one of the spots.

If the bee fixates upon the ring of spots as a whole, the spots will be projected to constant positions on the eye, and the result might be expected to be similar to that in Fig. 6. If the bee fixates on the reward hole, or with the aid of the geometry of the apparatus, however, all the spots change their positions systematically every 5 or 10 min and learning the location of a spot on the target would be impossible.

With this strategy, the results with some of the patterns are unexpected (compare Figs. 6 and 15). The result with three spots was consistently 55–58% all day after an initial training of 3 h. Only a few of the bees learned the task, and at a low level. With four and five spots [Fig. 15 (c,d)], the bees fail completely, although the training was continued all day. Pairs of up/down mirror images are certainly not favoured.

With six spots, however, after training for 3 h the result was 61%, *N*=300 and after 5 h was 64%, *N*=400 [Fig. 15(e)]. As a check, this training was repeated with a new group of bees and new patterns on a different day, with a result of 62.9%, *N*=240 after 3 h training. With seven spots in the ring, the result was 60.25%, *N*=400 after 3 h training. The results were better than those in Fig. 6. This experiment is a reminder that there is no special attribute of six axes of symmetry when the cues are from areas rather than edges.

With these pairs of patterns, we know from Fig. 6 that the patterns can be discriminated when fixed. With the off-centre rings, the additional task for the bee is to fixate on the circle, and only when this is done, the spots can be located. Considering the failures with three, four and five spots, a substantial ring is needed to make the fixation effective. Presumably the bee fixates on the centre with its filters for tangential or circular objects and is then able to locate one or more spots.

The same experiment was tried with only two spots, although they do not make a ring and the location of one spot relative to the other is an obvious cue [Fig. 15(a)]. There are four positions of the targets, in rotation, because one target is the mirror image of the other when the orientations are both vertical. The bees learn this task quickly. After 3 h training the result was 66% for the next 200 choices and 68%, *N*=400 later in the day. The bees discriminate the generalized positions of two spots side by side versus two spots one above the other irrespective of the shuffling of locations.

The trained bees were tested with two black and white plain gratings of period 16°, with the reward alternating

between the vertical and the horizontal grating, but they failed completely to respond to the orientation cue in these tests. They had not learned an orientation cue, and so they must have learned a spot location. The result suggests that they fixate upon one spot and discriminate the relative location of the other. With three, four or five spots in an off-centre ring with rotation (Fig. 15), the bees failed to discriminate patterns that they distinguished well enough with fixed targets (Fig. 6). The bees discriminate location with six or seven spots in an off-centre ring, and in these cases we infer that they fixate their attention on the ring of spots. All results are compatible with the idea that the eye is stabilized on the circle as seen from a distance. A similar conclusion follows from experiments with horizontally presented circles (Hertz, 1933).

4. Discussion

4.1. Historical

From the early work up to the present day, researchers have found that bees learn flower-like patterns easily. However, they did not inquire why this was so. Neither did they elaborate upon the finding that radial cues direct fixation innately. The very efficient discrimination of radial patterns from other patterns was not distinguished from the weaker discrimination between different radial patterns. Making these distinctions, and then looking for other properties of these patterns, throws light on the interpretation of pattern vision by bees.

4.1.1. The necessity of an innate fixation mechanism

To use radial and tangential cues, or to use location as a cue, the bee visual system functions in relation to a perceived centre which must be found before other cues can be used. Friedlaender (1931) stressed that radial symmetry enables the bee to find a vertically presented pattern. When the bees discriminate radially symmetrical patterns, the position of the pattern is not important, as if the bees are able to find it from the symmetry itself (Fig. 15). The same principle applies to targets shuffled on a flat table (Hertz, 1933).

When the pattern helps the bees to fixate and the cue is the location of spots or sectors, the number of axes of symmetry is not important (Figs. 5, 6 and 15). With patterns of edges, the system behaves as if initially all radial edges are detected and the responses summed to give maximum sensitivity. At a later stage, the orientations of axes and the differences between two, three or six axes may be discriminated if there is sufficient contrast [Fig. 3(f)].

If, after fixation on the centre, none of the filters detect a cue, and there are no outstanding differences between the patterns in the locations of areas of colour or black,

discrimination will fail. This happens with pairs of plain shapes such as a square, oval, or triangle (von Frisch, 1914).

4.1.2. Discrimination between two different radial patterns

Unfortunately, almost all previous workers with vertical patterns have used square crosses, so details of specific radial filters did not appear in their work. An exception is the finding that a fixed flower-like pattern with three blue petals was discriminated from those with other numbers, but four petals are not discriminated from five petals if both are rotated at random during the training (Baumgärtner, 1928; table 6 therein).

