11 DO BEES SEE SHAPES?[1]

When the human eye looks at an object, it is almost impossible to avoid seeing its shape. We cannot imagine how we would not see the shape. So it might be difficult for readers to accept the conclusions so far reached—that bees detect cues in simple patterns that they do not see, and remember the directions of cues that enable them to identify places.

It is usually assumed that bees probably remember vague, crude or fuzzy shapes, and that, because they have eyes, the onus of proof lies with those who would show that they do not. The opposite, however, is the case. It is very difficult—in fact, impossible—to show that they remember shapes and quite easy to show that they do not.

Bees can be trained to distinguish between a can of lager and a can of ale, or between a bottle of claret and a burgundy, even with the corks in, as long as the labels differ enough. They easily distinguish between photographs of two different human faces (especially if one has black hair, as in the published example), but it is impossible to show that they see or even detect the whole shape as a shape. In all cases, they might be detecting a small cue that has been learned especially for the occasion, and when tested, this proves to be so.

Going back to Mill's rules (Chapter 2), we see that the general statement that bees see shapes is not true, as shown by numerous examples of pairs of simple shapes or patterns that bees cannot distinguish. When compared with other pairs that were discriminated (Figure 9.14), these examples helped to reveal the cues (Chapter 9).

Having explained much of bee vision by the cues, however, we might have overlooked other ways to detect shape. The only way to find out is to search for them and investigate them one by one.

We have at least three ways to demonstrate that bees do not remember shapes as whole shapes. First, we can show that, when they appear to discriminate between shapes, they in fact use simple cues that can be demonstrated. This is an alternative explanation, but it says nothing about an additional memory of shape unless every example is thoroughly examined. Second, as previously described (Figures 9.14f–j), there are many examples of patterns between which bees cannot discriminate and we can investigate why they fail. This is Mill's method of 'agreement in absence' (of discrimination), which requires numbers of examples to be secure. Third, we can show that although they discriminate between two shapes, bees cannot remember the rewarded or the unrewarded shape that they were trained on when tested versus a different pattern that displays the same cues (as in Figures 11.1f and 11.1g). This positive evidence of absence of recognition of shape is the principal topic of this chapter.

One or several local regions of the eye

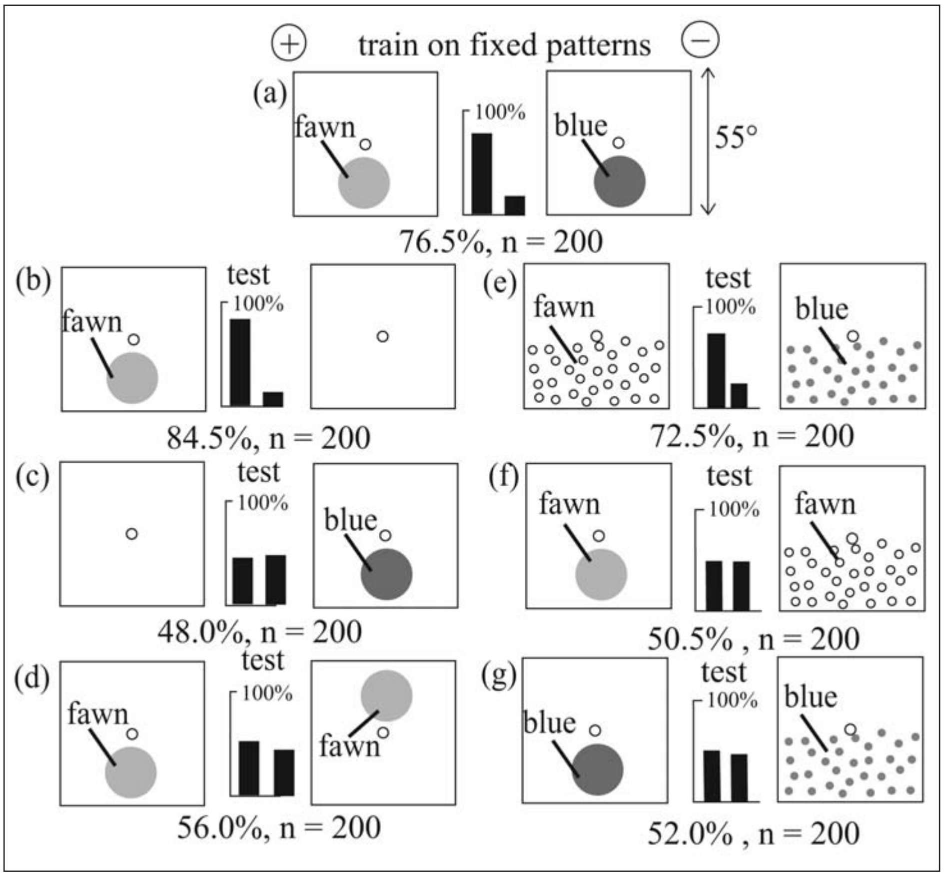
The division of the whole eye into local regions that detect separate cues complicates the situation. Therefore, very large patterns that overlap more than one eye region might be discriminated by the spatial layout of their parts, giving the impression that the whole shape is detected. This was the cause of the difficulties in Chapter 4 and the analysis of results with very large patterns was presented in Chapter 10. Therefore, the present discussion refers to small patterns that are covered by one local eye region. As will be seen, this is the whole story when we are discussing results of recent training with the Y-choice maze. The bees were trained to discriminate the patterns and not to look beyond them because the positions of the targets were changed every five minutes to make the bees look at them to identify the place.

The balance of preferences between two targets

When presented with a choice between two patterns, one of which is rewarded and the other not, the bees ignore most of the cues because they are displayed on both targets. The bees learn them on one target and unlearn them on the other. So, cues commonly displayed equally on both, such as average position, modulation, area or blackness, are not used.

The situation is also complicated by the different preferences for the cues. The bees learn first the most preferred cue, even if they learn to avoid it. This can give the false impression that they learn to prefer the rewarded pattern—for example, when all the cues displayed on the rewarded pattern are identical to those on the unrewarded one, but the unrewarded one displays a unique cue that the bees learn to avoid.

