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Some labels that are recognized on landmarks by the honeybee (*Apis mellifera*)

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Abstract

Freely flying bees were trained in a situation that resembled the natural task of a bee arriving at a foraging site that was located by a landmark. The bees' task was to locate the reward in the arm of the Y-choice apparatus, where a black pattern on a white background was displayed in one arm versus a white target in the other arm, at a range of 27 cm. The alternative patterns for the training included previously identified cues. They were: an oblique bar, three parallel oblique bars, an oblique grating, a square cross, six spokes, a large or a small spot, a spotty modulation, or a ring.

The trained bees were given a variety of interleaved tests to discover the labels they had used to identify the patterns. A label is defined as the coincidence of cues that contributed to the recognition of a single landmark. The bees learned, firstly, the black area at the expected place, secondly, modulation caused by edges at the expected place. These cues were quantified and always available. In addition, the orientation cue was learned from a grating that covered the target, but was ignored in a single bar. The bees learned the positions of the centres of black and of radial symmetry. In tests, they also recognized unfamiliar cues that were not displayed in the training. The cues and preferences were similar to those used to discriminate between two targets. The new experiments validate some old conclusions that have been controversial for 40 years.

Keywords: Honeybee; Vision; Learning; Landmark; Cues; Labels; Filters

1. Introduction

Over century ago, in the belief that it was used as a landmark by the bees, Bethe (1898) cut down a large tree adjacent to his beehive, only to find that there was no effect at all. Decades of more sophisticated efforts led to many descriptions of the bees' use of landmarks, to which the findings below relate, but the details that the bees actually remember have largely remained a mystery. In the long review of Thorpe (1963, p. 258) we find: "the first learning of the environment seems to involve a response in some way to a whole, and—with longer experience an increasing segmentation or articulation of the perceptive field is brought about". More recently, Collett et al. (2002) made artificial landmarks for the bees and concluded that they were used only in the proper panoramic context. This implied that the landmarks were individually recognized, but in a natural scene it is difficult to control the landmarks or the panorama to investigate how bees do this. The uncertainties, however, were more fundamental. The main block to progress was the belief that landmarks for bees were shapes in a scene, as in human vision. On the contrary, the vision of the bee is more like our sense of hearing and smell in being a coincidence of inputs in each direction, but without re-assembly of an image. How they actually discriminate between the landmarks is a continuing gap in our knowledge. What labels do landmarks display?

From the mid-1920s on through the last century, the feature detectors of the honeybee were slowly recognized and progressively described. The principal research strategy was to train bees to choose between two patterns and then, to see what they had learned, measure the responses to a variety of test patterns that may or may not display some of the components in the training patterns. Progress

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was slow because the cues detected by the bees were unknown and not obvious. In retrospect, many of the experimental patterns and tests were not optimal for bee vision.

Recently, it has become apparent that bees have arrays of a few types of local detectors of simple features that are detected in different proportions in all patterns, and nothing more. The feature detectors are labelled with their positions in eye coordinates and the type of feature. They detect local cues irrespective of the rest of the pattern (Horridge, 2005, 2006b). Therefore, we can expect the labels on landmarks to be coincidences of cues.

The following cues, in approximate order of discovery, were inferred from discriminations between two patterns presented on vertical surfaces—the orientation of a single bar or of a regular grating (Turner, 1911; Wiechert, 1938; Jander et al., 1970; van Hateren et al., 1990), the colour of an area and the relative positions of two colours (von Frisch, 1914; Gould, 1985), the area of a shape but not its shape, and the total length of edge or the modulation caused in the receptors by relative motion of the bee (Hertz, 1933; Cruse, 1972; Anderson, 1977), the presence of radial symmetry (Hertz, 1933; Horridge, 1994) or bilateral symmetry (Horridge, 1996c), a difference in the position of an area of black or colour (Friedlaender, 1931; Wehner, 1969, 1972), especially when close to the reward hole (Baumgärtner, 1928), absolute size (Horridge et al., 1992), a difference in the position of the centre of a black area (Horridge, 2003a), and a difference in the position of the centre of symmetry (Horridge, 2006a). The cues may be localized, like a spot or an edge, or span the whole target, like the modulation of a texture or the orientation of a grating. The bees recognized the cues irrespective of the test patterns in which they were embedded because their feature detectors detected cues, not patterns.