When offered a variety of radial patterns on a vertical surface, untrained bees preferred those with six bars (Lehrer et al., 1995). The new training experiments (Figs. 8–11) now show that the rotation of regular radial patterns with three or six axes of symmetry is discriminated. Other numbers of axes are discriminated only when the patterns are large and fixed during the training. When the locations of areas are randomized by rotation, targets with four, five, seven or eight bars are discriminated with difficulty (Figs. 8–12). A pattern of four bars is confused with a pattern of five bars, and one of seven bars with one of eight bars. The results are compatible with the idea that the bee visual system has a set of at least four high level specific radial filters with three arms and at least another two filters with six arms. New data [Fig. 10(f)] confirm that the filters with six arms function separately from the set with three (Horridge, 1999a).

We cannot say that the individual radial filters respond to radial patterns irrespective of rotation, because we do not know how many filters there are, and only one at the correct angle may be necessary to detect a cue. The idea of rotational invariance applies to performance of the whole group of filters, not yet to individual filters. The radial filters, however, explain many of the previously puzzling results with patterns laid out on a flat table (Hertz, 1933). It is tempting to suppose that this specific filter mechanism has a structure that retains the hexagonal lay-out of the eye.

4.1.3. Discrimination of radial edges from other edges

In his pioneering work, von Frisch (1914) found that bees could not discriminate geometrical patterns such as triangles, squares, diamonds, ellipses or different chequerboards, but they discriminated between sectors or other radial patterns presented on a vertical surface. The reward hole was at the centre of the pattern. Hertz (1933) found that radial patterns could be discriminated from circular patterns and blobs, of similar size and disruption, although shuffled about on a flat table to make their locations useless as cues. The reward and blanks (water) were placed beside each pattern. The bees flying above were able to fix their attention on these patterns.

Recent work has confirmed that bees efficiently discriminate radial from tangential cues when locations of edges and areas of black are randomized (Horridge and Zhang, 1995). With patterns of two or four bars, they do not focus their attention on the individual bars but are able to fixate the centre and detect radial and tangential cues (Horridge, 1996a). They also detect a radially symmetrical pattern after it has been displaced, whether presented vertically (Friedlaender, 1931), or on a flat table (Hertz, 1933). When randomly rotated radial edges are discriminated from other patterns presented on a vertical surface, the number of axes of symmetry is of little importance (Fig. 12). In these tasks, discriminations between a radial and a tangential cue, or between a radial and a random pattern, reach 90% correct, as if responses of all detectors of radial edges are summed.

There is therefore an innate robust mechanism that discriminates a radial cue from a different cue. Learning is relatively rapid, within 2 h, reaches a high performance and has a relatively low contrast threshold near 10–15% (Horridge, 1999c). On the other hand, the specific filters that detect angles between radial edges that are multiples of 30° are slower in learning, reach performances nearer to 65% and have contrast thresholds greater than 30% [Fig. 3 (f)]. These results suggest that there are many detectors for radial edges, of which some are specific filters for radial edges at angles of 30°, 60° and 120°. The others may be detectors for single radii or for radii at random angles to each other.

A remarkable parallel is found in the visual processing of the stick insect which is attracted to walk towards a vertical stem when the side branches are at angles of 30°, 60° or 120°, but repulsed when the angles are 45°, 90° or 135° (Jander and Volk-Heinrichs, 1970).

4.2. The difference between bars and spots or sectors

Bees have strikingly different responses to patterns of radial bars on the one hand and spots or sectors on the other. When their vision is stabilized well enough to use the location of some part of the image as a cue, the positions of fixed spots or sectors are well discriminated, with performance falling off as the size of the spots is reduced (Figs. 5 and 6). Patterns of well separated spots appear to contain no orientation cue. When patterns of spots are randomized by rotation during training, the bees cannot discriminate even two from three, or three from four spots (Fig. 7). Patterns of radial edges, however, are best discriminated from each other when there are angles of 30°, 60° or 120° in one of the patterns, with little difference between fixed (Figs. 2–4) and randomly rotated patterns (Figs. 8–11).

This distinction between bars and spots is the distinction between edges and areas which turns up regularly in a variety of work on insect vision (Horridge, 1999b). There are two processing pathways to visual discrimi-

nation. The first remembers the location of at least one area of colour or black when targets are fixed during training, with spatial resolution determined by the precision of fixation (Horridge, 1999d). This system discriminates left/right and up/down mirror images (Figs. 5 and 6). The second system discriminates certain patterns of edges irrespective of the location on the target, and is colour blind (Giger and Srinivasan, 1996; Horridge, 1999c), with rapid adaptation to intensity changes and spatial resolution limited by the modulation in individual receptors (Srinivasan and Lehrer, 1988). There is no evidence that the bees remember the individual edges, and locations of edges can be randomized during training. Only the edge cue is remembered, not the pattern (Horridge 1996a, 1997). The radial filters take their inputs from edges not from areas, but the fixation mechanism can also use a large spot or a substantial ring of spots (Fig. 15). When the pattern is made from black bars on a white background, the bees prefer cues from edges, but with fixed areas in colour they prefer locations as the cues.

