



Visual discriminations of spokes, sectors, and circles by the honeybee (*Apis mellifera*)

Adrian Horridge*

Research School of Biological Sciences, Australian National University, P.O. Box 475, Canberra, A.C.T. 2601, Australia

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Abstract

A new cue for visual discrimination by the honeybee has been demonstrated. Bees detected the position of the centre of symmetry of radial patterns of spokes, sectors, and circles relative to their point of choice in the learning process, irrespective of the pattern. When trained with one of these patterns versus a blank target, the bees discriminated a shift in the position of the centre of symmetry by as little as 5°, in some cases with unfamiliar test patterns. A pattern of spokes or rings also stabilized the vision of the bees in the horizontal plane so that the position of a plain black area could then be discriminated.

In other experiments, bees discriminated half of a pattern of radial spokes or concentric circles from the other half, cut either vertically or horizontally, and irrespective of scale. Therefore these patterns were not detected by preformed combinations of orientation detectors or global templates with a single output. Instead, the crucial cue for detecting edges as radial or circular was the coincidence of responses of numerous local edge detectors having the appropriate convergence to a hub. Edges that converged towards a hub were detected by the bees as radial, and edges at right angles to these were parts of circles, irrespective of the actual pattern.

Breaking the patterns of spokes or circles into rows of squares spoiled the discrimination if the squares were separately resolved. Alternatively, breaking the pattern into short bars that were separately resolved spoiled the discrimination when the bars subtended less than 3°. The local feature detectors for spokes and circles therefore resembled those of the orientation detectors in being short, independent, and unable to span gaps of more than 3°. In conclusion, radial and circular patterns were identified by the regional coincidences and convergence of local detectors of edge orientation, and the positions of the centres of symmetry were remembered as landmarks that helped locate the reward, but the patterns themselves were not remembered.

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1. Introduction

The topic is not new. In earlier work, bees discriminated between different patterns that were dominated by radial or circular edges, such as flower-like patterns with different numbers of petals (Baumgärtner, 1928; Wehner, 1981, Figure 67), or with different distributions of coloured sectors (von Frisch, 1914; Gould, 1985). Others found that radial patterns were very well discriminated from patterns of circles of similar size and area, irrespective of the exact pattern (Hertz, 1929–1931a–c; Horridge and Zhang, 1995). Untrained bees were attracted to radial spokes or sectors,

but avoided concentric circles (Lehrer et al., 1995). These discriminations were dependent on edge orientations (Horridge, 1999a). More recently it was found that radial patterns with 3 or 6 spokes were easily detected, but radial patterns with 4, 5 or 7 spokes were not (Horridge, 2000d). Radial and tangential edges appeared to be separate cues that were distinguished irrespective of the pattern, but the cues were not defined by experiment.

Recent work on the orientation detectors for straight edges and bars showed that they were short (3° long) and independent, and would not bridge gaps of more than about 3°. Equal lengths of edges at right angles cancelled the orientation cue, so destroying some aspects of texture and pattern, and no global orientation cue could be detected in a line of spots or squares that were resolved

*Tel.: +61 2 6281 2762; fax: +61 2 6125 3808.

E-mail address: horridge@rsbs.anu.edu.au.

(Horridge, 2000a, 2003b). The local orientation detectors behaved as if they responded independently and fed in parallel into large-field collector neurons that indicated something like an average orientation irrespective of pattern. The techniques used in these studies of the orientation detectors will now be used for measuring the edge detectors for radial patterns.

In parallel with orientation cues were quite different cues that were independent of edges. When they learned to discriminate a black shape versus a blank target, bees learned the position of the black area relative to the coordinates of the apparatus, although it was an unnecessary part of the learning process. They discriminated the positions of the centre of black with a spatial resolution of about 5° in the vertical direction, irrespective of the test pattern (Horridge, 2003c). We will later investigate whether they remembered the position of the centre of radial symmetry.

In previous work, bees could not discriminate the left/right interchange of two coloured spots with no green contrast (Horridge, 1999b) or between a target with a rectangle of grey, black or colour on the left versus one with the rectangle on the right (Horridge, 2000c). The explanation was that the bees in flight scan continually in the horizontal plane and they fail to detect the position of an image that is not stabilized on the retina. Friedlaender (1931) discovered that the addition of a radial pattern of spokes made possible the discrimination between the left versus right positions of two black areas. When the bees had been trained with radial spokes adjacent to the rectangles, however, they could discriminate their positions and then retained the discrimination without the spokes. Moreover, patterns that included radial spokes could be moved up or down on the targets without spoiling the discriminations. Her explanation was that the centre of symmetry of the spokes was salient and it provided a reference point. As an introduction to the new work, this experiment was repeated (see Figs. 2a–c) and extended to circles (Figs. 2f–g).

The discrimination of edges as radial or tangential when they lay at different angles to each other was at odds with the discovery that equal lengths of edges at 90° to each other cancelled the orientation cue (Srinivasan et al., 1994). To resolve the discrepancy, I proposed that some edge detectors in radial or circular directions on the eye were grouped into compound detectors that might be called global templates for spokes or rings (Horridge, 1994, 2000b). This proposal was merely compatible with the data, not the result of further analysis. The numerous discriminations of different radial and tangential edges presented a problem because they were independent of the size and details of the patterns, so that many templates would be required. New experiments, described below, now show that numerous small independent detectors of edge orientation converge upon large-field collectors that respond to the coincidences caused by several radial or tangential edges, and the bees remember the position

of the centre of symmetry irrespective of the pattern or scale.

2. Methods

2.1. The apparatus

The apparatus and methods have been unchanged for 10 years (Horridge, 2003a, c and earlier work), and the data published here was collected over the period 1999–2005. The experiments were done under a roof with open front 3 m wide and 3 m high in indirect sunlight. The Y-choice apparatus was made of clear Perspex, the walls lined with clean white paper (Fig. 1). The transparent baffles, 1 mm thick with a 5 cm hole in the centre, were set in a white frame 1 cm wide, 27 cm from the targets. The range from the baffles to the targets controlled the angle of 55° that was subtended by the target at the bees' decision point and allowed the observer to make a sharp decision at each choice. The bees usually exited via the slots over the tops of the baffles.

The targets displayed the patterns on white cards, which could be rotated. During training the target that displayed the rewarded pattern together with the reward, was interchanged with the non-rewarded (negative) target every 5 min to prevent the bees from learning which arm of the

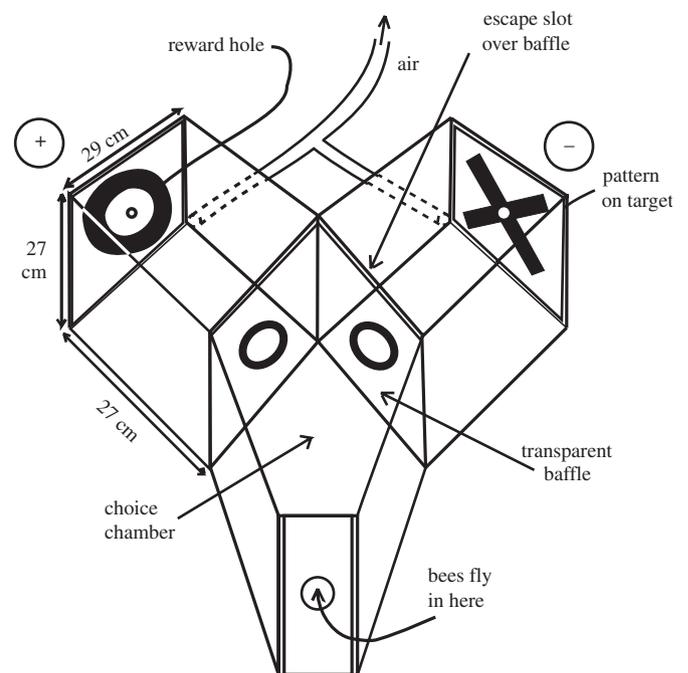


Fig. 1. The modified Y-choice apparatus. The bees entered at the front through a hole 5 cm diameter into a choice chamber from which they saw both targets. They chose to enter through one of the baffles via another 5 cm hole, and usually departed over the baffles into the choice chamber and out the way they came. To prevent the bees from learning which side to go, the targets and the reward changed sides every 5 min. Odours were extracted by the air pipes.

apparatus to choose. In the illustrations the rewarded pattern was always shown on the left (labelled + at the top).

The bees required only 8–12 visits to build up a discrimination between most pairs of simple black patterns on a white background. It took at least 5 min for the bees to return for another reward. After an initial training period of 2–4 h, depending on the difficulty of the task, each first choice in each 5 min period was recorded while training continued. These results were labelled “train”. In other experiments, labelled “test”, a different pair of patterns was substituted for those in the training, and the bees’ first choices towards these were recorded in each period of 5 min. Many test periods on different days were required to build up a count of 200 choices. In the tests it was essential to give a reward, otherwise the bees continued to search in the Y-maze, and would not go away. To prevent the bees from learning during the tests, several different tests were interleaved during continued periods of training. Also, tests were made with one pattern rewarded and then at another time with the other pattern rewarded. At least 6 different tests were interleaved in this way on any 1 day. In most of the critical tests the bees failed to discriminate, so they learned nothing from them anyway. In the tests the bees were rewarded after they had made their only choice in that 5 min period, and they returned to find the training situation again.

Before the experiments started, the bees were familiar with coming to the reward holes at the centres of plain white targets with a reward on both sides of the apparatus. On the morning when training started, a group of 10–15 bees were individually marked with fabric paint and other bees were excluded. The training targets were then put in place. At first the bees did not know where to look or what to look for, so choices were random but after 2 h of training it was possible to start the scoring.

2.2. Scoring and statistics

A new group of 10–15 bees was used for each experiment. Each bee was identified by one of five colours painted on the thorax and on the abdomen, and the criterion for the score was when the bee passed through the hole in one baffle or the other. Unmarked bees were removed. Only one bee at a time was allowed into the apparatus, others had to wait. Only the first choice made by each bee in each period of 5 min was recorded, not the first choice of each arrival. When the next choice was recorded for each bee the patterns and the side of the reward had changed so that the choices were independent. It is far better to design a conclusive test than to struggle with marginally significant test results. The main requirement was a decision whether the bees could or could not discriminate the critical tests. Two statistical calculations were made with samples of constant size. In the first, the correct choices were counted in each block of 20 successive choices, for the tests and the training. The standard deviation (s.d.) between 10 of

these blocks was calculated and placed after each score. The method was arbitrary because the size of the blocks was arbitrary, and any change in the performance made the s.d. too large.

In the second method used in most studies following Friedlaender (1931), the value of $\sqrt{[p(1-p)/n]}$ was an estimate of the s.d., where p was the fraction of correct choices and n was the total number of choices. This method assumes that there were no trends, that the individual choices were independent and they had a binomial distribution about the mean. The s.d. estimated from this formula was given in brackets after each score. By this method a score of 57% based on 200 choices was twice the estimated standard deviation away from the null (random) hypothesis of 50%, and considered to be just significant.