The above references track the fundamental historical shift in paradigm away from the outdated template/snapshot/eidetic image theories of insect vision (Wehner, 1969, 1972; Cartright and Collett, 1982; Collett and Cartright, 1983; Gould, 1985) toward a modern electrophysiological/feature detector/wavelet theory based on modelling the fields of different neurons in superimposed arrays (Jander, 1964; Srinivasan et al., 1994; Horridge, 2005, 2006a).

The strategy of training to discriminate between two targets worked well for the discovery and description of the various cues used by the bees, but a landmark was usually a single pattern, not a choice between two patterns. It was inconvenient to control the cues in natural landmarks, but it was possible to train bees with a single pattern in an otherwise white apparatus and then test them to see what combinations of cues they had preferred.

As part of a curious train of events, training on a single pattern versus white targets was used as a new strategy in the period 1968–1977. Bees were trained to come to a single broad black bar versus one or more white targets, and then tested with the training bar versus the same bar that had been rotated by various angles (Wehner, 1969, 1972). The bar was huge, subtending $53^\circ \times 130^\circ$ at the point of choice. The test scores fitted the idea that the trained bees responded to a function of the area of overlap and non-overlap of the two patterns (Wehner, 1969, 1972). The orientation of the edges was not mentioned because earlier experiments had shown that changing the orientations of the edges of the arms of a square cross by cutting them into steps made little difference to the memory of the angular position of the cross (Wehner, 1967). The bees remembered the retinotopic positions of areas (the larger the better) irrespective of the edge orientations.

At about the same time, edge orientation as a cue was demonstrated in wasps trained on a vertical black bar versus an oblique one. Discrimination persisted in tests with unfamiliar patterns, and even with white bars on a black background, supporting the idea of oriented edge detectors (Jander et al., 1970). At the time it was not noticed that the memory of edge orientation resulted from training on one pattern versus another, but the memory of the position of an area of black resulted from training with a very broad bar versus a white target. The data on both was valid, but the opposing theories were not compatible because each was presented as exclusive.

Towards the end of the century our ideas about the bees' discrimination of bars, gratings and crosses were again thrown into confusion by three discoveries. First, bees discriminated the orientation of a grating although the widths and positions of the bars were randomized during the training (van Hateren et al., 1990). This was convincing evidence that the discrimination of orientation of areas or edges depended on superimposed arrays of differently oriented local edge detectors, as in vertebrates.

Secondly, in contrast to the earlier results of Wehner (1967), a square cross was not discriminated from the same square cross that was rotated by 45° in the Y-choice apparatus (Srinivasan et al., 1994). This was evidence that the detectors of orientation of edges or areas (or both) fed into collector neurons with very large fields within which the different orientations cancelled out. Subsequently, it was found that any edges of equal length at right angles on the same side of the target cancelled the orientation cue (Horridge, 1996a, 2000a).

Thirdly, when trained on a single bar versus a white target, the bees did not recognize the shape or orientation of the edges of the bar (see Fig. 2, below). They responded to any area of black where they expected to see it, and were less able to detect it the more it had been displaced vertically from the training position (Horridge, 2003a). The most important cue with a single target was the bar's position.

From 1988 onwards, bees were trained on one black pattern versus another, both on a white background in the Y-choice apparatus (Fig. 1). The baffles were introduced in 1996 to control the angle subtended by the target at the point of choice, and it was shown that the rotation of a square cross was in fact discriminated when the bars