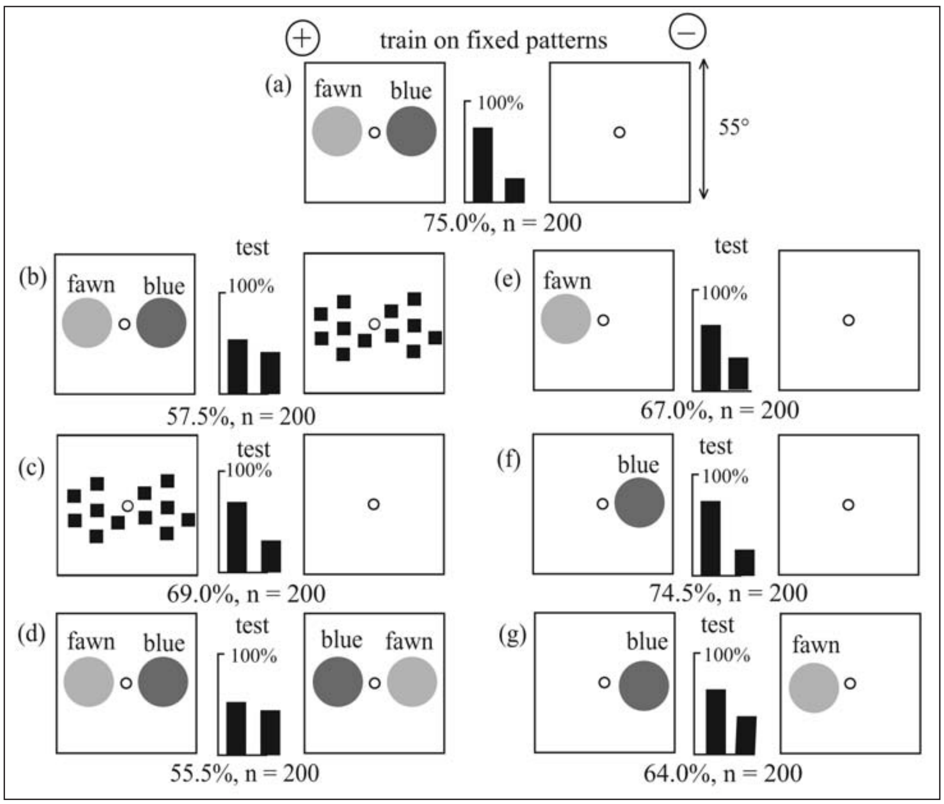
Figure 11.1 The colour cue is detected but not the pattern. a) Training patterns. b) The score was higher when the attraction of the blue spot was removed. c) The blue spot alone was not recognised because the preferences were balanced on the two targets. d) The position of the rewarded spot was not remembered because the training spots were in corresponding positions. e) The trained bees distinguish between the colours of groups of small spots of the same total area. f) and g) They cannot distinguish the large training spots from a scattering of small spots of the same colour; + = rewarded training pattern; – = training pattern without reward.



For example, before training, bees preferred a blue spot to a fawn spot, each subtending 20° at the choice point. When trained to go to the fawn spot (Figure 11.1a) then tested against a plain white target, they in fact preferred the fawn spot more than in the original training (Figure 11.1b), but they could not tell the difference between the plain white target and a blue spot (Figure 11.1c). At first sight, this seems strange, until we realise that the innate preference for the blue spot was not completely removed, but only reduced by the training to the same attraction as a white sheet. The bees' training for the fawn spot was fully revealed when some residual attraction for the blue was removed. What mattered was the balance of preferences.

Because the two spots were in the same place on the targets, the trained bees had not learned their position, as shown by a test (Figure 11.1d). They also had not learned their shape. When tested with the original spot versus a scattering of 40 small spots of the same colour with a total area the same as the area of the large spot (Figures 11.1f and 11.1g), they did not distinguish the targets, showing that they did not remember that they had been rewarded on the large spot. They had learned only the colour cue, not its shape, position or modulation.

Figure 11.2 The landmark indicating the reward displays two different colours, versus a blank white target, but the bees learn only that something lies at the right place. a) Training patterns. b) The trained bees failed to distinguish the training pattern from a group of black spots. c) The black spots are sufficient. d) The trained bees scarcely notice if the colours are reversed. e) and f) The fawn and blue spots alone are adequate. g) In a forced choice between the two, the innate preference for the blue spot was unchanged by the training.



Source: After Horridge (2007), with (g) corrected.

Similarly, when the trained bees were tested with a scattering of 40 small fawn spots versus 40 small blue spots on white backgrounds, the score was as high as in the training (Figure 11.1e). The cue did not have to be in a large spot, implying that a colour learned from a flower nearby could be transferred to the same colour in many scattered flowers further away. There are obvious implications for the evolution of flowering bushes.

In the above training with two coloured spots, the bees clearly detected the fawn and the blue cues separately, because one was rewarded. On the other hand, when bees were trained with the same two spots on the rewarded target versus a blank white target (Figure 11.2a), they appeared to have learned very well. In a test, however, they could scarcely tell the difference between the coloured spots and a black and white neutral pattern (Figure 11.2b) and they responded just as well to the black spots versus a white target (Figure 11.2c). They could scarcely distinguish the training target from its mirror image (Figure 11.2d), so they had not learned much at all. When tested with the fawn and blue spots separately against the white target (Figures 11.2e and 11.2f), the bees' results tell us only that they preferred something to nothing and the blue more than the fawn. When the blue spot was tested versus the fawn one (Figure 11.2g), they preferred the blue, as expected from their innate preference, as though they had learned nothing about the colours in the training.

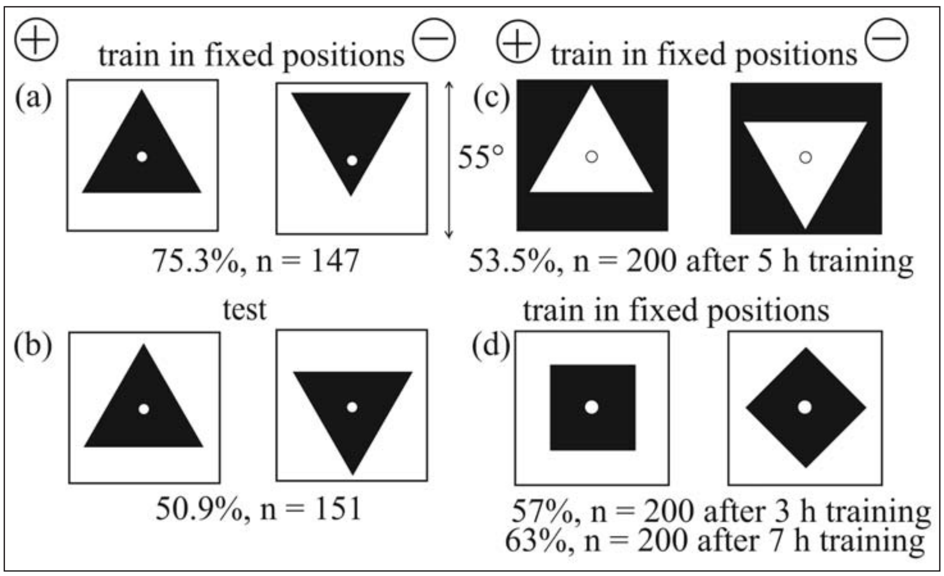
This example reveals very well our initial mistaken trust in the intuitive conclusion that the bees had learned the shapes and the colours. When you first read the early results illustrated in Chapter 1, no doubt you concluded that bees saw the entire pattern and the colours in their places (Figures 1.2a, 1.2b, 1.3)—as indeed was believed and taught for almost a century. There were, however, no tests of what the bees detected and the uncritical conclusions were based on the intuition that was, according to Mill, 'the intellectual support of false doctrines' that he predicted would ruin society. Well, it ruined the science of bee vision—and no doubt a lot else besides.

So, was all the fine talk about scientific method in Chapter 2 just pub talk and *post hoc et ergo propter hoc* claptrap? Did understanding of bee vision advance in fits and starts by myopic steps guided by anthropomorphism and prejudice? Yes, sometimes it did.