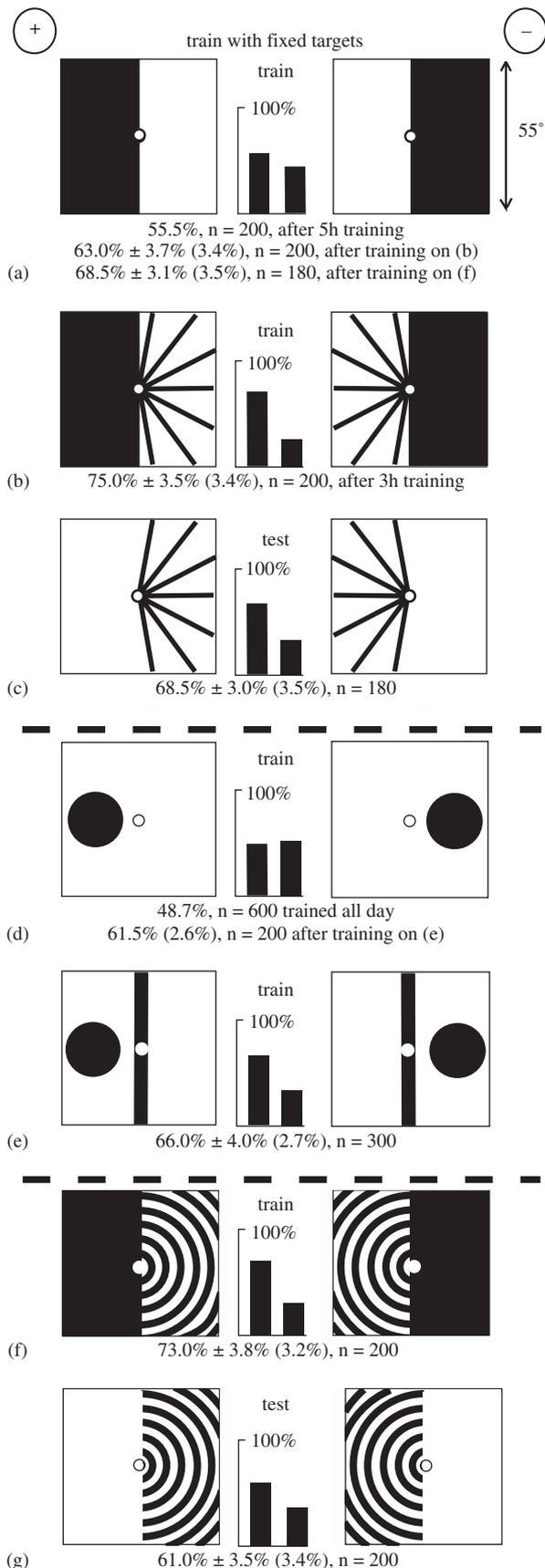
3. Results

3.1. The stabilization of vision in the horizontal direction

Bees in flight are relatively stable about two axes, roll and climb, but their scanning from side to side in the horizontal plane interferes with learning the positions of isolated contrasts. Bees had great difficulty in learning to discriminate between a large black rectangle (subtending $54^\circ \times 27^\circ$) on the left hand side of one target versus a similar rectangle on the right hand side of the other target (Fig. 2a). As already shown by Friedlaender (1931), but not given due credit in the past, when the training was repeated with an additional pattern of 6 spokes radiating from the reward hole at the centre of each target, the score reached 75% correct in 3 h (Fig. 2b). The trained bees could then discriminate the positions of the rectangles when the spokes were removed. They had been trained to look in the right place relative to other landmarks. They were also able to discriminate the positions of the spokes alone (Fig. 2c), and therefore had learned more than one cue.

Similarly, a new group of bees could not be trained with a large black spot (subtending 20°) on the left versus a similar spot on the right (Fig. 2d). However, the positions were easily discriminated when a vertical black bar was added down the middles of the targets (Fig. 2e). The trained bees were then able to discriminate when tested with the spots alone.

In the next experiment a new group of bees was trained with a pattern of concentric half-circles beside each black rectangle, with the same success as with spokes (Fig. 2f). When tested on the rectangles alone, they discriminated well (Fig. 2a). Similarly, they discriminated between the two patterns of concentric half-circles when these were presented in isolation (Fig. 2g). The results in Figs. 2c and g were not consistent with the idea of large preformed global composite feature detectors or symmetrical templates for spokes or circles with a single output, because a single template would not distinguish between left and right sides of the patterns.



3.2. Cues in patterns of thin radial spokes

It is already known that bees did not discriminate the rotation of a right-angled cross (Srinivasan et al., 1994) or between different patterns with equal lengths of orthogonal edges (Horridge, 1996, 2000a), but they discriminated between radial patterns based on a symmetry of 3 or 6 versus others (Horridge, 2000d). The next experiment was designed to elucidate what the bees detected in radial patterns of 4 or 6 spokes.

Bees were trained on a rewarded pattern of 4 thin spokes (each subtending 18° long and 3° wide) versus 6 thin spokes (each $18^\circ \times 2^\circ$) on the unrewarded side (Fig. 3a). Thin spokes were used to avoid substantial areas of black that would be remembered by position. This was a difficult task for the bees and scores reached only 60% after 4 h training, but 65–70% on the second day. Training continued for 3 days, interspersed with numerous tests.

When tested with the 4 spokes versus an unfamiliar pattern of spots of the same total area of black (Fig. 3b), the trained bees failed to recognize the previously rewarded pattern as if they had never seen it.

In tests with the spots versus the pattern of 6 spokes (Fig. 3c), the performance was equal to that in the training, showing that the bees had learned to avoid the 6 spokes. This was an example where the whole of the learning was apparently an avoidance of the unrewarded target.

When tested with pairs of targets displaying straight lines at various orientations, taken from the training patterns, it was clear that the bees avoided the oblique orientations taken from the pattern of 6 spokes (Fig. 3d, e, and other tests not illustrated). In these tests, the lines were duplicated to strengthen the stimulus. The bees had not learned the spokes at 45° to the vertical, or the horizontal one in the pattern of 6 spokes (Fig. 3f).

In this experiment, the bees demonstrated no learning about the pattern of 4 spokes although it was the rewarded one, but avoided the oblique orientations from the 6 spokes. The strong preferences for certain cues and the avoidance of the unrewarded target were familiar from other experiments (e.g., Fig. 10).

In the next experiment the rewarded pattern consisted of 12 radial spokes symmetrically arranged around a central reward hole (Fig. 4a). When trained with this pattern versus a blank target, the bees performed extremely well and discriminated the spokes from an unfamiliar pattern of

Fig. 2. Spokes, vertical edges, and circles acted as reference centres. (a) The left-right reversal of the positions of two black panels was difficult to discriminate in isolation. (b) Addition of radial spokes made the task easy, and the trained bees discriminated the panels alone. (c) The trained bees also discriminated the spokes alone. (d) New bees also found the left-right position of large black spots hard to discriminate. (e) Addition of a vertical bar made the task easy, and the trained bees discriminated the spots alone. (f) New bees easily discriminated when concentric half-rings were added to the panels in (a). The trained bees then discriminated the panels alone. (g) They also discriminated the half-rings alone.

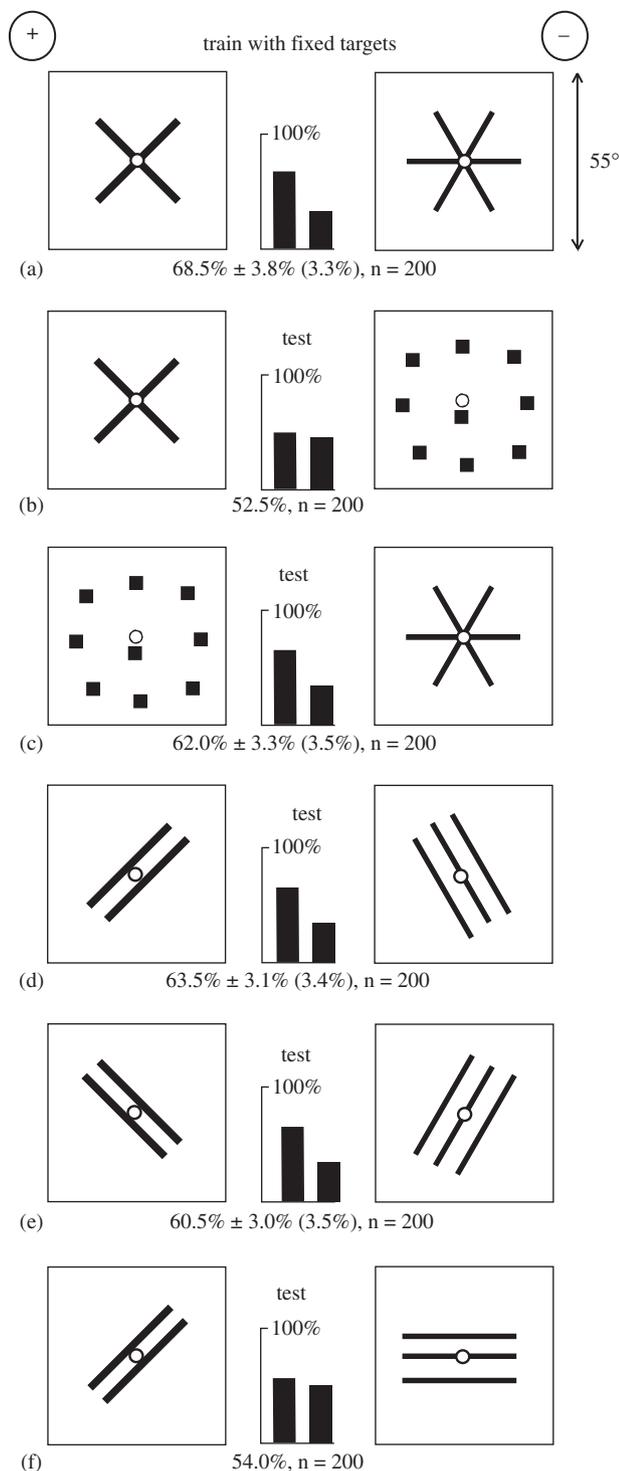


Fig. 3. Learning to avoid the component orientations. (a) Bees were trained to discriminate the 4 spokes from the 6 spokes. (b) The trained bees failed to discriminate between the rewarded pattern and an unfamiliar pattern of spots of the same total area. (c) The spots were discriminated from the 6 spokes. (d–f) Two of the component orientations from the spokes were discriminated.

small squares of the same total area (Fig. 4b), showing that the presence of black or the receptor modulation were not the only cues in the training pattern.

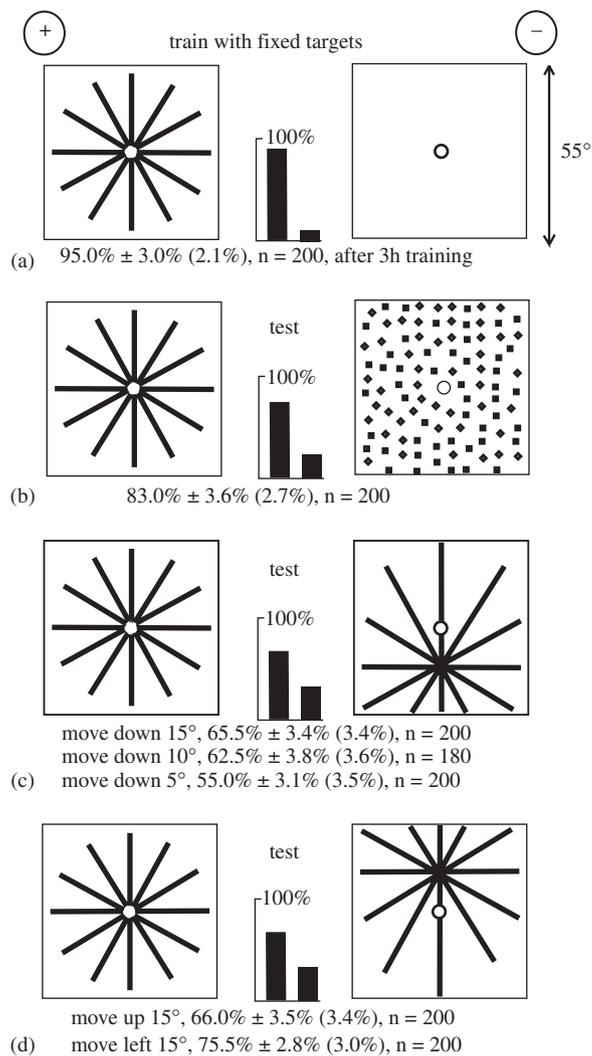


Fig. 4. Bees learned the position of the centre of a pattern of spokes. (a) Bees were trained with a pattern of 12 spokes (1.5° wide) versus a blank white target. (b) The trained bees discriminated the spokes versus a scattering of small squares of the same total area. (c) The trained bees discriminated a downward shift of the spokes. (d) They also discriminated an upward shift.