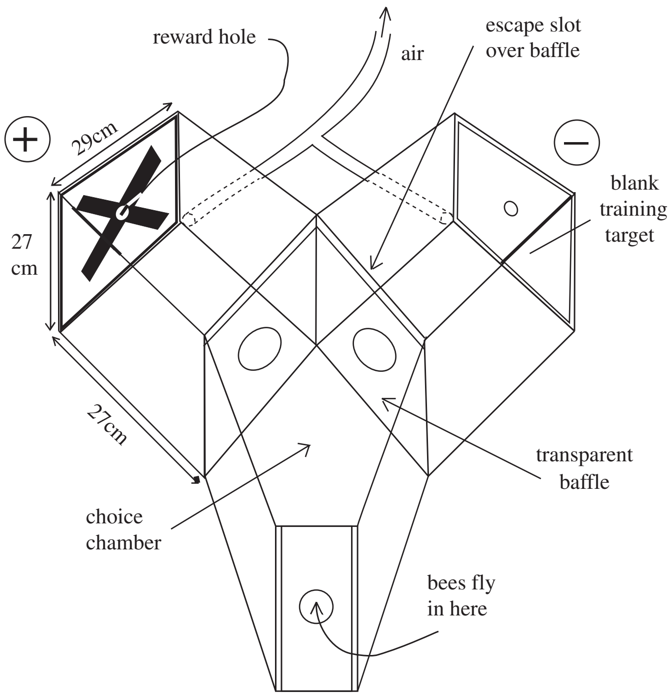


Fig. 1. The Y-choice apparatus. The bees enter through the hole 5 cm in diameter at the front and pass through one of the transparent baffles. The targets and their patterns with the reward change sides every 5 min, to prevent the bees from learning which side to go. Odours are extracted by the air pipe. As in all the figures, (+) and (−) indicate the rewarded and unrewarded patterns.

subtended very large angles (Horridge, 1996b). With thin bars, the edge orientation was learned but the edges had to be compared in corresponding positions on the two targets (Horridge, 1998). The more the width of a fixed bar exceeded 5°, the more the bees learned the difference in positions of black on the targets. When the positions of the bars were shuffled during the training, the bees were able to discriminate them in any of their expected places.

So, from 1966 to 1977, bees were trained with one pattern versus a white target, or with two patterns side by side, and the area of black and its location was the most popular cue. From 1988 to 2002 bees were trained with a simultaneous view of two patterns centred at the same place, and orientation was the most popular cue, while modulation and position of black were usually ruled out because they were similar on the two targets. The reward hole was not a useful cue because it was always the same on the two targets.

Until recently it was never clear whether the bees learned the rewarded pattern, the difference between two patterns, or to avoid the negative pattern. There were also insufficient tests to reveal the cues, or the sparse memory, and it was not understood that a failure to discriminate could indicate the lack of a crucial cue that could be supplied to make the test successful. The discussion was always based on successful tests, which suggested that the bees saw the two patterns. This anthropomorphic error actually obscured the nature of the recognition process, which acts on both targets with several different detector arrays in parallel and detects the preferred cues on either target. All observations are now explained by the finding that a few preferred cues were learned at the retinotopic places where they were displayed in the training.

The present research began as a reinvestigation of single black patterns on a white background, and concludes that some old ideas about areas as labels on landmarks were nearer the truth than some recent ideas about orientations of edges.

2. Methods

The bees came from a local hive within 100 m of the experimental apparatus, and could return in 5–10 min for another reward. The experiments were done in the Y-choice apparatus (Srinivasan and Lehrer, 1988), modified by the addition of the baffles and a circular entrance hole 5 cm in diameter that helped to keep out newly recruited bees (Fig. 1). The apparatus was placed outside under a roof with an open front 3 m wide and 3 m high, with the targets facing bright daylight. The walls of the apparatus were of white card; the top was of clear Perspex. The baffles, of transparent Perspex 1 mm thick, with a 5 cm hole at the centre, were set in a frame 1 cm wide. They controlled the angle subtended by the target at the bees' decision point, and allowed the observer to make a sharp decision about the success or failure of each choice. The bees could also exit by walking under or over the baffle. The black patterns were printed by computer on white paper of constant quality. The targets had a hole 2 cm in diameter at the centre, on the positive side for access to the reward and on the negative side leading to a blind tube. From the choice chamber the bees could resolve this hole on both targets (Fig. 1).

The bees were individually marked with a code of two colours. The reward was a fresh aqueous solution of sucrose sufficiently concentrated to keep the marked bees making regular visits without attracting recruits. During the training and tests the side of the positive target and of the reward with it were changed every 5 min to prevent the bees from learning which arm of the apparatus to choose, but in the illustrations the rewarded pattern (labelled +) was always shown on the left.

A small group of 10–15 bees from a local hive was trained to select one of the two targets while in flight in the central chamber (Fig. 1). They usually spent some time looking through the baffles. Each bee was identified by its colour code, and the criterion for a score was when it passed one baffle or the other. With the baffle at a distance of 27 cm, the targets subtended an angle of about 55° at the point of choice. The bees required about 20 visits to build up a memory of a single pattern. After an initial training period, the first choice of each identified bee in each period of 5 min was recorded while training continued. These results were labelled "train". To obtain the results labelled "test", a different pair of patterns was substituted for those in the training, and the bees' choices were recorded individually for 5 min on each side of the apparatus. All tests were made with one pattern rewarded, and then at a different time with the other pattern rewarded. In tests it was essential to give a reward, otherwise the bees continued to search. All tests were repeated with the patterns reversed in the two arms of the apparatus to compensate for possible side preferences. Different tests were interleaved during continued periods of training, so the trained bees did not become familiar with any one test.