In the past, there have been other examples of training with two or more colours on a rewarded target in which researchers have concluded that the bees learned the colours, although no tests were done. They should all be revisited and tested, in case the conclusions were nonsense. Please don't conclude, however, that bees cannot learn two colours. In Figure 11.1, it was shown that the bees could learn a difference between the same two colours. If trained on a pattern displaying two colours versus the same with the colours interchanged (Figure 11.2d), they would learn the difference in the positions of blue, but perhaps no more. The point is that the task in Figure 11.2a did not require them to learn anything about the pattern or colour, which is the common situation when bees learn to detect a solitary landmark.

More clearly than with black and white shapes, these experiments with colours show that the bees learn very little, sometimes as little as learning to avoid one preferred cue, or that anything is preferred to nothing, or everything else is avoided when they are trained to prefer a blank white sheet. We are now in a sufficiently critical mood to doubt whether bees really see shapes, symmetry or anything else that could be graced by an abstract noun. Fortunately, not many examples have so far been proposed.

Figure 11.3 Position is discriminated but not the shape of the triangle or square. a) Bees discriminate the inversion of the black triangle if the centres are at different positions in the vertical direction. b) They fail in tests or fail to learn when the centres are at the same height. c) They also fail when black and white are interchanged. d) They have difficulty discriminating the rotation of a square.



Source: (b) Horridge (1999a).

Bilaterally symmetrical triangles and squares

In 1997, I found that an equilateral black triangle subtending up to 40° at the point of choice was easily discriminated from the same triangle inverted (Figure 11.3a) unless their centres were at the same height (Figure 11.3b). This result made me suspicious of claims of discrimination that required pre-training on other patterns. Even bees that were trained to discriminate the triangles in different positions failed when tested with the centres carefully placed at the same height. The same applied to white triangles on a black background

(Figure 11.3c). The bees detected a difference of about 8^o vertically, but not a horizontal shift. The averaged edge orientation on each side of these triangles is vertical, so cannot be a cue.

Bees are very slow to learn to discriminate between a black square subtending 40^o at the point of choice and the same rotated by 45^o (Figure 11.3d) when the centres are at the same height. Eventually, they learn but the cue is not obvious because edge orientations at right angles cancel out. Of course, very large squares are more easily discriminated.

Mirror-image triangles

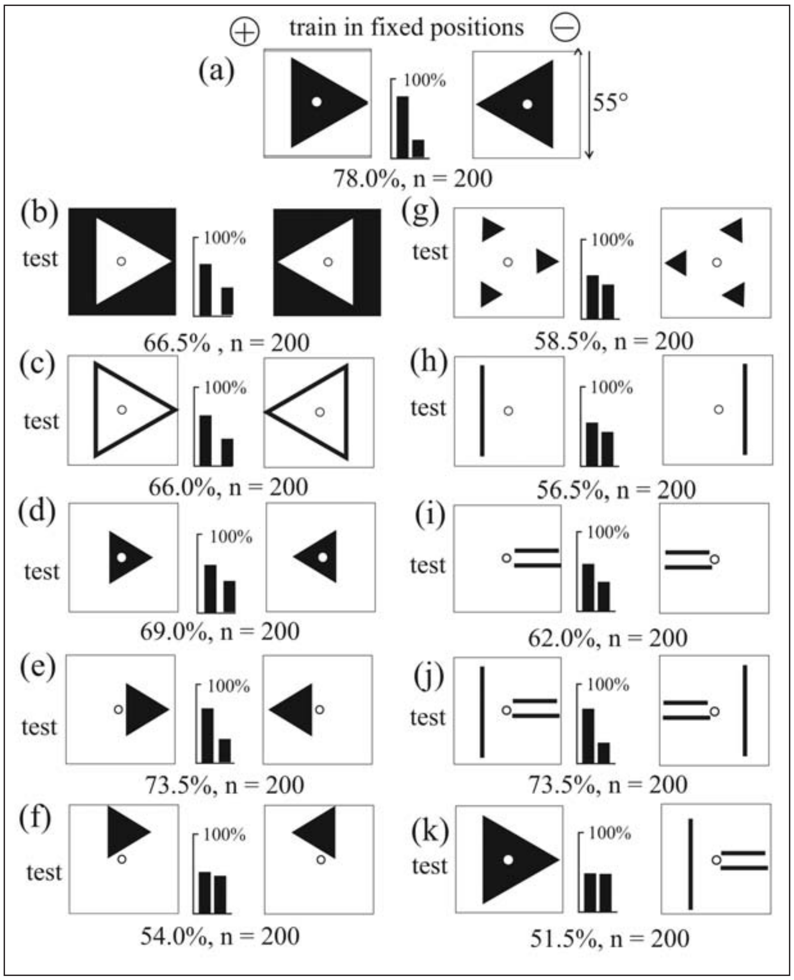
In the past, there have been claims that mirror images are variously favoured in training or confused in discriminations, but the trained bees were not tested to reveal what they had learned. In cue theory, mirror images are nothing special.

Bees very readily learn to discriminate between the black triangle when one side is vertical, versus the mirror image of the same (Figure 11.4a). The trained bees were given a variety of tests. They distinguished the triangles when white on a black background (Figure 11.4b) and with edges only (Figure 11.4c), so the cue was probably in the edge orientation. This cannot be the whole story, or else the triangles in Figure 11.3b would be easily discriminated.

The trained bees easily discriminated smaller versions of the two triangles (Figures 11.4d and 11.4e), unless they were moved in the vertical direction (Figure 11.4f), so positions of parts of the areas were not likely cues—as confirmed by testing with the corners only (Figure 11.4g).

A test of the trained bees with the isolated vertical edges revealed some discrimination (Figure 11.4h). In the training, however, there was a vertical edge on both targets, so the bees must have discriminated the difference between their positions. Following the same idea, the trained bees were tested with isolated horizontal edges (Figure 11.4i) and also with vertical edges on one side of the target and horizontal edges on the other side (Figure 11.4j), with surprising success. Clearly, the difference in the positions of the average orientations of the edges on corresponding sides of the two targets was a cue. Finally, in the crucial test, the trained bees failed to discriminate between the original training triangle versus the horizontal and vertical edges without the area of black (Figure 11.4k). They could not recognise the target they were trained on when it was presented versus a different pattern displaying the same cues in the positions where they had been trained to look for them.