It was surprising, however, to find that the trained bees readily discriminated the training pattern from the same pattern that was moved down by as little as 5° (Fig. 4c). Similarly, a shift upwards was also discriminated (Fig. 4d). Also, when the training pattern was tested versus the same pattern shifted 15° to the right (not illustrated), the score was 75.5% correct, n = 180. The bees had learned the position of the centre of the radial training pattern, although this detail was not essential to their success in the training.

As they stand, these tests do not show whether the bees discriminated the shift in the centre of black or the point where the spokes converge (the centre of symmetry). Subsequent experiments with sectors or concentric circles showed that they discriminated the positions of the centres of symmetry (see Figs. 8d, 11g, 13b, 14g, 15c, d, g).

The examples of failure to discriminate were more informative. When the trained bees were tested with the thin spokes versus six thicker black bars at 60° to each other (Fig. 5a), they could not tell the difference, at a time when the training score was over 95%. The suggested explanation was that the test patterns both displayed the same total of preferred cues although they were very different.

The trained bees discriminated well between the rewarded training pattern and a radial pattern composed of separately resolved squares that lacked the radial cue (Fig. 5b). They could not distinguish between the training pattern and four small radial patterns of six bars (Fig. 5c), as if both displayed a similar total of cues. The trained bees also confused the training pattern with a similar pattern that was re-arranged into symmetrical parts (Fig. 5d), with a the test score of 58% at a time when the training score was 95.5%. These results showed that the trained bees did not remember the lay-out of the patterns of radial spokes. As long as the orientations of edges, the modulation, and the position of the centre of symmetry were similar, they confused the unfamiliar pattern with the training pattern. However, when tested with the training pattern versus a square cross (Fig. 5e), or versus four small square crosses (Fig. 5f), they discriminated quite well. As already known (Horridge, 2000d), these results confirmed that that six spokes carried a strong cue but four spokes did not (see also Fig. 3).

3.2.1. The local detectors of radial edges

Next, a group of bees was trained with the 12 radial edges versus a scatter of small black squares of the same total area of black (Fig. 6a). This negative pattern was selected with the subsequent tests in mind, so that the bees would not be attracted to disrupted patterns. To determine the size of the local feature detectors for radial spokes, the trained bees were tested with the twelve spokes versus a similar pattern of 12 spokes composed of small squares ($2^\circ \times 2^\circ$) of the same total area, that were separated by small gaps. On different targets, the gaps were adjusted so that the pattern of spokes was progressively changed to a pattern of squares. When the gaps were 4° (Fig. 6b) the score was 80.5% correct, but when the gaps were 2° the score fell to 58.5%. With gaps of 1.5° (Fig. 6c) the bees could not distinguish the two patterns. This result showed that the cue was not the distribution of the areas of black in the patterns, and that the edge detectors could not bridge a gap of more than about 3° . In earlier work, similar results were obtained for the maximum length of the local orientation detectors (Horridge, 2003b).

In the next series of tests (interleaved with the others) the arms of the spokes were composed of short bars of adjustable length that were separated by gaps of 4° to ensure that they were separately resolved. The trained bees were tested with one of these patterns versus the unrewarded training target, which was a scatter of small

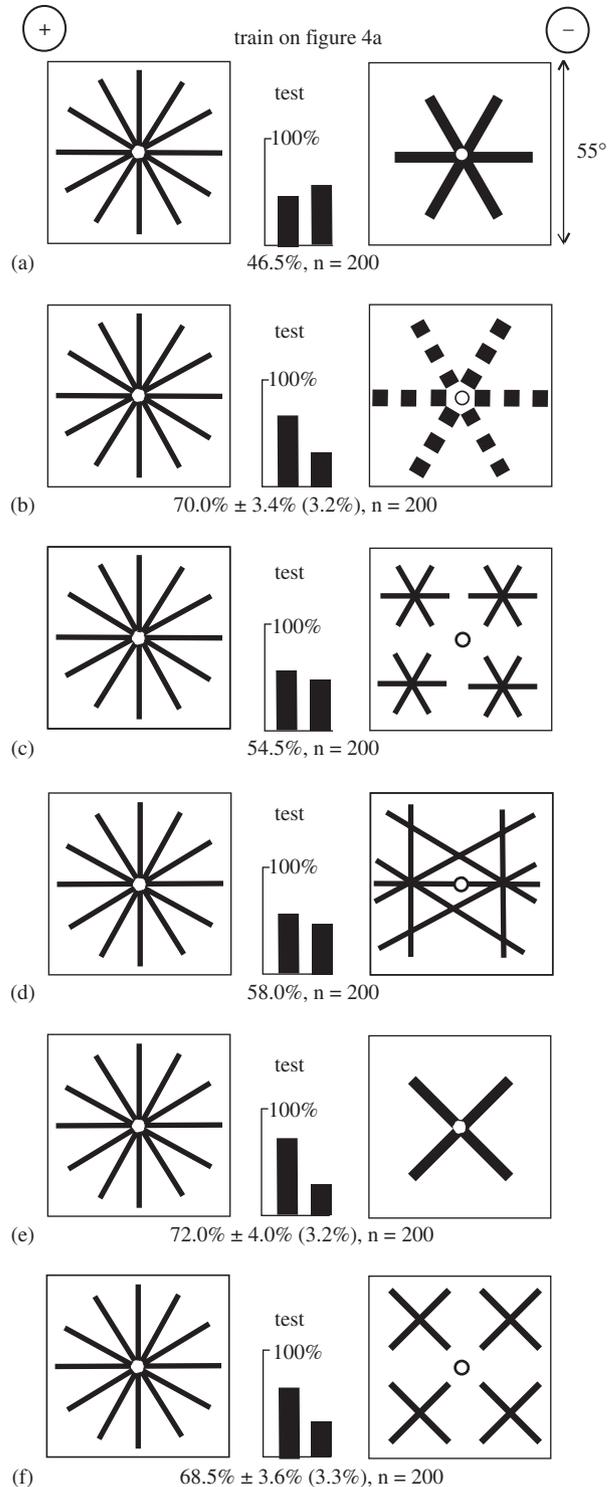


Fig. 5. Continuation of the tests after training on Fig. 4a. (a) Six radial bars were similar to 12 spokes. (b) When the six radial bars were broken into small squares, they differed from the spokes because the radial cues were lost. (c) Four small patterns of six spokes were not distinguished from the training pattern. (d) The training pattern was similar to a pattern with a different lay-out. (e) A large square cross was easily discriminated. (f) Four small square crosses were also discriminated.

black squares (Fig. 6d). When the short bars were 4° or more long, the trained bees discriminated the spokes, but with 3° bars they were unable to do so. Similar results were

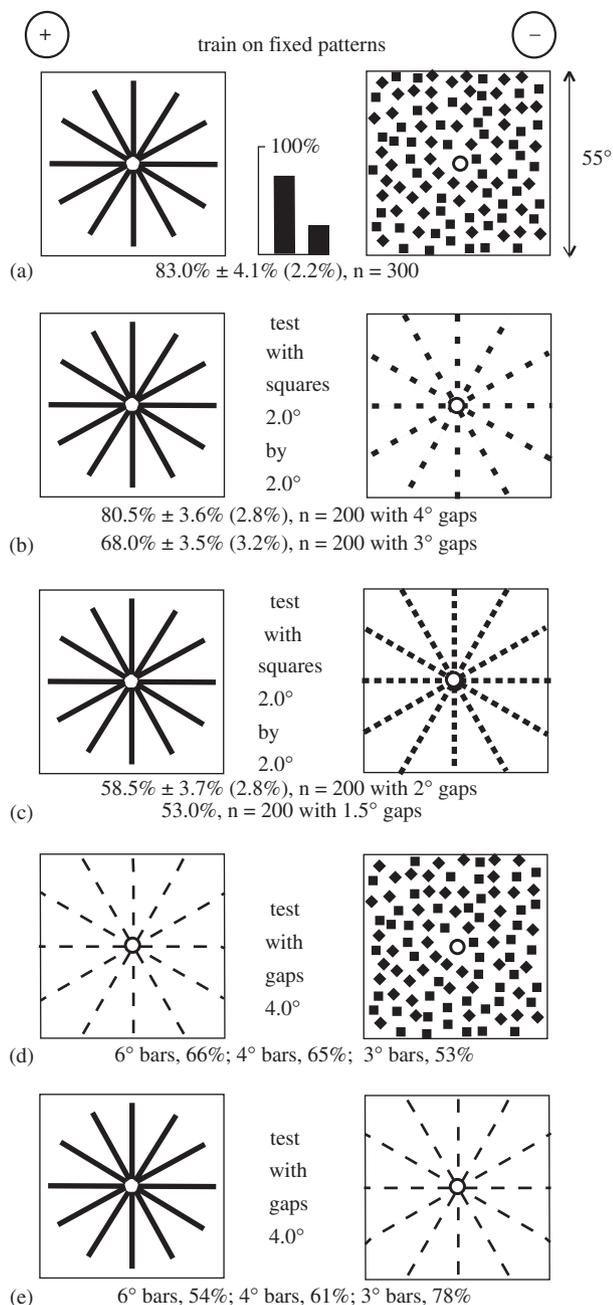


Fig. 6. Measurements of the local feature detectors for radial edges. (a) The bees were trained with 12 spokes (1.5° wide) versus a scattering of small squares of the same total area. (b) The trained bees discriminated between the training pattern versus the same pattern broken into lines of black squares when the gaps between the squares were 2° or more. (c) They failed when the gaps were less than 2°. (d) When tested with the 12 spokes composed of dashes that were separated by gaps of 4°, versus the scatter of small squares, they failed to detect radial patterns with dashes of 3° or less. (e) When tested with the 12 spokes versus the same pattern composed of dashes separated by gaps of 4°, the trained bees failed with dashes of 6° or more.

obtained for the minimum length of the local orientation detectors (Horridge, 2003d).

Similarly, when the trained bees were tested with the training pattern of complete spokes versus the patterns of short lengths (Fig. 6e), they could not tell the difference

between the smooth pattern and the broken pattern with lengths of 6°, but with lengths of 3° the score was 78.0% correct. These results showed that the minimum length of the local edge detectors was about 3°, which was the same as inferred for the local detectors of orientation of straight edges.

3.3. Training with radial sectors

In many of the following experiments, the patterns were 50% black and 50% white, with both black and white areas in all parts of the targets, so that a shift of the centre of symmetry of the pattern on the target had little effect on the position of the centre of the black areas.

In the next experiment the bees were trained to discriminate between a pattern of sectors (period 30°) versus a plain grey target (50% black). Learning was rapid and performance was excellent (Fig. 7a), reaching 90% correct. Discrimination was equally good when the trained bees were tested with the rewarded training pattern versus the same pattern with the centre shifted upwards by 14° (Fig. 7b). There was nothing remarkable in this, because the rewarded pattern was the same in each case, but when the bees were tested with a large spot on each target (Fig. 7c) or with concentric circles (Fig. 7d), they still preferred the pattern with its centre of symmetry at the centre of the target.