Training began in the early morning and usually continued for several days between repeated tests, until 200–250 choices had accumulated for each test. By watching the bees in the choice chamber, one could see whether they decided quickly. If they were baffled they spent a long time examining first one target then the other. In many of the tests the bees failed, so they learned nothing from the test. In the tests the bees got a reward after they had made their only choice in that 5 min period, and when they returned the patterns had always changed, ensuring that choices were independent.

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 training or the tests. The mean score and its standard deviation (s.d.) was calculated for 10 of these blocks. These values are printed in all the illustrations. The method was arbitrary because the size of the blocks was arbitrary, and any change in the performance during the experiment made the s.d. too large.

In the second method (Friedlaender, 1931), an estimate of the s.d. was the value of $\sqrt{[p(1-p)/n]}$ where p was the fraction of correct choices and n was the total number of choices. This method assumed that there were no trends during counting, 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%.

Almost all samples were of 200 successive choices, so the following p values applied. If the s.d. was used, $p<0.05$ for a score of 57%, $p<0.01$ for a score of 60%. If the chi squared test was used, $p<0.05$ for a score of 60%, $p<0.01$ for a score of 62.5%, and $p<0.002$ for a score of 65%.

Quantitative comparisons of the scores in different tests are not as valid as might be thought, because each test involves a different mixture of several cues for which the bees have different preferences, and the bees switch between cues as the tests require. The main requirement was a decision as to whether the bees could or could not discriminate in the tests. It was far better to design a conclusive test than to struggle with marginally significant test results.

3. Some definitions

As the subject matter developed, some of the terminology changed its meaning. Therefore it is essential to note the intended meaning of some of the terms.

The black *patterns* on a white background were displayed on one *target* (Fig. 1). The two targets are exchanged every 5 min during the training to make the bees look at them.

A *landmark* is a single pattern that is fixed relative to the reward and to the place where the bee makes its choice, as in Fig. 1.

The *image* (as detected by the visual system) is the pattern of modulations in the receptor layer.

The *modulation* at the receptor level is caused by the change in the light intensity in the receptor, and can be measured as the amplitude and frequency of the electrical signal there. The simplest feature detector for modulation has the shape of a single peak with an inhibitory surround, as commonly used in computer vision. It detects the edge of a contrast edge irrespective of the orientation or direction. In the pattern, the modulation has been measured as the total length of edge or contour (Hertz, 1934; Cruse, 1972; Anderson, 1977) and is related too the spatial frequency.

A *feature detector* is a neuron or group of neurons in the peripheral optic lobe that is coarsely tuned to detect a primary local feature in the pattern, e.g., a local modulation of the receptors, a unit of edge and its local orientation, a coloured patch, or a black patch. Each feature detector has a local retinotopic position on the coordinates of the eye and each edge detector has a *feature vector* that defines its orientation.

A *cue* is an abstracted part of the pattern that is detected by a local group of feature detectors together with its position, e.g., the averaged edge orientation, modulation or colour in a region. Because the bee has an incomplete set of feature detectors, not all details in the panorama contribute to the cues. The cues are best discriminated when they are in corresponding positions on the two targets, i.e., they are compared in the same direction from each point of choice.

A *hub* (in machine vision) is a local concentration of the extensions of vectors at right angles to the tangents at an edge. Each hub indicates a position near the centre of a discrete object. In bee vision it lies near the centre of symmetry of radial or circular patterns.

A *label* is the combination of cues that are detected, remembered, and recognized in a pattern, according to the order of preference of the bees. The rest of the landmark is irrelevant.

The *features, cues, hubs and labels* act with progressively increasing specificity in the visual recognition mechanism. They are the letters, words and sentences that are detected on the landmarks. They do not correspond to the human idea of a visual stimulus.

A *filter* is a neuron or group of neurons that detects a particular coincidence of its inputs. In vision it is always a spatio-temporal pattern of modulation. It can be represented as a mathematical operator that extracts a component of the pattern. Feature detectors are filters.