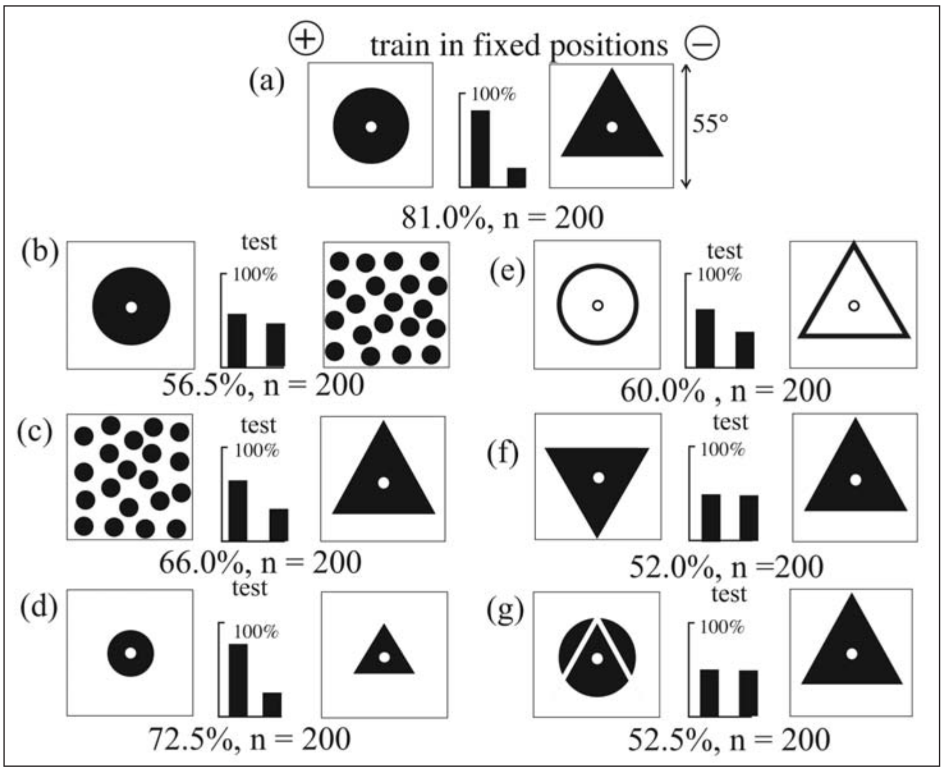
Figure 11.4 In contrast with Figure 11.3, the rotation of the same triangle is easily discriminated when one edge is vertical. a) Training patterns. b–e) The trained bees discriminate when black and white are interchanged, when only the edges are displayed or when the triangles are smaller. f) They fail when the small triangles are moved 12° upwards. g) The differing positions of the areas at the corners have little effect. h–j) The average edge orientation on the two sides of the target is a good cue. k) The trained bees fail to distinguish between the rewarded black triangle and the edge orientations alone, so its shape or black area was of no consequence.



A disc and a triangle

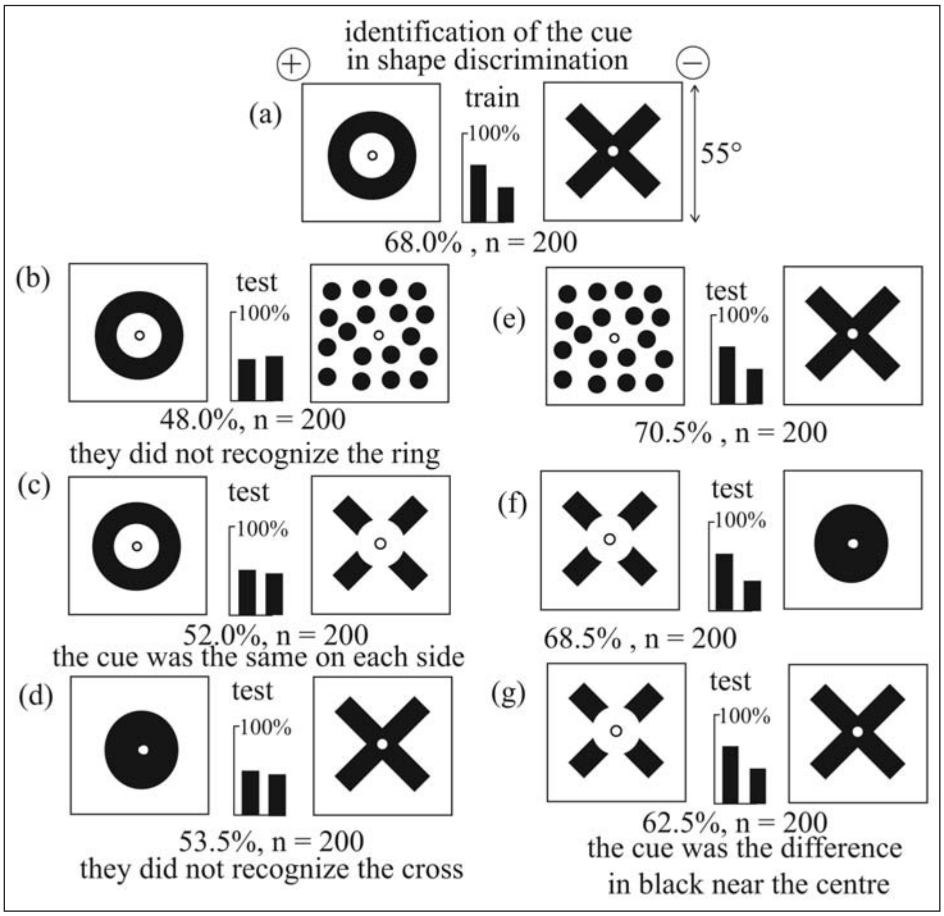
Bees learned to discriminate between a black disc and a triangle of similar area (Figure 11.5a) presented in the Y-choice maze. When the trained bees were tested with the disc versus a random pattern of spots, however, they scarcely recognised the difference (Figure 11.5b). Clearly, they had not learned to go to the disc, as one might suppose from the performance in training. When tested with the spots versus the triangle, they avoided the triangle (Figure 11.5c). Therefore, they did not recognise the disc but they had learned to avoid the triangle.

Figure 11.5 An identification of the cue after training to discriminate between two black shapes. a) Training patterns. b) No preference for the disc versus the spots. c) A similar test reveals an avoidance of the triangle. d) Discrimination does not depend on size or area of black. e) The cue is related to the edges of the empty shapes. f) The black inverted triangle and the triangle at the same centre are equally preferred, so the exact layout of edges is not relevant (compare with Figure 11.3). g) When two oblique lines are added to the disc, the equal preference shows that the cue is the oblique edges on the unrewarded target.



The trained bees discriminated a smaller disc and triangle (Figure 11.5d) and also the isolated edges (Figure 11.5e), but could not distinguish the triangle from the same inverted (Figure 11.5f). This result was similar to that in Figure 11.3b, showing that the bees had not learned the positions of the edge orientations. When white oblique lines were drawn on the disc, however, the bees could not distinguish it from the triangle (Figure 11.5g). Vertical lines serve equally well. Therefore the cue was the average edge orientation on each side. In this case, they did not need to learn the positions of the oriented edges. There was 'absence of proof' that they had learned anything besides the cue, but more importantly, there was a direct demonstration in the tests that they had not learned the shape of either the disc or the triangle.

Figure 11.6 Identification of another cue on the unrewarded target in the discrimination between a ring and a square cross. a) Training patterns. b) and c) The trained bees fail to distinguish the ring from a pattern of spots or a hollow cross. d) A solid black disc is not distinguished from the cross. e–g) The cue is the black around the centre on one target but not the other, irrespective of the pattern; there is clearly no discrimination of shape as assumed by Zhang et al. (1995).



Source: After Horridge (2006a).

A ring versus a cross

This example has an interesting relation to some of the conclusions of previous authors, who assumed that bees discriminated these two shapes. Bees were trained to recognise a large fixed, broad black ring (ID 18°, OD 33.4°) on the rewarded target versus a black cross of similar area (Figure 11.6a). Initially, they avoided the ring innately, but then slowly learned the task. When the trained bees were tested with the ring versus a pattern of spots (Figure 11.6b), however, they could not tell the difference, which suggested that they had learned nothing about the ring.