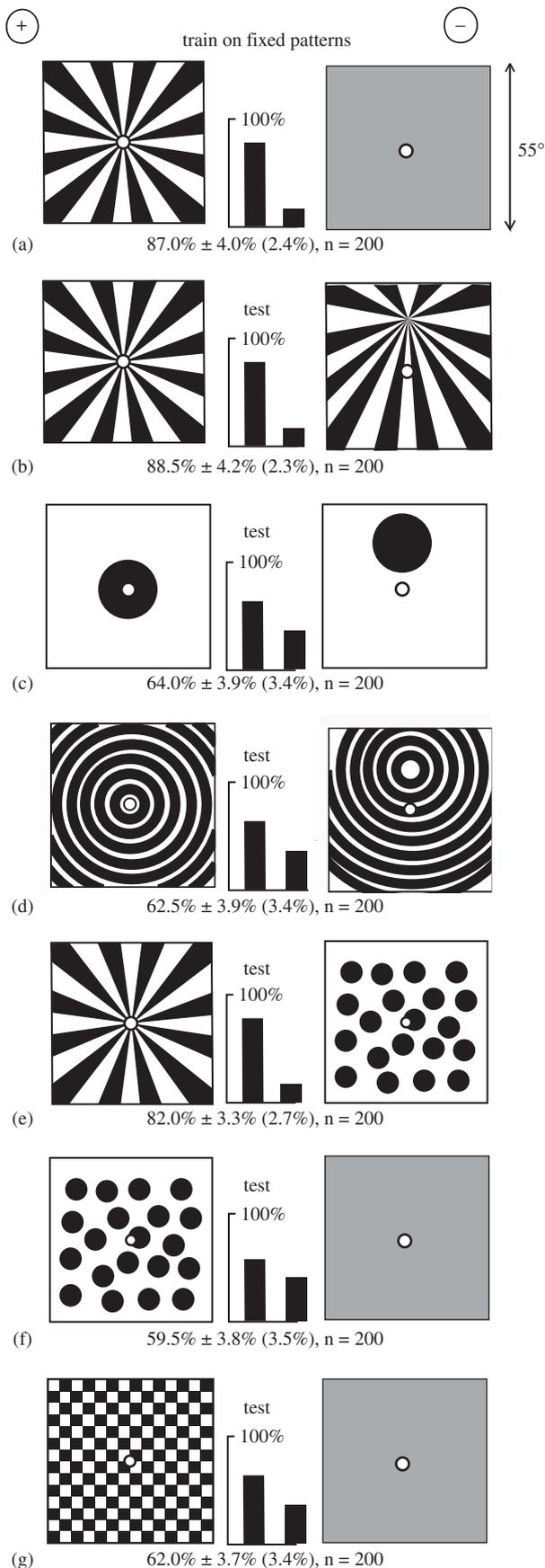
With the rewarded pattern versus 20 black spots (Fig. 7e), the performance was as good as in the training, but with unfamiliar patterns versus plain grey, the scores were low (Figs. 7f, g). Therefore, when the trained bees learned to discriminate the targets in Fig. 7a, the cues came principally from the rewarded pattern.

In the next experiment, the bees were trained with the pattern of 12 sectors versus a pattern of 20 black spots each subtending 6° (Fig. 8a). Performance was excellent, reaching 90% between subsequent tests. The trained bees were tested with the rewarded training pattern versus the same pattern with the centre shifted upwards by 14° (Fig. 8b). The performance was now poor compared to that in Fig. 7b, as if the position of the centre was a less important cue in Fig. 8a. However, the trained bees preferred a spot (Fig. 8c) or a pattern of concentric circles (Fig. 8d) with the centre of symmetry at the centre of the target. They had learned the position of the centre irrespective of the test pattern.

With the training patterns in Fig. 8a, there was some learning to avoid the negative pattern, as shown when the trained bees were tested with a unfamiliar checkerboard and plain grey patterns versus the negative pattern. One of the unfamiliar patterns had a much greater modulation than the training patterns, the other much less modulation, and both were weakly discriminated (Figs. 8e, f).

3.4. Training with halves of patterns of sectors

The next result suggested that a significant cue was derived from the responses to oriented edges that



converged to a centre, and the bees learned the position of this centre.

The rewarded pattern was a half of the sector pattern (Figs. 7 and 8) versus the same inverted (Fig. 9a). Learning was rather slow; 72% after 2 h of training and 80% after 7 h. In the afternoon, the trained bees were tested with the rewarded pattern versus a pattern of black spots each subtending 6° (Fig. 9b), and also with the spots versus the unrewarded training pattern (Fig. 9c). The results showed that both patterns contributed similarly in the training.

With the patterns moved down on the targets (Fig. 9d), the bees discriminated well but they preferred the pattern with the familiar directions of the oriented edges on each side of the targets, not the pattern with its centre of symmetry at the reward hole (see also Figs. 15b, c).

To test this further, the trained bees were tested with a pattern of 3 thin parallel bars on each side of the target, with fixed orthogonal orientations, with similar results (Figs. 9e, f). The trained bees selected the pattern with the correct relative position of the centre of convergence of the bars, irrespective of the training pattern, as shown by testing them also with two black spots in different positions (Fig. 9g).

3.5. Discrimination between a sector pattern and the same rotated

Bees discriminate between a vertical sector pattern and the same pattern that has been rotated by half a period, whether trained on a single pattern versus a blank (Wehner, 1981, Fig. 59) or on one pattern versus the other (von Frisch, 1914; Horridge, 2000d, Fig. 5 therein). For decades, this discrimination was cited as an example of retinotopic memory, but it was merely compatible with that idea and there was no analysis of the mechanism.

A new group of bees was trained with a rewarded pattern of six equal black sectors on a white background versus the same pattern rotated by half a period (Fig. 10a). Performance reached 70–80% in the periods between the subsequent tests after the first day of the experiment. When tested with the rewarded training pattern versus an irregular pattern of the same sectors that were shuffled on the target (Fig. 10b), however, the trained bees could not tell the difference. Clearly, they had not learned much about the rewarded pattern.

When tested with the irregular pattern of sectors versus the unrewarded training pattern, the result was 62% in favour of the irregular pattern (not illustrated), so the bees

Fig. 7. The bees learned the position of the centre of a sector pattern and generalized it to other patterns. (a) When trained on a pattern of 12 sectors versus a blank target the performance was excellent. (b) The trained bees discriminated a shift of the centre. (c) They discriminated a difference in the positions of two black spots. (d) They also discriminated a shift of the centre of concentric rings. (e) They discriminated between the sectors and an unfamiliar pattern of spots. (f, g) Unfamiliar patterns were weakly discriminated from the negative training target.

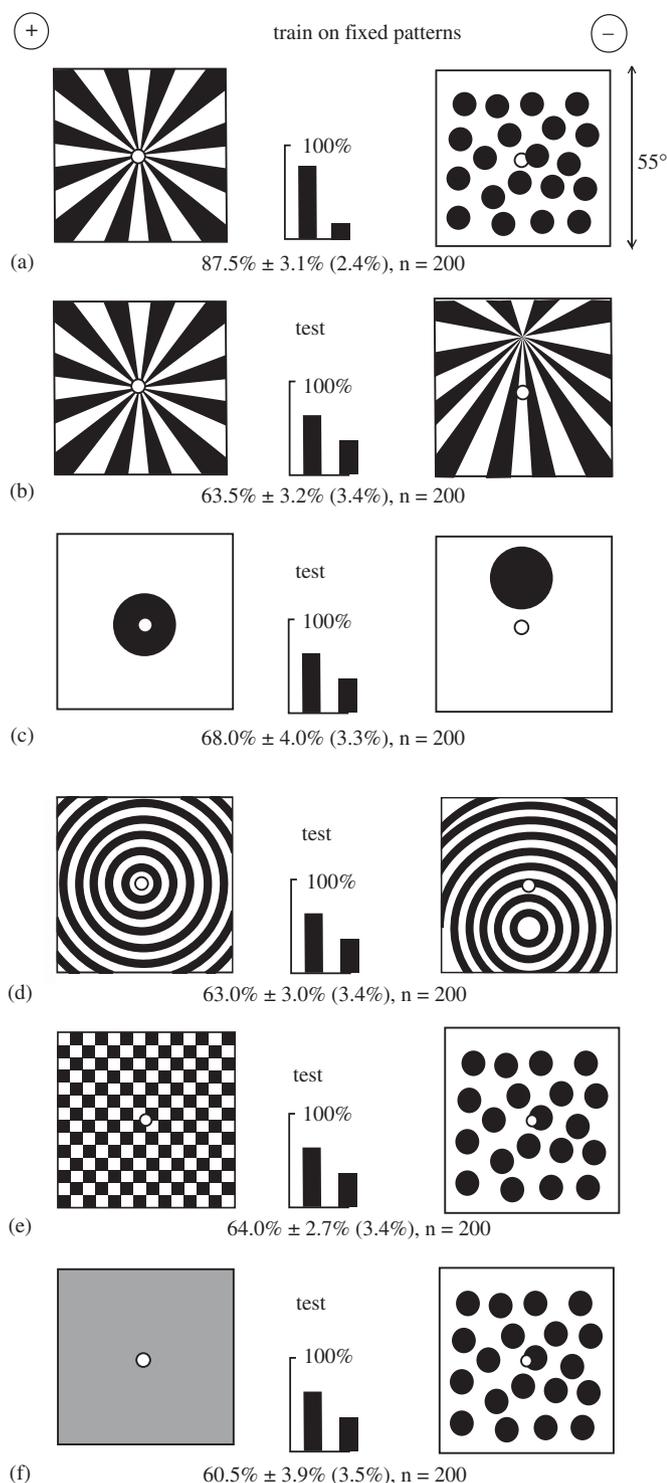


Fig. 8. The bees learned cues from both patterns. (a) The training patterns. (b) The trained bees weakly discriminated a shift of the centre of symmetry of the sectors (compare Fig. 7b). (c) They discriminated a shift of the centre of a black spot. (d) They weakly discriminated a shift of the centre of concentric rings. (e, f) The trained bees discriminated two unfamiliar patterns from the negative training pattern.

had learned to avoid the unrewarded training pattern. The trained bees were also tested with the unrewarded training pattern with the centre shifted upwards by 14° versus the

unrewarded training pattern (Fig. 10c). They did not use the position of the centre as a cue because it had been the same in both training targets.

The trained bees were also tested with the training patterns from which some sectors were removed, to see which were essential. They discriminated well with only two horizontal sectors in the negative pattern (Fig. 10d), but not when these two sectors were removed (Fig. 10e). When tested with the rewarded training pattern versus a ring of six round spots of the same area as the sectors, no part of the negative target was displayed except the positions of the edges. The trained bees preferred the sectors to the spots even though the major areas of black were in the same positions on the two targets (Fig. 10f). Therefore the edge orientations aroused something in the memory. In a similar test with the spots versus the unrewarded training pattern (Fig. 10g), they much preferred the spots, as expected because we already know that they avoided the other. In a forced choice between the two sets of spots, there was a slight preference for the pattern that most resembled the rewarded training pattern (Fig. 10h). The difference in performance between Figs. 10a and h, together with other tests, showed that the bees avoided the near-horizontal sectors in the unrewarded training pattern, with a small contribution from the positions of black.

In this example, principal cues came from the near-horizontal sectors in the unrewarded training pattern, and these would have been relatively stable in horizontal scanning. The bees had not learned the position of the centre of symmetry because it was the same in both training patterns.