By techniques described elsewhere (Giger and Srinivasan, 1996), sector patterns can be made of two coloured papers that give no contrast to the blue receptors or alternatively no contrast to the green receptors, where they meet. As long as the bees can fixate in the horizontal plane, the resolution of fixed patterns is little affected by lack of either blue or green contrast (Srinivasan and Lehrer, 1988; Horridge, 1999d), showing that the cue is the location of coloured areas, not the contrast at edges at all. On the other hand, when the cues are derived from edges, discrimination is colour blind (Giger and Srinivasan, 1996; Horridge, 1999c).

4.3. The significance of symmetry

The filters are part of the innate mechanism for the detection of symmetry in the first place. Previously it has been shown that untrained bees prefer a pattern with any symmetry rather than a similar asymmetrical one, and a vertical axis of bilateral symmetry is preferred to an inclined axis (Free, 1970; Lehrer et al., 1995). Bees learn to discriminate bilaterally symmetrical patterns from asymmetrical ones on a vertical surface (Horridge, 1996a,c). Bees use radial symmetry to assist fixation before the pattern is learned or discriminated. They innately detect the axis of bilateral symmetry as they land on a flower, irrespective of pattern (Jones and Buchmann, 1974). Long ago, Friedlaender (1931) found that a square cross is discriminated from a square patch irrespective of its location or rotation relative to the geometry of the target, as if the radial symmetry assists the finding of the pattern. The actual experiments do not show, however, that the bees have discriminated the square cross, only the cue in the radial symmetry of it.

Whether these principles of symmetry detection apply

to other insects or only to honeybees will have to await appropriate experimental tests. Visual responses of insects are closely tied to the behavioural repertoire of the particular insect, and reflect its need to find a mate, a food plant or a prey. In experimental work, the stimulus has usually been a spot, a vertical edge, a light or a natural object, so analysis has not gone far. The need for a general purpose visual system by flying insects, enabling them to chase mates or prey, avoid collisions and land safely, appears to be satisfied by a system that detects moving contrasts of the right size and measures the range and direction of moving edges without an analysis of pattern at all (Horridge, 1987; Lehrer et al., 1988).

4.4. Radial filters and flower shapes

Flowers evolved after the insect visual system had been functioning for about 300 million years, so their radial symmetry must have been adapted to the existing visual circuitry of the insects of the time. Probably insects which became pollinators first modified their system for detecting the visual flow field in flight by adding a non-specific mechanism for detecting any radial symmetry to assist fixation on the flowers. This is now the strongest system that uses radial edge cues. It is colour blind and detects contrast against green, not flower colour (Horridge, 1999d).

The detection of a radial pattern with a radial filter is independent of range, which is such a favourable combination for discrimination that it is unlikely to be fortuitous. The flowers, correspondingly, have radial and tangential edges or a ring of petals. They are not spiral, as in Fig. 12, or striped or randomly spotty. Flower symmetry appears to be adapted to the innate fixation requirements of the bee and promotes landing on the centre.

The radial and orientation detectors depend upon edges and are colour blind. The flat colours of flower petals are adapted to the bees system that detects locations of areas in colour, about which we know little as a pattern discriminating mechanism. For the bee the edges of the flower usually have green or yellow contrast against a background of foliage or dirt, but the results with artificial patterns suggest that radial edges in the pattern play a small part in the bees' choice of flowers.

With vertical presentation, bees can discriminate many fixed patterns that are unrelated to the proposed filters based on symmetry. The cues could be a vertical petal or a tongue below the reward hole (Baumgärtner, 1928) or a contrast at one side, or above or below it (Friedlaender, 1931) or the location of any outstanding contrast. Bilaterally symmetrical flowers, however, often present themselves in the vertical plane. In this case, the bee detects the orientation of the axis of symmetry innately before it lands (Jones and Buchmann, 1974), fixates on it, and each eye looks at one side of the pattern

(Horridge 1996c, 1998). A detector of a vertical axis automatically acts as a measure of the perfection of bilateral symmetry.

Flowers are frequently flat to land on and the arrival directions of the bees vary, so that their features are effectively randomized by rotation in the horizontal plane. The weight of evidence affirms that odour and colour are much stronger signals than shape or number of petals, and I know of no controlled experiments with random rotation of the patterns when the numbers of petals have been manipulated to test the preferences of foraging bees. The results with artificial patterns suggest that some preferences would be found (Fig. 7). The specific filters for three and six radial arms that assist in the separation of some radial patterns of black bars require high green contrast to function at all (Horridge, 1999c). They are probably imperfect and still evolving.

The radial filters could detect the regularity in the first place, promote fixation on it, detect the centre, or fill in a partially obscured outline. But there is a more recently evolved function that has not been considered. The non-specific detectors of radial symmetry are analogue devices, which respond in a graded way. Their responses therefore measure the perfection of the radial symmetry. It is known that the more symmetrical flowers produce the most nectar, and bumblebees prefer flowers that have the more perfect symmetry (Møller, 1995). This is a behaviour pattern that requires a mechanism for the measurement of the perfection of radial symmetry.

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