The trained bees were tested with the ring versus the cross with the centre removed (Figure 11.6c). Now, neither of the test patterns displayed a black area near to the reward hole and the trained bees failed to discriminate. When a black disc (D = 28°) of similar area was tested versus the black cross (Figure 11.6d), there was black around the reward holes on both targets, and again the trained bees failed to discriminate. This result showed that they did not recognise the cross. With the pattern of spots versus the cross (Figure 11.6e), with the cross minus its centre versus the black disc (Figure 11.6f), and with the cross minus its centre versus the intact black cross (Figure 11.6g), they performed as well as in the training, showing that cues were available although the patterns were so altered. Therefore, the necessary and sufficient cue was the white versus black around the reward hole and the real shapes were of no significance at all.

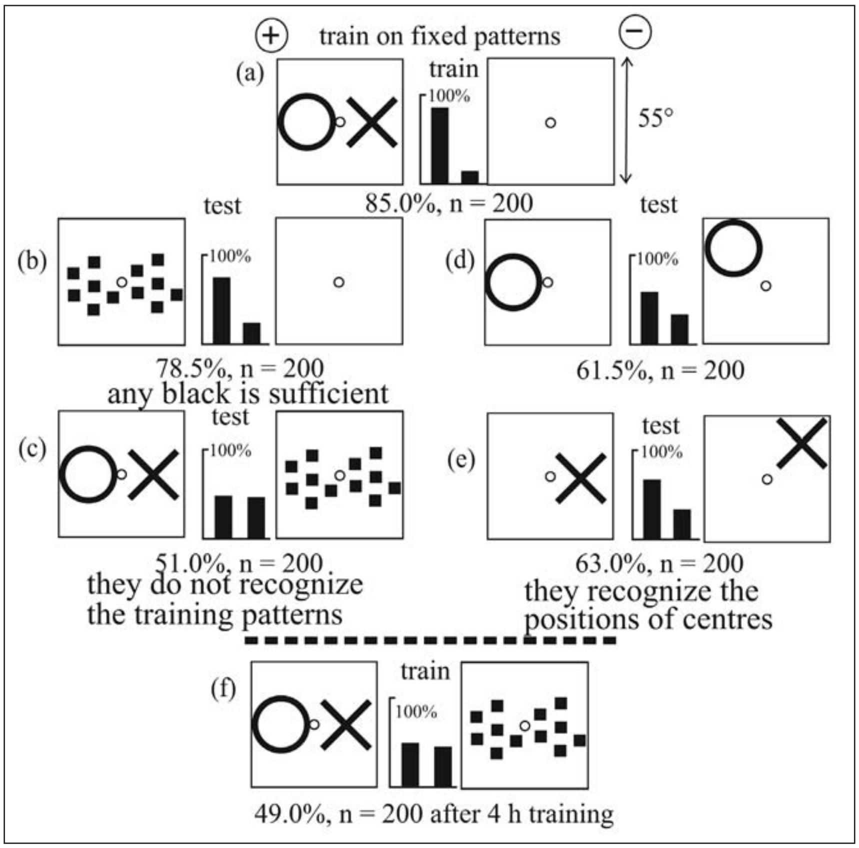
The bees demonstrated quite a subtle way to distinguish between the two patterns. Although we can correct the error of thought that they detected the shape, we cannot say that the bees did not have any other ability to detect something abstract about the patterns. In fact, they picked out the difference in the amount of black around the reward hole, which was a salient detail in the most important direction for them to look (see Figure 1.3).

A ring and a cross versus a white target

The previous experiment showed that when given a ring versus a cross, the bees used the difference in black at the centre as the cue, but learned neither pattern. In the next experiment, the bees were trained with both patterns together versus a white target (Figure 11.7a), as was the normal situation for an isolated landmark. The trained bees performed just as well when tested with a pattern of spots versus a blank (Figure 11.7b), but they failed when tested with the ring and cross versus the spots (Figure 11.7c), so they cared little for the training pattern. They had taken some notice of the position of black on the target, however, as shown by testing with either the ring or the cross in a different position (Figures 11.7d and 11.7e). In a separate experiment, they could not be trained to discriminate between the ring/cross pattern and a pattern of spots (Figure 11.7f).

This result illustrates that the training score is high because the task is easy. The bees detected little more than something on one target and nothing on the other.

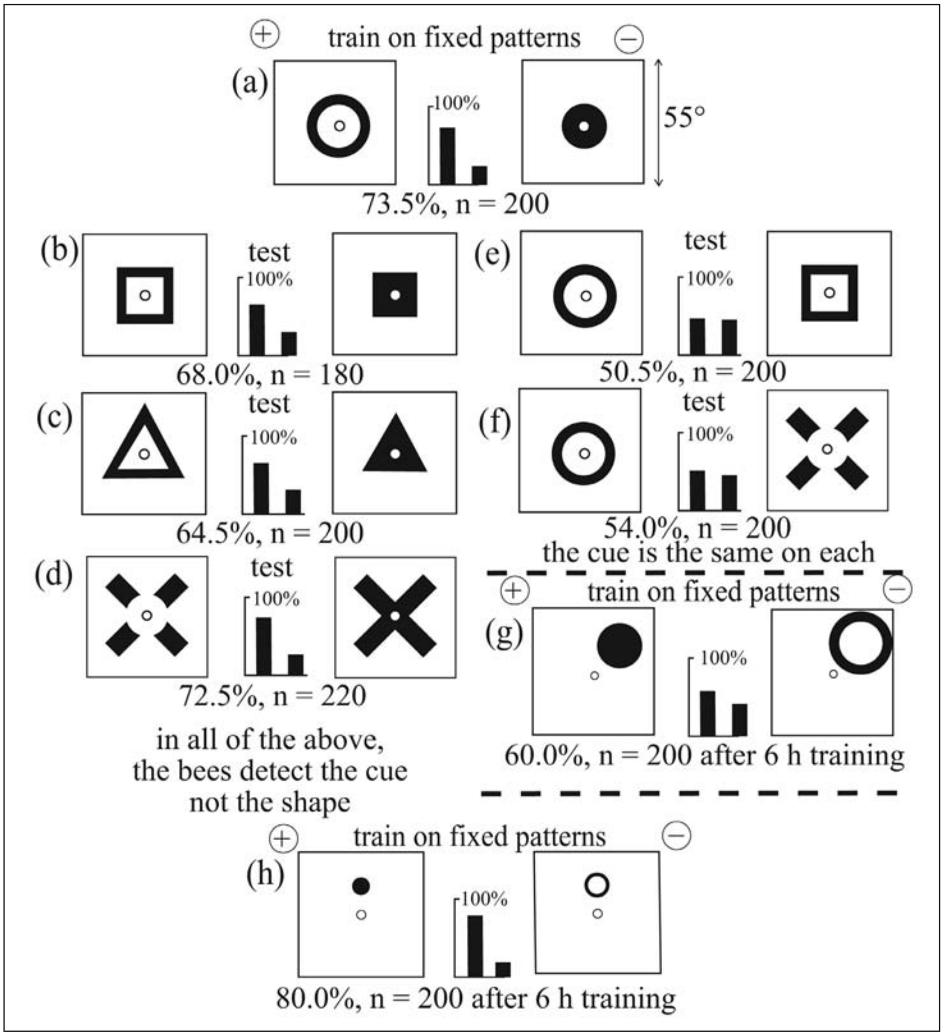
Figure 11.7 Excellent recognition of the place, but failure of the bees to recognise either of two simple patterns—one with circular and the other with radial symmetry—when they were presented together on a landmark. a) The bees readily learned the task. b) The trained bees discriminated 12 squares equally well from the white target. c) They failed to discriminate the ring and the cross from the 12 squares. d) and e) The ring and the cross were discriminated separately from the same moved upwards on the target, so something had been learned about the position of the black areas or the radial hubs. f) In a new experiment, the bees could not learn to discriminate the ring and the cross from the 12 squares.