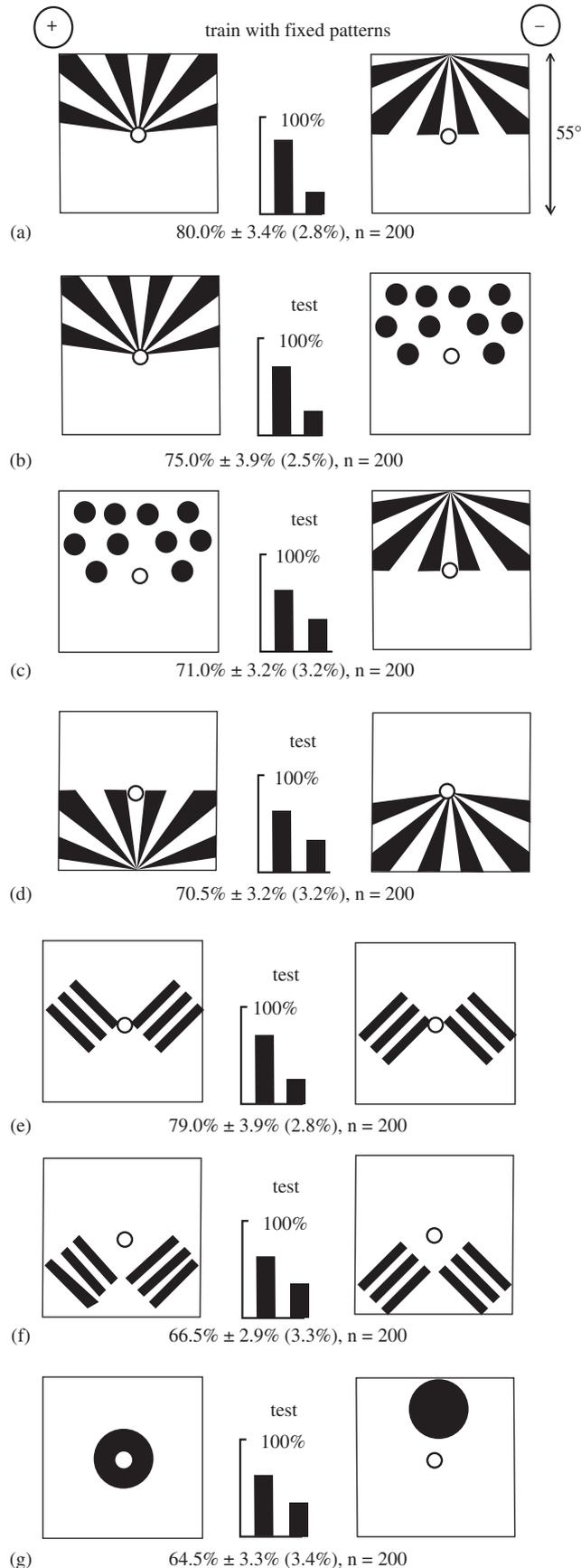
3.6. Circular patterns

3.6.1. Preference against memory of a ring

One might suppose that a bee would recognize a circle or ring with great ease, as is usually assumed in the literature. After all, bees frequently fly through a round hole or approach a circular flower. If you have this view, you will find the following experiments disconcerting.

When a new group of bees was trained with a rewarded thick black ring (ID 18° , OD 33°) versus a blank white target (Fig. 11a) they performed extremely well, as might be expected because they had only to aim for something black. When tested with the training ring versus a pattern of black spots of equal total area, however, they could not recognize the ring that they had been trained on (Fig. 11b). This result scarcely suggested a discrimination of shape.

At another time, a different group of bees was trained with the same thick black ring versus a thick square cross of similar area (Fig. 11c). Discrimination was not easy. The result was 62.5% after 5 h of training. When the trained bees were tested with the ring versus the pattern of spots, they could not tell the difference (Fig. 11d). In both of these examples (Figs. 11a and c), it could be inferred that the bees had learned to avoid the negative targets, and they



failed in the tests because whatever they had learned was not displayed.

Next, a new group of bees was trained with a pattern of concentric rings versus a blank grey target (50% black). The result was 71.5% correct after 4 h of training (Fig. 11e). When the trained bees were tested with the same concentric rings versus a checkerboard of the same spatial period (8°), they could not distinguish between the two targets (Fig. 11f). Again, the bees had not remembered the pattern. The trained bees were therefore also given a choice between the rewarded training patterns versus the same pattern with the centre moved up 15° on the target (Fig. 11g). The score, 62.0% correct, was poor compared to the training score, but it demonstrated that the trained bees could detect the difference in position of the centre although they did not recognize the rings. As in the experiments with radial patterns, they remembered the kind of cue and the position of its centre of symmetry, but they could not remember the lay-out of the pattern. It was another example of the extraction of exactly the minimum requirement for a landmark.

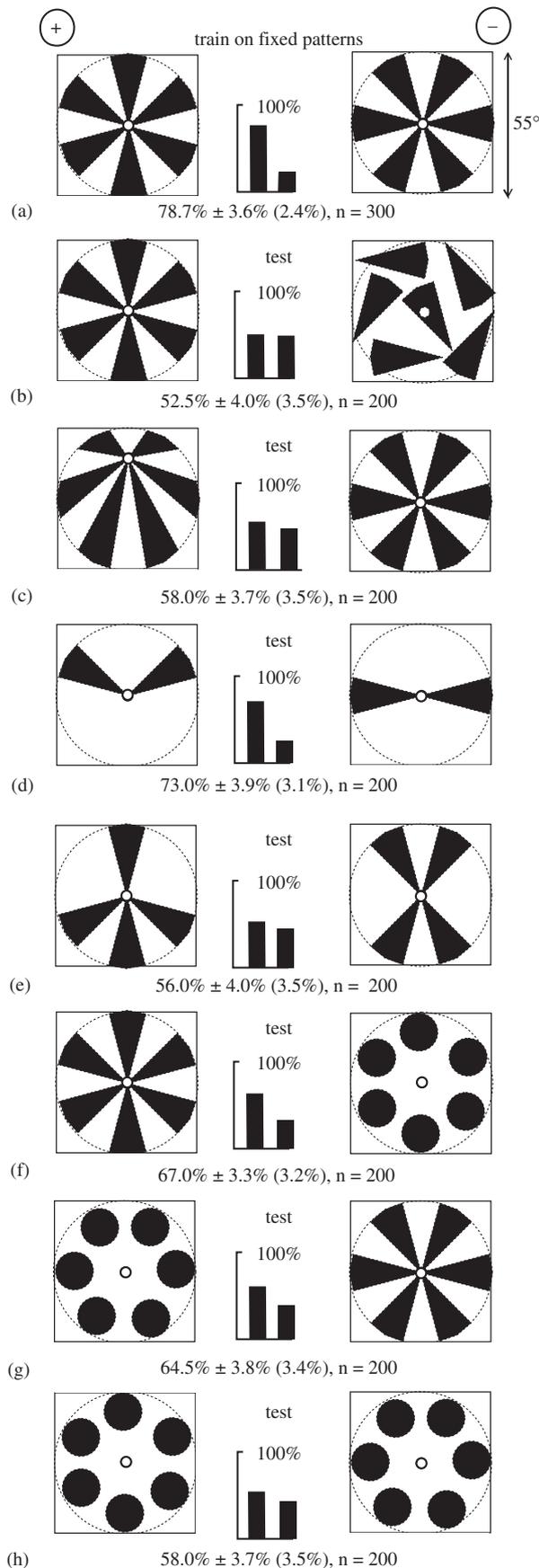
In a new experiment at a different time, a group of bees was trained with two concentric rings versus a scatter of 4° black squares of the same total area of black (Fig. 12a). The trained bees were tested with the two concentric rings versus a diamond pattern of similar total area (Fig. 12b) and also versus a pattern in which the rings were split and turned around (Fig. 12c). In both tests the trained bees failed to recognize which was the pattern that was rewarded in the training. Clearly there was no memory of shape or lay-out. The trained bees were also tested with the pattern of 12 spokes, as an example of an orthogonal image, versus the negative training target of small squares. The result showed that they were not attracted to either target (Fig. 12d). However, they could just distinguish the circles from the radial pattern of spokes (Fig. 12e). These tests, taken together, showed that the bees discriminated the area of black, the modulation in the pattern, the position of the centre, and whether the edges were tangential or radial, but not the shape of the circles.

3.6.2. The units that detected rings

The above experiments show that the bees must have detected the circles because they remembered the positions of the centres. They could abstract this cue from circles, although they did not remember the pattern.

To measure the size of the feature detectors that were excited by circular patterns, the two concentric rings of the

Fig. 9. The bees detected the relative positions of the centres of convergence in two salient patterns, irrespective of the centres of black. (a) The training patterns. (b, c) A test with each pattern in turn versus a neutral pattern of spots showed that both training targets were recognized. (d) When both patterns were moved down, the relative positions of the centres were remembered, showing that both patterns were salient. (e, f) The convergence towards a centre was detected with bars. (g) The relative positions of the centres were remembered when tested with black spots.



rewarded training pattern were divided into short curved bars 2° wide, that were separated by gaps of 4° and were of adjustable length (Fig. 12f). The trained bees were tested with one of these patterns versus the scatter of small black squares. When the short segments were 4° or more long, the trained bees discriminated the rings, but with segments 3° or less they were unable to do so.

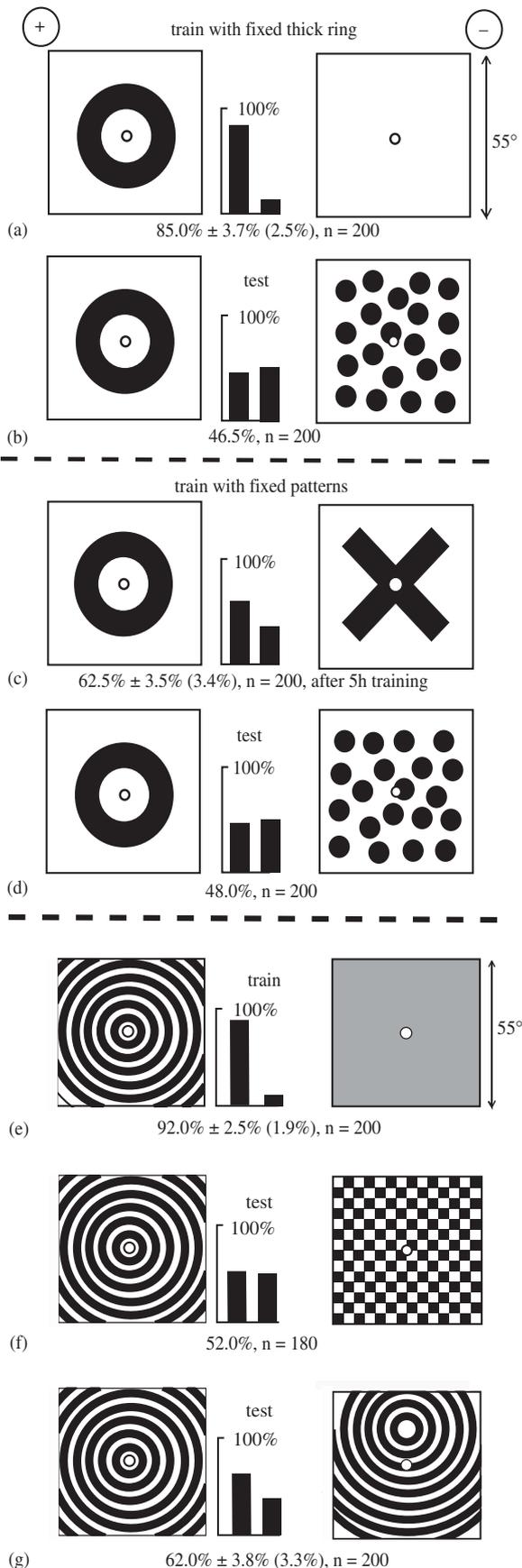
The trained bees were also tested (in interleaved tests) with the two concentric rings composed of small squares ($4^\circ \times 4^\circ$) versus the negative training target (Fig. 12g). The squares were separated by gaps of controlled size, which were different in different test targets. When the gaps were 1.5° the bees detected the rings, as in the training, but when the gaps were 3° or more, the bees could not distinguish the two patterns. These two sets of tests showed that, as with the radial patterns of thin spokes (Fig. 6), the cue was not in the lay-out of the areas of black but it depended on the orientation of each segment of the edges. As with earlier work on the orientation cue, the feature detectors were about 3° long, and could not be strung together to span gaps.