4. Results

4.1. Training on a single fixed black bar

Beginning with a simple pattern, the bees were first trained to come to a single oblique black bar (subtending $36^\circ \times 8^\circ$) on a white background versus a white target (Fig. 2a). The bar was deliberately oblique so that its mirror image was at right angles with no change in modulation (Fig. 2b). After 3 h training, the score exceeded 80% and over the next 2 days the trained bees were given several interleaved tests. When tested with a half size bar (a quarter the area) versus a white target, the result was 60.5%, $n = 200$ (not illustrated). It is already known that the area of the bar and the total length of edge were strong cues (Cruse, 1972; Anderson, 1977).

When tested with an orthogonal oblique bar, centred at the same place, versus a white target (Fig. 2b), result was 81.5%, $n = 200$. The orientation of the training bar counted for nothing. Even more striking, the trained bees could not tell the difference between the training bar and a similar bar at right angles centred at the corresponding place on the other target (Fig. 2c).

The bees responded to the bar only in its expected position. When the bar was moved 12° down on the target and tested versus the white one, the result was 54.5%, $n = 200$ (not illustrated), and when it was moved down 25° and tested against the white target (Fig. 2d), the result was 48.5%, $n = 200$. Incidentally this test showed that the bees had not simply learned to go to a black area or to avoid the white target.

When the oblique bar was tested against the same bar moved down by 25° (Fig. 2e), the trained bees distinguished the training bar very well. When tested with a pair of orthogonal gratings of period 14° that filled the targets, there was no preference for either orientation (not illustrated).

In conclusion, the trained bees were excellent in the training task, and they remembered the area and position but could not remember the orientation. Similar results were obtained when bees were trained on either a horizontal or a vertical single fixed black bar versus a white target. The height of the bar was not a cue, and discrimination was less sensitive to a shift of the bar in the horizontal than in the vertical direction (Horridge, 2003a). The position of the black area, the length of edge (not tested here) and the area of black, were the only cues in the label. In different terms, each was described long ago (Friedlaender, 1931; Wehner, 1968; Cruse, 1972; Anderson, 1977).