A ring versus a large spot

This is a pair of shapes like the ring and the cross (Figure 11.6), with a large difference in pattern to the human eye but not for bees. In an earlier study that assumed the discrimination of shape, it was claimed that bees trained on a rewarded ring versus a large round spot could transfer the discrimination to patterned targets raised over a patterned background without further training and could discriminate the shapes by the parallax as the eye moved (Zhang et al. 1995).

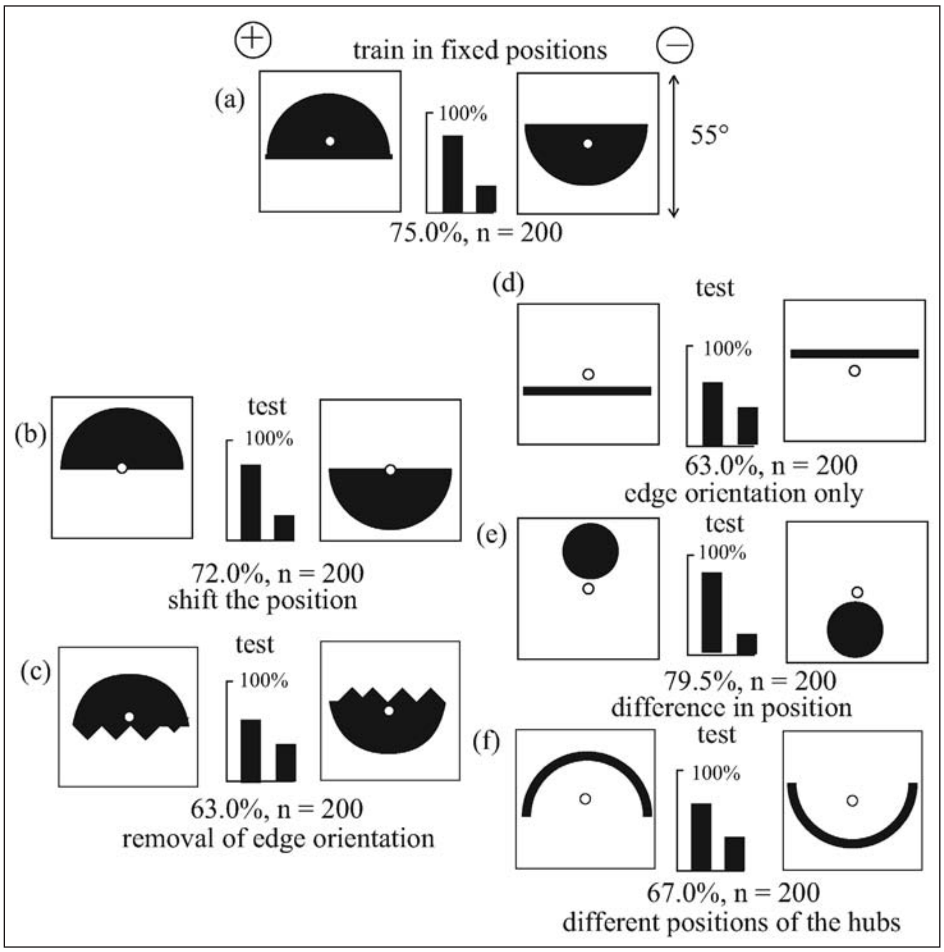
Figure 11.8 With a ring versus a spot, the cue is the black near the centre. a) Training patterns. b–d) As long as the cue is present, the shape is of no consequence. e) and f) Failure to distinguish between the training ring versus a hollow square or a hollow cross because the cue is lacking. g) The poor discrimination of a ring from a large spot when both are offset from the centre, even when the ring is on the unrewarded target. h) Discrimination was excellent between a small offset spot and ring.



In the new experiments, learning was slow because at first the bees avoided the ring, but the score reached 70 per cent after two hours of training (Figure 11.8a). In tests, the trained bees cared nothing about the patterns presented as long as there was a difference in black around the reward hole (Figures 11.8b, 11.8c, 11.8d). When this cue was lacking, the bees failed, irrespective of the test shapes (Figures 11.8e and 11.8f).

The cue works only near the reward hole and bees do not detect it in other positions on the targets. They bees will not learn when trained with the ring and spot offset and the ring rewarded. They learn very slowly with the spot and ring offset and the spot rewarded (Figure 11.8g). They probably detect the modulation difference, which in the spot is half that in the ring. Interestingly, they learn the off-axis task better when the spot is very small (Figure 11.8h), but the cues have not been investigated.

Figure 11.9 A discrimination task in which the bees remembered three cues. a) The training patterns—one inverted relative to the other. b) Moving the patterns in the vertical direction had little effect (compare with Figure 11.4f). c) Removing the orientation of the straight edge reduced the score. d–f) The positions of the straight edges, the positions of the centres and the directions of the curvature were all adequate cues. The modulation, the area of black and symmetry were not learned because they were the same on both targets.



The D shape versus the same inverted

The bees learn this task easily (Figure 11.9a). A small shift of the pattern vertically has little effect (Figure 11.9b), but removing the orientation cue from the straight edge has a greater effect (Figure 11.9c). Three types of cue were easily demonstrated with the trained bees: the difference in position of the horizontally oriented edge (Figure 11.9d), the difference in position of the area of black (Figure 11.9e) and the difference in the direction of the curvature of the curved edge (Figure 11.9f). Each of these differences functioned separately, irrespective of the pattern in the test. In these tests, the bees accepted patterns that were different from those in the training as long as they displayed no unfamiliar cues.