3.6.3. Detection of vertical shifts of the centres of rings

To eliminate modulation as a cue by displaying it on both training targets, a new group of bees was trained to discriminate between the concentric black and white rings and the checkerboard of similar period (Fig. 13a). These patterns are so rich in detail that the bees could never remember them. The score reached 85% correct after 4 h training, however, and was 85–95% correct in some of the training periods between the subsequent tests. When tested with the training pattern versus the same pattern that was moved upwards or downwards by various amounts (Fig. 13b), the minimum discernible shift was about 5° . The discrimination at first improved as the shift was increased to a maximum near 12° , but then fell off at larger angles. When tested with the radial pattern of sectors versus the same pattern that was moved upwards by 15° (Fig. 13c), or with a black spot versus the spot shifted down by 15° (Fig. 13d), the position of the centre was weakly discriminated in these unfamiliar patterns.

When the trained bees were tested with an unfamiliar pattern of sectors (Fig. 13e) or spots (Fig. 13f) versus the unrewarded training pattern, they preferred the unfamiliar pattern, showing that they had remembered to avoid the

Fig. 10. In the discrimination between a pattern of six sectors and the same rotated by half a period, there was no retinotopic memory of sectors, and the cues were the positions of the horizontal sectors in the unrewarded pattern. (a) The training patterns. (b) The trained bees could not tell the difference between the rewarded training pattern and a pattern of shuffled sectors. (c) The trained bees avoided the unrewarded training pattern even in favour of the same pattern with a shifted centre. (d) When tested with two sectors from each pattern the cues were in the horizontal sectors. (e) They could not discriminate when the horizontal sectors were removed. (f) They preferred the radial pattern to the spots when the cues were removed. (g) When tested with six spots they avoided the unrewarded training pattern. (h) The patterns with spots in the positions of the sectors were scarcely discriminated.



negative pattern in the training, but the scores were only 65–70% compared to the training scores of 80–90%. In the training, therefore, both the rewarded and the negative patterns contributed to the score.

3.6.4. Horizontal shifts of the centres of rings

To investigate the effect of a lateral shift in the position of the centre, half of each training target was a blank white rectangle and the other half was a half of the pattern of concentric circles from Fig. 13. Bees trained with the centre at the reward hole versus the centre at the right side (Fig. 14a), reached a score of 75% correct, $n = 200$, by 11.00 am on the first day.

When tested with the mirror images of the training targets (Fig. 14b), the trained bees reversed their preference. As in Fig. 9d, they did not prefer the half of the pattern with its centre at the reward hole. Instead they preferred the half-pattern with its centre of symmetry on the left of the curved lines, as in the rewarded training pattern. This result suggested that the cue lay in the convergence of the orientations of scattered detectors of tangential edges, not in the absolute positions on the target. The detector was a sum of separate responses, not a fixed template with a single output.

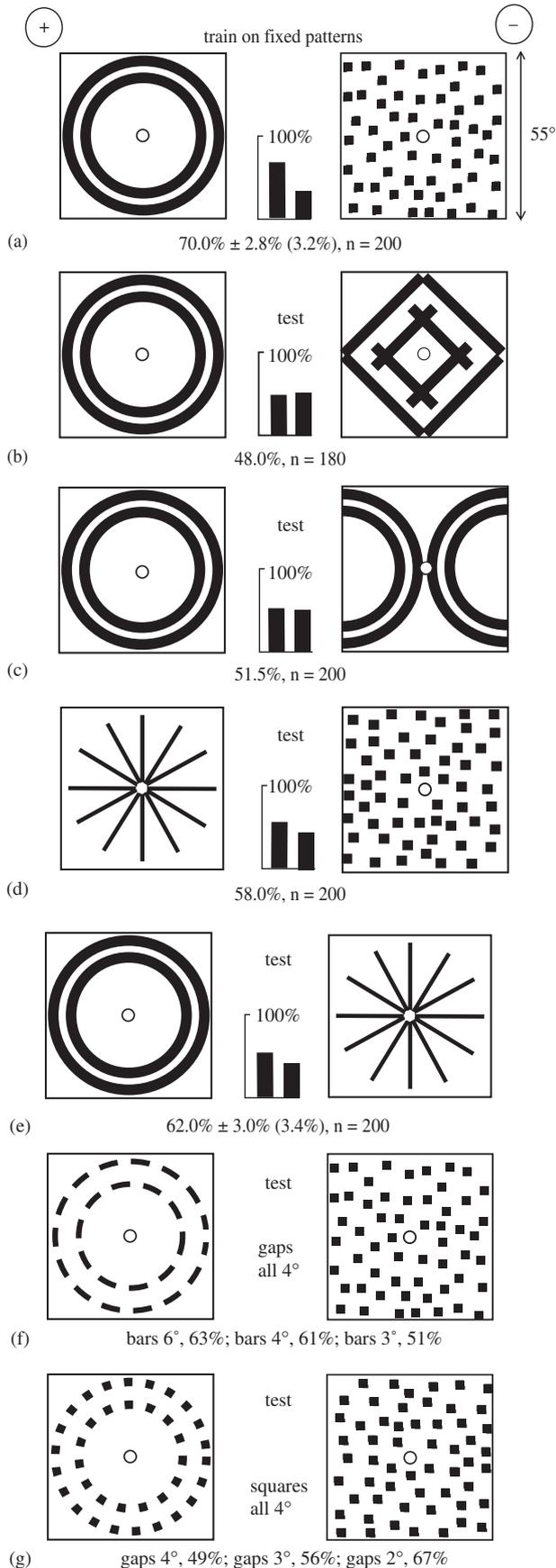
The trained bees were also tested with the mirror image of the rewarded training pattern versus the original negative pattern, so that the both centres of symmetry were on the right of the patterns (Fig. 14c). The bees avoided the negative training pattern, but with a weak score.

To investigate whether the edges had to be curved to indicate the position of the centre, they were replaced by straight bars at right angles to each other (Fig. 14d). Discrimination was not so good as in the training, but still significant. In other experiments, the trained bees could not discriminate between the rewarded training pattern and parallel straight bars that had the same position of the centre (Fig. 14h).

In a further test, interleaved with the others, the black areas around the reward hole were removed in case a difference there had provided a cue (Fig. 14e). The response was 64% correct, showing that these regions of the targets were not vital.

In an effort to find the minimum curvature that indicated a centre of symmetry, bees were trained with the centre of the rings at the reward hole versus a target with the centre of the rings at the top (Fig. 14f). By 10.45 am the score was 66% correct, $n = 200$, and 85%, $n = 100$ by 11.45 am.

Fig. 11. The bees did not learn to recognize a ring. (a) Bees were trained with a black ring versus a blank white target. (b) When tested versus scattered spots of equal total area, the trained bees failed to recognize the pattern they were trained on. (c) New bees were trained with the black ring versus a thick black square cross. (d) In a test versus the spots, the bees failed again. (e) New bees were trained with concentric rings versus a blank grey target (50% black). (f) In a test versus a checkerboard, they could not tell the difference. (g) The trained bees discriminated the upward shift of the centre by 15°.



There is no doubt that this was an easy discrimination. The trained bees were tested with parallel parts of concentric rings of various curvatures. With a radius of 60° (Fig. 14g), the response was 70.5%, $n = 220$. With a radius of 90° (not illustrated), which must have been close to the limit, the response was 55%, $n = 160$. Only small fractions of these rings could be displayed on the targets, but they showed that the bees had a mechanism that detected the curvature of the contours and remembered the position of the centre, or at least the direction in which the centre lay.

3.7. Concentric circles versus sectors

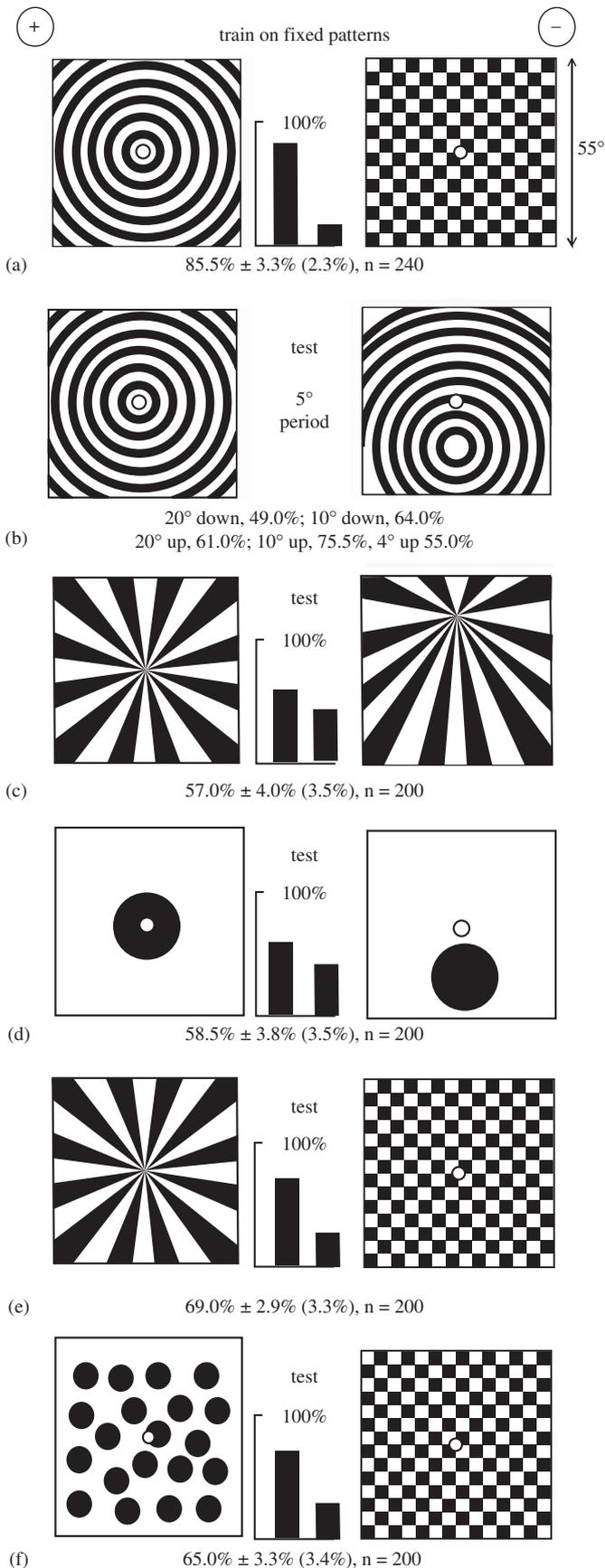
Finally, a group of bees was trained to discriminate between concentric circles versus sectors, with the centres displaced above and below the reward holes, respectively (Fig. 15a). The naïve bees at first strongly preferred the unrewarded target. When tested with both patterns inverted, the trained bees ignored the positions of the centres but remembered the kind of cue and were attracted to the concentric circles (Fig. 15b). They remembered the correct positions of the centres, however, when tested with only the circles (Fig. 15c), or only the sectors (Fig. 15d).

As shown by testing with each of the training patterns versus a blank, they had learned to go to the concentric circles (Fig. 15e), but the training had not completely overcome their innate attraction to the sector pattern (Fig. 15f). They could also discriminate the positions of the centres of black spots (Fig. 15g).

4. Discussion

In all the experiments, the discrimination of the position of the cue required a set of coordinates that were provided by the panorama inside the apparatus as the bees looked through the baffles (Fig. 1). With the apparatus lined with white paper, a contrasting vertical edge or a radial pattern was sufficient to stabilize the visual system in the horizontal direction in flight (Fig. 2). Learning was facilitated by presenting the cue at corresponding positions on the two targets so that it was detected at the same position on the eye in each arm of the apparatus. The most preferred cues on the targets became landmarks in the panorama. Other features of the patterns were irrelevant.