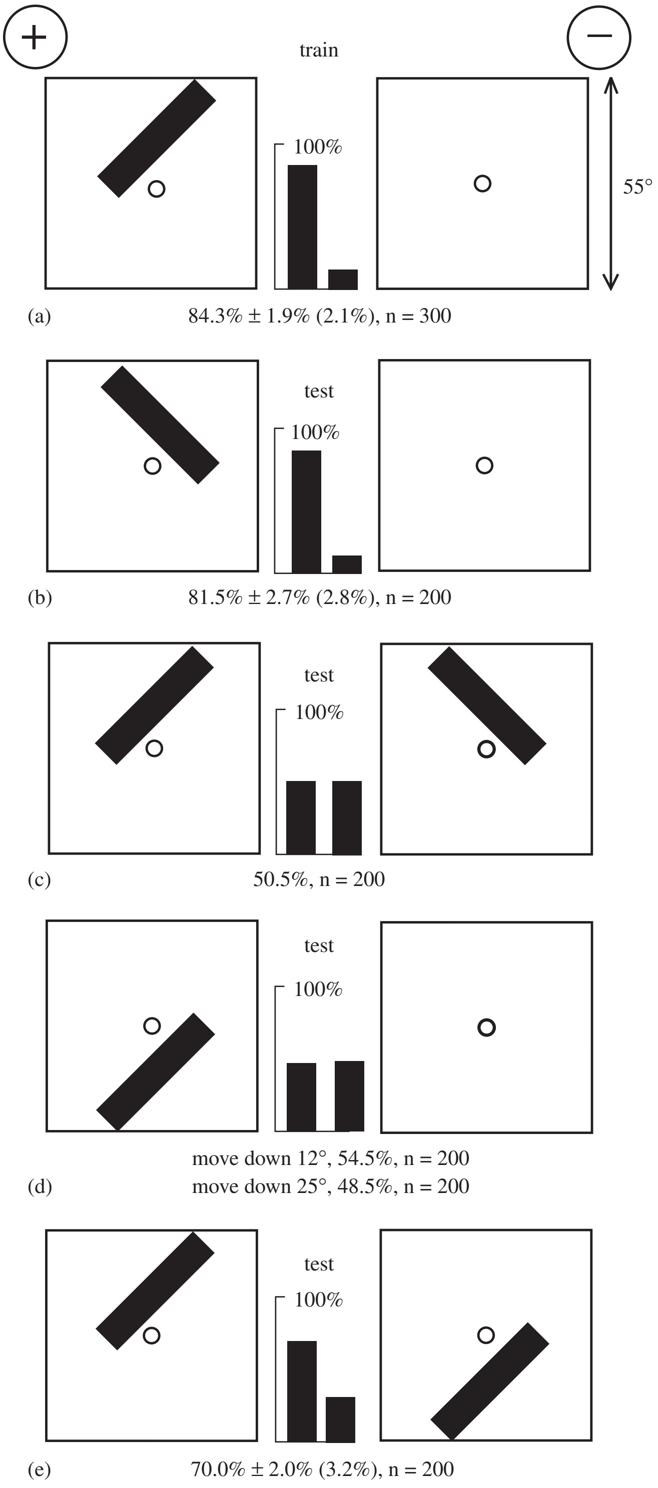


Fig. 2. The position, not the orientation, is learned when training with a single bar versus a white target. (a) A single oblique bar versus a white target. (b) Discrimination of an orthogonal bar versus the white target. (c) No discrimination with the training bar versus the orthogonal bar. (d) No discrimination with the bar moved down, versus the white target. (e) Discrimination with the training bar versus the same bar moved down.

4.2. Training on three oblique bars versus a white target

To increase the length of edge and therefore the modulation of the receptors, the bees were next trained on a target that displayed three oblique bars (each subtending 6° in width) that were fixed in position, versus a white target (Fig. 3a). Scores over 95% were reached in 2 h of training.

The first test of the trained bees was a forced choice between the rewarded training pattern and the mirror image of the same pattern (Fig. 3b). Unlike the situation with a single bar (Fig. 2c), the bees could discriminate, with a score of 71.0%. This was a large drop in performance, showing that they had learned more than the orientation of the bars. There were a number of other features in the training, such as the black area and the modulation on both targets, which were unchanged in the test. Further tests helped to separate these possibilities.

The rewarded training pattern was preferred with a score of 65% when tested versus a pattern of small squares (each side subtending 6°) of the same total area (Fig. 3c). The score was similar when the small squares were tested versus the white target (Fig. 3d), however, showing that the bees had learned more than the orientation cue and an orientation cue was not essential.

In the next test, the training pattern was drawn as three lines of squares (each side subtending 12°) to remove the edge orientation, as done by Wehner (1967), but leaving the distribution of black areas relatively unchanged (Horridge, 2000a, 2003c). The trained bees were given a forced choice between this pattern versus the mirror image of the same pattern (Fig. 3e). Discrimination was lost, showing that the exact distribution of the area of black on the training target was not remembered.

The trained bees could easily detect a difference between the rewarded training pattern and the same pattern with similar modulation but edges in large steps (Fig. 3f), suggesting again that orientation was a significant cue. Steps of 6°, however, were too small to destroy the orientation cue (Fig. 3g). The test scores in Fig. 3(b–g) were all much less than the training score between the tests, because the bees could no longer rely on the easy choice between a white target and one displaying orientation, modulation and black.

When presented with the rewarded training pattern versus the same pattern with more bars (Fig. 3h), they slightly preferred the one with more of each cue. In conclusion, with three well-separated bars versus a white target, the label was a mix of area and position of black, together with modulation and edge orientation.

4.3. Training on an oblique grating versus a white target

As in the previous experiment, the bees rapidly reached a very high score when trained on an oblique grating of period 10° versus a white target (Fig. 4a). When forced to choose between the training pattern and its mirror image (see Fig. 4(i) right pattern), the test score was 90.5%,