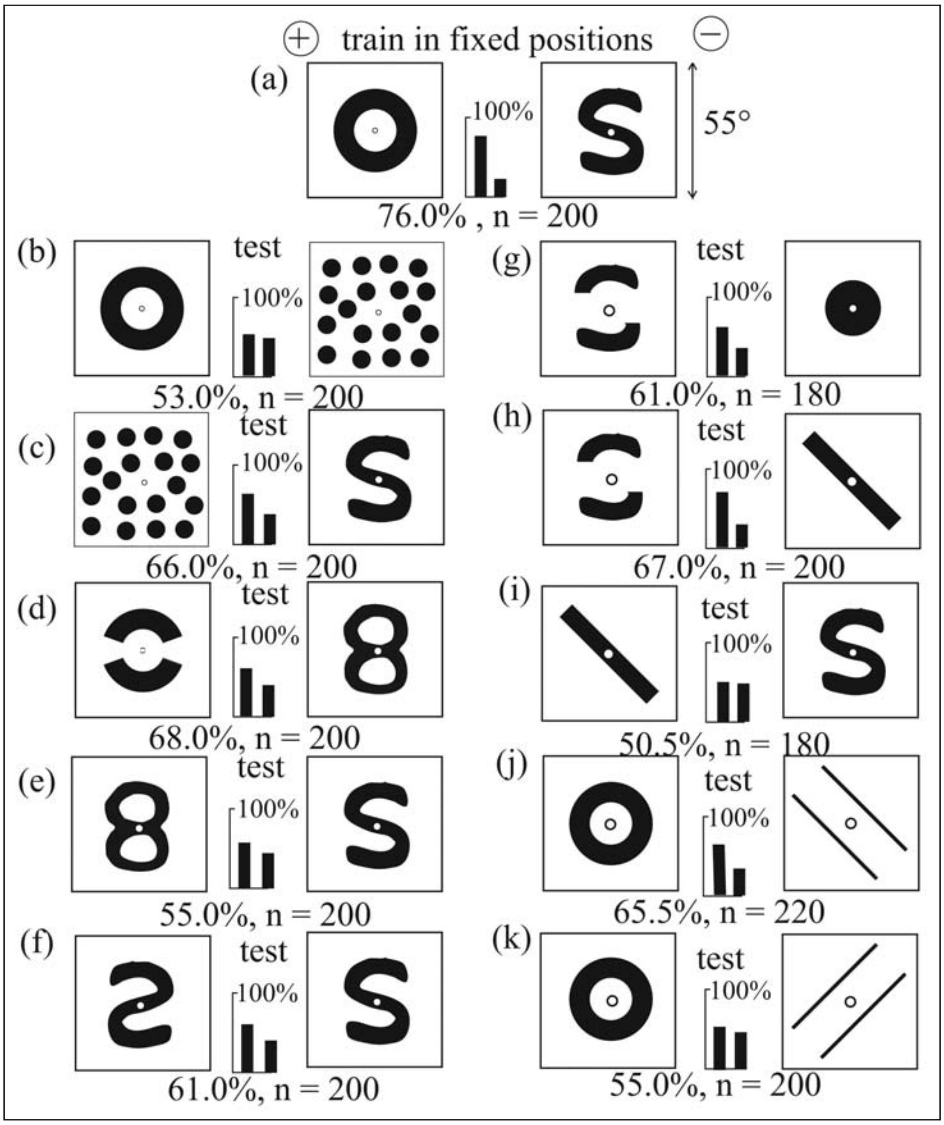
A thick black O versus a large letter S

In this experiment, the bees were trained with a large black O (as in Figure 11.8) subtending OD = 33.4^o and ID = 18^o at the point of choice, versus a large black letter S of the same area (Figure 11.10a). The patterns were the same as those used by Chen et al. (2003). The naive bees detected the O and at first avoided it. As a result, they learned very slowly. After two hours' training, the score was 65 per cent. On subsequent days, tests were done only when the training score was more than 70 per cent.

The bees learned the unrewarded pattern. When the trained bees were tested with the training O versus a pattern of randomly arranged spots of the same total area (Figure 11.10b), the result was 53.5 per cent at a time when the average training score was 78 per cent, so clearly the bees had not learned to go to the O. When the trained bees were tested with the pattern of spots versus the S (Figure 11.10c), the result was 66 per cent in favour of the spots when the average training score was 78 per cent, so the bees had learned to avoid the S more than the O.

The cue was not related to the topology of the shapes. Two gaps were made in the O, each subtending angles of 40^o at its centre, and the broken O was tested versus a figure of eight (Figure 11.10d), with a score of 65.5 per cent. When the figure of eight was tested against the S (Figure 11.10e), discrimination was very poor (55 per cent). Finally, the mirror image of the S was weakly discriminated from the S (Figure 11.10f), with a score of 61 per cent, which suggested that there was an additional cue beside the black near the centre. The topology was not a factor because the trained bees responded similarly to the eight and the S, and it was irrelevant whether the O was open or closed.

Figure 11.10 The cues were unrelated to the topology. a) The training task. b) Failure with the O versus a pattern of spots. c) Test with the pattern of spots versus the S. d) Test with a broken O versus a figure of eight of similar area. e) Test with the figure of eight versus the S. f) Test with the mirror image of the S versus the S; in each of these tests the bees discriminated irrespective of the topology. g–k) The identification of the cues. g) Discrimination of a broken S versus a black disc. h) Discrimination of a broken S versus an oblique bar. i) Failure to discriminate the oblique bar from the S. j) The O was discriminated from the thin bars. k) Failure to discriminate the O from the thin bars rotated through 90°. The cues were therefore the black near the centre and the orientation of the central bar of the S—both in the unrewarded target.



Quite different tests were required to demonstrate the real cues. The same trained bees were tested with the S with the middle section deleted versus a black disc of similar area (Figure 11.10g). They were also tested with the S with its middle section deleted versus an oblique bar with the same orientation as the middle section of the S (Figure 11.10h). These tests, taken together with the tests in Figures 11.10d–f, showed that white near the reward hole was preferred to black near the reward hole irrespective of the rest of the pattern.

This idea was corroborated by showing that the trained bees failed to discriminate the oblique bar versus the S (Figure 11.10i). They had certainly not learned the shape of the S. The O was then tested versus two thin bars with no black near the centre (Figure 11.10j). There was excellent discrimination, showing that a cue was detected, but discrimination was lost when the thin bars were turned through 90º (Figure 11.10k). Taken all together, the results were consistent with the detection of two cues already familiar from earlier work: the black near the reward hole and the average edge orientation at a certain position. The bees did not learn the difference in the topology of the O and the S, although, in the absence of appropriate tests, that was an earlier conclusion (Chen et al. 2003).

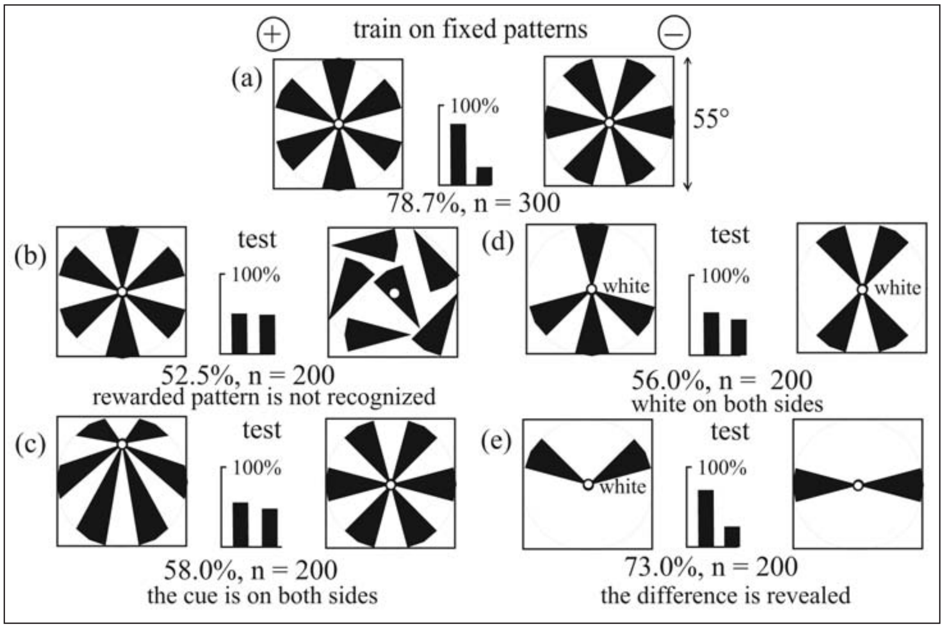
Discrimination of the rotation of a sector pattern

Until quite recently, it was accepted that bees could be trained to remember the layout or the global aspects of a pattern. For example, with reference to a proposed eidetic image of a sector pattern (as in Figure 11.11a), 'insects are able to compare a stored neural image…with a current neural image…has directly been shown in honeybees…The only factor that can account for the bees' ability to discriminate…is the exact retinal position of the black and white sectors' (Wehner 1981:476). In fact , for 25 years, no factors were tested.