Fig. 12. The bees detected a modulation difference and tangential edges but not the shape of circles. (a) Bees were trained with two concentric rings versus a scattering of small squares of the same total area. (b) There was no discrimination versus a diamond pattern. (c) No discrimination between the training pattern and the same pattern re-arranged. (d) The trained bees showed a preference for a radial pattern versus the negative training pattern. (e) The training pattern was discriminated from the radial pattern. (f) In tests with the rings composed of dashes separated by gaps of 4° , versus the negative pattern, the trained bees discriminated when the dashes were more than 4° long. (g) The trained bees failed to discriminate the training pattern when it was broken into squares separated by more than 3° .



4.1. Detection with and without memory of it

The experiments in which the bees detected the spokes or parts of circles as radial or tangential, and located the centres but did not recognize the patterns, helped to clarify the contrast between detection and memory. The detection of all local orientations of edges was the essential first step. The outputs of the edge detectors were integrated to give only the average orientation in each region and to locate the centres of spokes and circles, which were remembered. Other cues, such as the position of the centre of black, the modulation in the receptors induced by the whole pattern, the area or size, could also be abstracted by parallel pathways from the same pattern, and remembered according to a scale of preferences.

The cues that the bees detected were the inputs of numerous feature detectors that were not remembered individually. The parameters that they remembered were derived from various scalar and vector sums of the responses of simultaneously excited feature detectors, but without memory of the spatial lay-out. The bee visual system could abstract several parameters from the sums and differences of the feature detector responses in large fields but stopped short of any re-assembly.

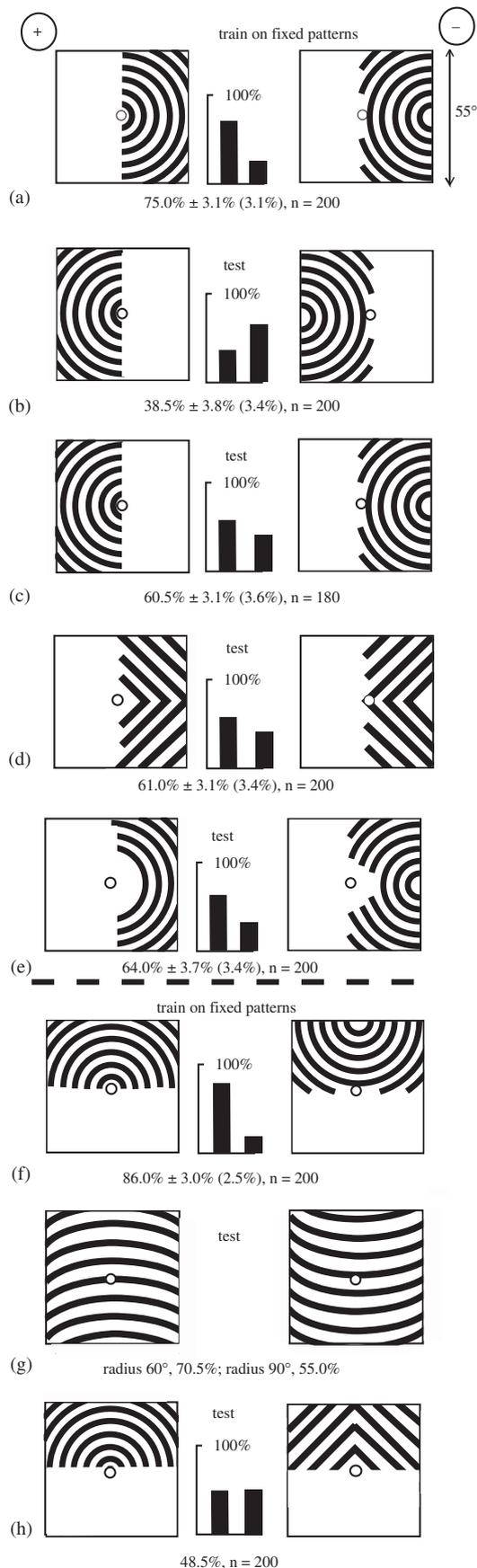
4.2. The bees learned the cues not the pattern

Almost a century ago, von Frisch (1914) worked with fixed radial and circular patterns presented on a vertical surface. The principle that the parameters were detected irrespective of the pattern was inherent in the work of Mathilde Hertz, with many experimental patterns laid out flat on a white table (Hertz, 1929–1931a–c). The parameters identified were the modulation generated by edges from the relative motion of the flying bee, related to length of edge or spatial frequency, and the size, related to area of black (Cruse, 1972; Anderson, 1977). Hertz was convinced that radial and circular patterns also had special characters based on symmetry.

Summarizing a variety of responses of ants and bees, Jander (1964) proposed that simple feature detectors could be the universal mechanism in arthropod vision, in line with new ideas of that time about sensory processing. In his theory, the parameters were detected by feature detectors. It was possible to train with arbitrary patterns, and to test the trained bees on other patterns, because the feature detectors responded to cues, not to patterns. At no time



Fig. 13. Bees learned the position of the centre of symmetry of concentric circles and to avoid the unrewarded pattern. (a) Bees were trained with a pattern of concentric rings of period 5.5° versus a checkerboard of similar period. (b) The trained bees discriminated downward shifts of the centre of symmetry by 6° to 16° and upward shifts of more than 4°. (c) The trained bees failed to discriminate different positions of the centre of symmetry of a sector pattern. (d) There was some discrimination of a shift of the position of a black spot. (e, f) Two unfamiliar patterns were easily discriminated from the negative training pattern.



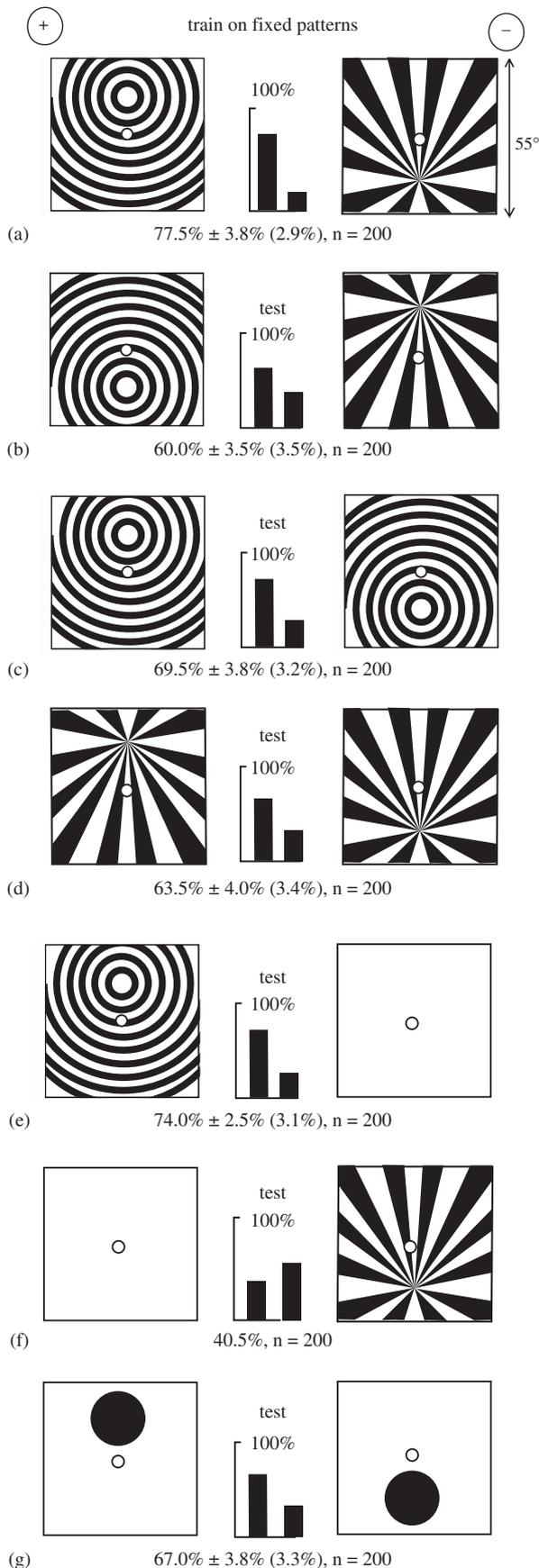
was there solid evidence that pattern or shape was recognized.

A decade ago, we found that bees discriminated well between radial and circular patterns although the targets were regularly rotated (Horridge and Zhang, 1995). Also, naïve bees preferred to go to radial patterns but avoided circular ones (Lehrer et al., 1995), and it was inferred that they had innate feature detectors adapted to these patterns. The mechanism was colour-blind and required green contrast, therefore green detectors alone were involved (Horridge, 1999a). Trained bees could not distinguish between some radial patterns and quite different ones that displayed the same cues (Horridge, 2005a). Now it has been shown that the bees remembered the positions of the centres, irrespective of the patterns.

When bees were trained with a black shape versus a blank target, they learned the position of the centre of black together with other preferred cues, but not the shape (Horridge, 2003a,c). In the new work, when bees were trained with spokes or rings versus a blank target, they were remarkably effective in the discrimination of a shift of the centre of symmetry, but did not recognize the actual pattern. Perhaps we should forget the supposed appreciation of flower patterns by bees. They were interested mainly in the positions of their centres, to use them as landmarks along with other cues.

The limited variety of cues in radial patterns can be inferred now that the appropriate experiments have been done, but it took many trial efforts before the proper experimental strategies were found. The bees learned the most preferred cue, depending on what was available, which could be different in different experiments. In the course of this work, it was realized that thin bars or spokes displayed orientation cues (Fig. 3), but the position of the area of black or colour was also a cue in thick bars. This distinction can be seen in old work (Baumgärtner, 1928; Friedlaender, 1931; Wehner, 1968) but was not explicit at the time. In the present work with thin spokes, the centre of symmetry was derived from the edge orientations (Fig. 3), but with sectors the positions of areas of black also contributed to the discriminations (Fig. 10). A phasic processing channel for edges and a tonic channel for areas have been recognized in arthropods for 40 years (Horridge, 1966a, b).

Fig. 14. Bees learned the position of the centre of symmetry from half-patterns of rings. (a) The training patterns. (b) The trained bees reversed their preference when tested with the mirror images of the training patterns. (c) The trained bees preferred the centre of symmetry to be at the reward hole versus the negative training pattern. (d) Discrimination persisted when the curves were replaced by straight lines at right angles. (e) They discriminated when there was no black around the reward hole. (f) A new group of bees was trained with similar patterns that differed in the vertical direction. (g) When the trained bees were tested with parallel curved lines of radius up to 90°, they responded to the positions of the centres of the curves. (h) The trained bees failed to discriminate the curved edges from straight ones at similar angles.



4.3. Avoiding the unrewarded pattern

Even when bees were trained with a pattern versus a blank target, they did not necessarily learn to go to the rewarded pattern. When presented with a ring versus a blank white or grey, for example, they learned to avoid the blank target (Figs. 11 and 12), but nevertheless they learned the position of the ring (Figs. 11g, 13b).

The preferences were recognized long ago. Bees learned most readily those patterns that they spontaneously preferred (Hertz, 1929–1931a–c). There was an order of preference for the cues, so that when two or more were displayed at the same time, the bees learned one first and more strongly than the others. The order was approximately that found for the spontaneous preferences of untrained bees (Lehrer et al., 1995). Bees in training may learn to avoid the unrewarded target (Figs. 3, 10, 11c, 12) even if it is blank (Figs. 11a, e).

4.4. The significance of the centre of symmetry

The trained bees remembered with high priority the kind of cue and a difference of 5° to 15° in the position of the centre of symmetry in the vertical direction, but not the actual pattern. The position of the centre of a black area (the centroid) was also a cue of high priority that was learned irrespective of pattern with a similar resolution of position (Horridge, 2003c). These were mechanisms that enabled the bees to look for the expected cue in the expected place at the next visit. In general, bees looked for cues only in the places where they occurred during the training. As previously reviewed in detail, the bees recognized a familiar place by the memory of several cues and their positions relative to each other and to other landmarks at the same time (Horridge, 2005a).

4.5. Detecting radial spokes

In earlier work, bees discriminated a symmetrical pattern of six thin spokes from the same pattern that was rotated by 30°, so they had a mechanism that was sensitive to the angles of the feature detectors to the vertical. In the present study, further examples showed that bees had a mechanism that detected that edges converged upon a hub. More detailed tests showed that they detected the orientations of individual edges in the patterns (Fig. 3). The detectors were the same as those measured for the orientation cue. They



Fig. 15. The type of pattern is a more preferred cue than the position of the centre, and sectors are preferred over concentric circles. (a) The training patterns. (b) The trained bees followed the pattern type, not the position of the centre, when tested with the inverted training patterns. (c, d) The trained bees discriminated the positions of the centres when tested with only circles or only sectors. (e, f) The trained bees preferred the concentric circles and also the sectors rather than a blank target. (g) In a forced choice with spots, they remembered the training positions of the centres.

were about 3° long in the centre of the eye and spanned three ommatidia in a row, flanked by inhibitory zones (Horridge, 2005b). To identify a radial pattern and the position of its centre, the experiments suggested that a number of collector neurons detected coincidences between responses of oriented detectors that converged towards a hub, and the edges were then accepted as radial (Fig. 16). The binding that defined the template was not hard-wired but depended on coincidences of responses anywhere.

4.6. Detecting that tangential edges are parts of circles

In the experiments above with circles, there was evidence that the bees detected the area of black (Fig. 11b), the existence of a centre (Fig. 11g), or presence or absence of black around the reward hole (Fig. 11c), and they may have learned to avoid the negative target (Fig. 11, but not in Fig. 12d). There was evidence that a centre of curvature was located by detectors of tangential edges (Figs. 11g, 12f, 13, 14). There was no evidence, here or elsewhere, for the idea that the bees detected the lay-out of whole rings or long curved edges, and much evidence against it (Figs. 11, 12, 13, 14). Rather than learn to recognize a circle, the bees preferred to avoid the negative target.

Regional differences in orientation could be used to indicate the presence of a circle. Vertical edges at the sides, coupled with horizontal ones at the top and bottom, indicated a circular pattern, but this alternative mechanism would not work for small or offset circles.

Bees certainly were able to learn the position of the centre of a ring or of concentric circles when trained versus a blank (Figs. 11e, g) or against a neutral pattern (Fig. 13). They even detected the direction of the centre of parallel curved lines (Fig. 14g), which implied that they detected the direction of the curvature of the edges. And yet I can find no demonstration that bees discriminated a ring or concentric circles by curvature or shape. The parameter was that a majority of the edges were detected as tangential to a hub.

To identify a circular pattern and the position of its centre, there would have to be collector neurons (called hubs) that responded to coincident activity of tangentially arranged orientation detectors. Whether the centre of symmetry was detected first and then the radial or tangential natures of the edges followed, or vice-versa turned out to be the wrong question. The coincidences bound both together in the response of a hub neuron.

There was no evidence for a global template that detected a circle of a given size and the position of its centre; instead, there was a diffuse and flexible mechanism that would find an average centre even for an incomplete pattern.

4.7. A model of the system

For a long time, I thought that radial or tangential patterns were detected by innate compound feature

detectors composed of hard-wired combinations of simple edge detectors (Horridge, 1994, 2005b), but this idea failed to explain the independence from the size or lay-out of the pattern. We need a new model that is independent of pattern or scale. The new experiments have shown that thin spokes and rings were detected by coincidences of typical local orientation detectors. Global feature detectors were ruled out by the successes with radial or tangential half-patterns (Figs. 9 and 14). The global cue was derived from the local orientations of all the edges that were bound together by temporal coincidences.

Three types of feature detectors for edge orientation, each composed of 7 ommatidia, have been previously proposed (Horridge, 2005b). Modulation of the receptors excites a central ridge of three ommatidia and inhibits four flanking ommatidia. One type has the axis vertical and the other two have the axis at 120° to the vertical (Figs. 16a–c). Each of these types forms an array behind the retina (Fig. 16d). These detectors interact locally and signal the local average orientation and its position on the eye. Collectively they feed into collector neurons with large fields that are the global detectors of average orientation in each region.

In addition, each orientation detector feeds into an array of collector neurons for radial edges (feathered arrows) and another array for tangential edges (simple arrows) which sum the inputs. The axes point towards the centres of radial edges and the cross-axes point towards the centres of circles. When edges excite the arrays, a selection of the feature detectors are excited (Fig. 16e), and the coincidences between these excite the appropriate higher order neurons that signal the type of pattern and the position of the centre. The original responses to edges are lost. This general plan, with selections of local feature detectors feeding into large-field higher-level neurons, is characteristic of all sensory processing.

The mechanism of locating a centre by convergence to a hub is independent of pattern and scale. It still requires validation by critical tests. It is familiar in computerized pattern vision when projections at right angles to the tangents converge towards separate hubs that identify positions of objects, but in the bee there is no evidence of a further stage towards of re-assembly of shape.

4.8. The minimum landmarks

As inferred elsewhere, the function of pattern discrimination in the bee is to recognize a place by the coincidences of a few landmarks in different directions around the eye (Horridge, 2005a). They do not see textures, shapes, circles or spokes, but rely on the coincidences of a few types of feature detectors and their retinotopic positions.

Given an array of detectors of modulation and edge orientation but no mechanism of re-assembly of the lay-out of the whole pattern, the visual processing system can still obtain a large amount of information from each region of a visual scene. As in all nervous systems, higher order

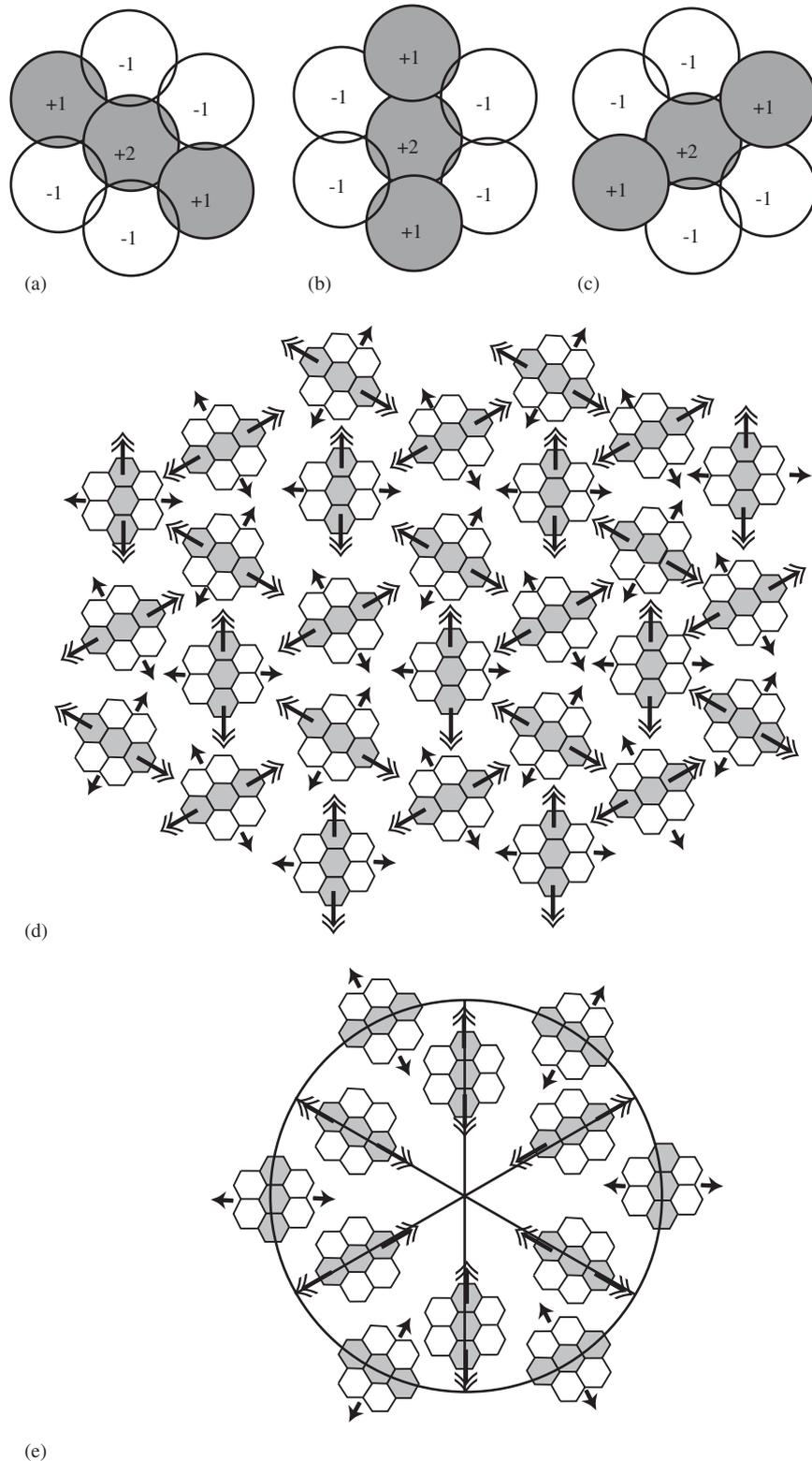


Fig. 16. A model of the feature detectors for radial/tangential cues and their centres of symmetry. (a–c) Three hypothetical orientation detectors as proposed for the honey bee. The circles are equally spaced fields in angular coordinates based on the hexagonal grid of the retina. These detectors are similar to Canny filters as used in machine vision. (d) The edge detectors form arrays. The orientation tangents (feathered arrows) point towards the centres of radial patterns. At right angles to the tangents, the simple arrows point towards the centres of circles. (e) When a pattern is displayed, there is a coincidence of the edge detectors that are excited. The coincidence signals the type of pattern and the position of the centre but not the actual pattern.

neurons detect the temporal coincidences of each kind of feature detector in the array, and the retinotopic positions of the higher order neurons identify the positions of the centres of the groups of feature detectors, or hubs. Different feature detectors are summed by different higher order neurons. The coincidences of the responses of the higher order neurons are remembered and they identify the place. Only a minimum memory of these outputs is required.

In the bee, full use is made of every way that responses of labelled feature detectors can be summed to assist meaningful recognition. Small feature detectors provide good resolution and the enormous convergence improves the signal/noise ratio. The size of the field of each higher order neuron determines the size of the region that it covers. Each feature detector feeds into many different higher order neurons. This circuitry is ideal for locating pre-determined cues quickly on-line. It implies that the feature detectors and the higher order neurons are matched to the useful cues in the image.

Almost all the cues that have been identified so far are insensitive to the range; that is, they are independent of scale or apparent size. The common cues were regions of strong modulation, one dominant orientation, a solid area of black or a colour, a radial or circular pattern, a centre of symmetry, or a small black spot, within each region about 20° across. All cues were linked to a position to identify a place.

5. Conclusion

Vision in the bee, and perhaps insects in general, is apparently based only on the sums and differences of responses of a limited variety of simple labelled feature detectors and their coordinates on the eye. The orientation detectors project parallel to the spokes upon higher level neurons to indicate a centre of symmetry of radial patterns, and are directed at right angles to each edge towards a centre of circular patterns. The coincident responses of each kind converge to separate hubs irrespective of the rest of the pattern. They produce an indication of the type of pattern and an averaged position of the centre, but the layout of the pattern is lost. Patterns of contours of other shapes, on average, also generate hubs on the concave sides of edges. The position of the centre of symmetry is another economical landmark that can be found by a coincidence of feature detectors without re-assembly of shape.

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