To analyse the situation, bees were trained on two patterns of six sectors—one rotated by half a period relative to the other (Figure 11.11a). It was most interesting to discover that the trained bees failed to recognise the rewarded pattern versus the same pattern that was seriously rearranged (Figure 11.11b). The bees had not learned the position of the hub because this cue was the same on both training targets (Figure 11.11c). The trained bees failed when the horizontal sectors were removed from the training patterns (Figure 11.11d), but they discriminated very well when only the horizontal sectors were displayed (Figure 11.11e). This test gave the game away.

So, after 25 years of support for eidetic vision, when the tests were done the positions of the horizontal sectors on the negative target were a sufficient cue (Figure 11.11).

Figure 11.11 The curious discrimination of patterns of sectors. a) Training patterns, one rotated by half a period relative to the other. b) The trained bees failed to recognise the rewarded pattern versus the rearranged pattern. c) The bees had not learned the position of the hub because it was the same on both training targets. d) The trained bees failed when the horizontal sectors were removed. e) They discriminated with the horizontal sectors displayed. The cue in the training was therefore the position of the horizontal sectors on the unrewarded target.



Source: After Horridge (2006a).

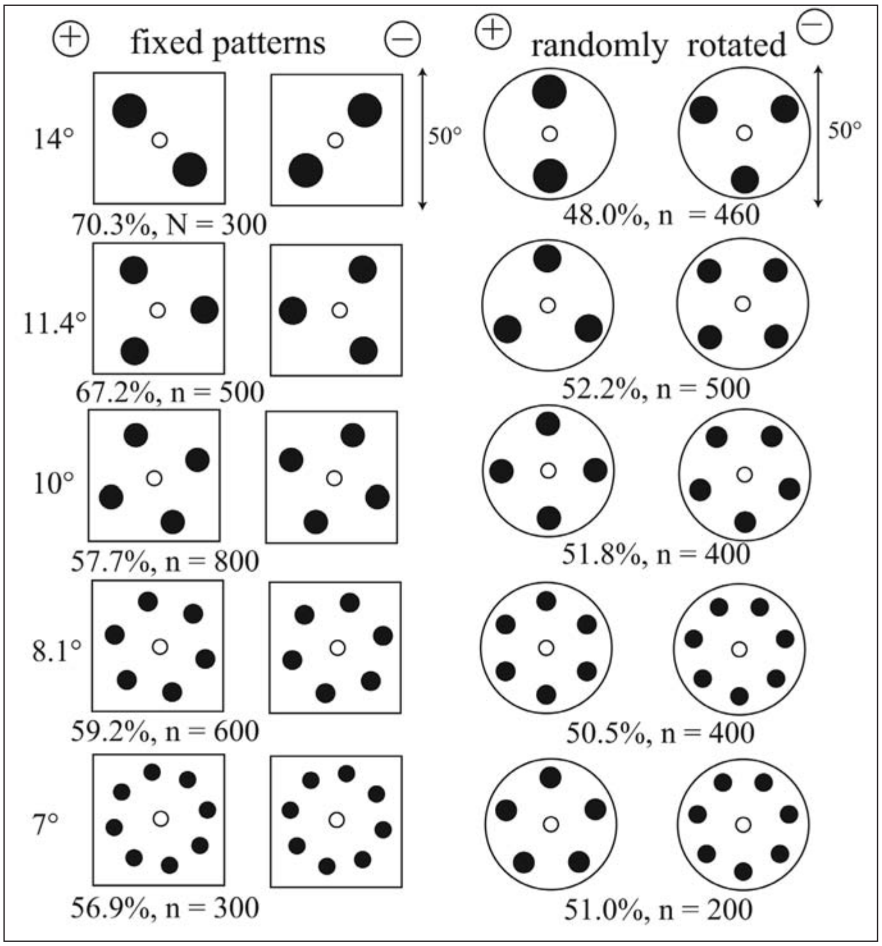
Spots

Lest it be thought that the bees or I favour solitary shapes rather than patterns, I have searched for evidence that bees can count or remember regularities or patterns displayed in groups of spots. Black spots are suitable units because individually they display few cues—namely, area, modulation and position.

First, when the training spots are fixed in position during the training, the bees learn to distinguish between two spots and three of the same total area and something about their positions. The performance depends strongly on the size of the spots but is reduced as the number of spots is increased (Figure 11.12, left side). The performance also depends on the size of the targets and is improved when the spots fall into different local regions of the eye.

When the training patterns are rotated randomly during the training, the bees cannot even learn to distinguish between two spots and three of the same total area, no matter how large the targets or how long they are trained (Figure 11.12, right side).

Figure 11.12 Failure to learn to discriminate the number or spatial layout of patterns of spots. Bees were trained on each pair of patterns separately. Those on the left were fixed in position during the training; the pairs on the right were rotated at intervals during the training. On the left, the positions of a few large spots were learned better than more spots with the same total area. On the right, even the difference between two and three spots was not learned. Previous claims that bees could count had no controls for the position effect.



The same few cues are used every time

The choice of tests was the result of a long history of progressive understanding of the way that bee vision worked. Once a way was found for defining the test set for each pair of patterns that was discriminated, it was possible to discover exactly what the bees had learned in each case. Each example yielded the same general conclusions. They learned to ignore cues that were the same on both targets and they remembered one or more simple cues in order of preference, but nothing about the layout or shape.

This implies that for each pair of patterns that is detected in each local eye region, the bees learn a selection from the same small repertoire of cues. When a new pair of patterns was substituted, the bees were obliged to learn the new situation, using the same order of preference of a few cues. In each context, therefore, they could learn only one task, but in a different context, there would be other cues in other local regions of the eye.

Conclusion

The strategy was to present two fixed training shapes that differed in a simple way. The trained bees were given numerous tests, which progressively identified and refined the cues that they used. Tests that resulted in failures to discriminate were an essential part of the analysis. This process was not a test of a theory of vision; it was a logical investigation of what the bees really detected.

The trained bees did not learn shape in general; they learned to discriminate by detecting and learning the position of one or more simple cues. There are only a few of these cues and they are used over and over again. Different pairs of shapes displayed the cues in different combinations in different strengths. Discrimination of shapes involved the coincidences of cues that were detected together in a local region of the eye, not the reassembly of the layout.

Endnotes

1. It follows from the results in this chapter that when bees discriminate between two shapes they learn something for that occasion only, not the recognition of shapes in general, and also that the performance does not imply cognition.