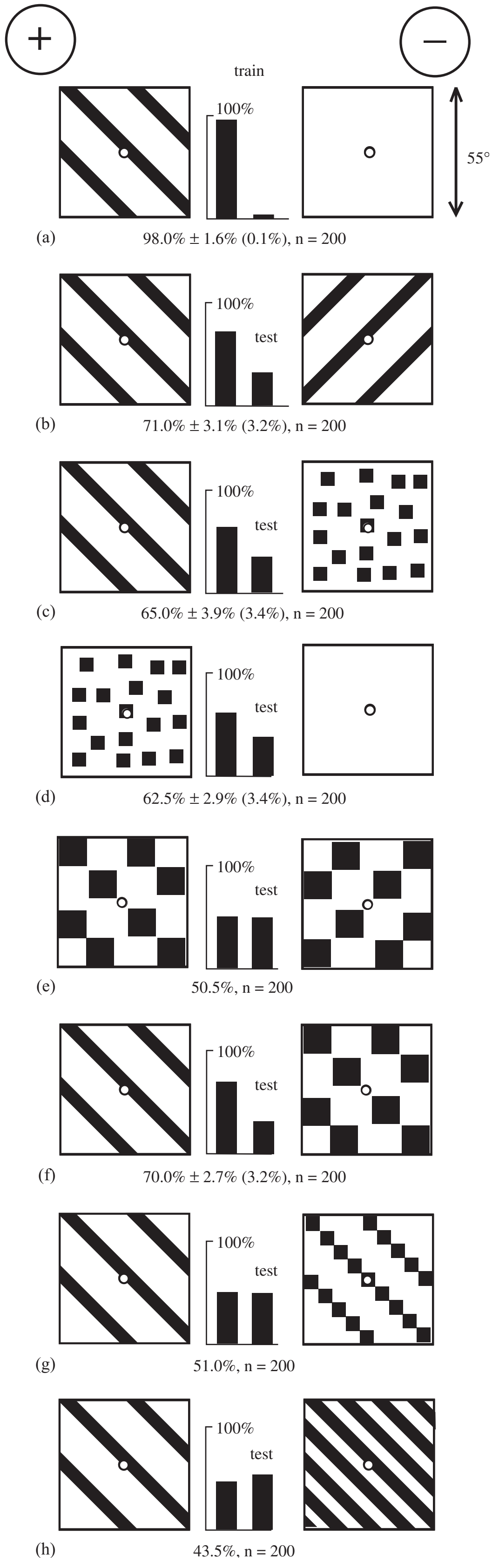


Fig. 3. Low scores in the discrimination of edge orientation with three oblique bars versus a white target. (a) The training targets. (b) The training target was discriminated from the same turned through 90°. (c) The training target was discriminated from the small squares of the same total area. (d) The small squares were discriminated from the white target. (e) Orthogonal stepped bars were not discriminated. (f) Good discrimination between the training pattern and the same with 12° steps. (g) No discrimination between the training pattern and the same with 6° steps. (h) Some preference for an oblique grating with the same slope as the training pattern.

showing that the bees did not rely on avoidance of the white target or attraction to black or modulation, and that they remembered the orientation very well.

When tested on an irregular pattern of black spots versus a white target (Fig. 4b), however, the test score was 75.5%, showing that the trained bees had learned an attraction to black or to modulation. It is not possible to say that they avoided the white target. When tested on the training pattern versus the irregular pattern of black spots (Fig. 4c), the bees strongly preferred the oblique grating to the spots. In a test with the training grating versus a checkerboard of similar period but with a greater total length of edge (Fig. 4d), the test score was less, although the modulation was greater, suggesting an attraction to black and modulation on both targets.

In the next test the trained bees were given a forced choice between three lines of squares (each side subtending 12°) to remove the edge orientation, versus the mirror image of the same pattern (Fig. 4e). The test score was 50.5%, showing that the cues were equally attractive on the two targets and that the global orientation difference was irrelevant. With bars cut into smaller steps of 6° versus the mirror image of the same pattern (Fig. 4f) the test score was 62.0%, so there remained a weak orientation cue in this test.

In a test with the training grating versus three smooth bars (Fig. 4g), the trained bees preferred the grating. However, when tested with the training grating versus a grating of period 5° but similar slope (Fig. 4h), the test score was 88.0% in favour of the training grating. These two tests taken together suggested that the bees had learned a quantitative measure of the modulation in the training pattern. Finally, when a single bar was placed across the training grating, versus an orthogonal training grating (Fig. 4i), the test score was reduced to 74.0%, showing that the bees responded as if to the averaged orientation.

It was concluded from this experiment that, as a label for the grating, the bees learned the edge orientation, the actual level of modulation and the presence of black.

4.4. Training with a square cross versus a white target

In this experiment, the rewarded target displayed a large square cross of two black bars (each bar subtending

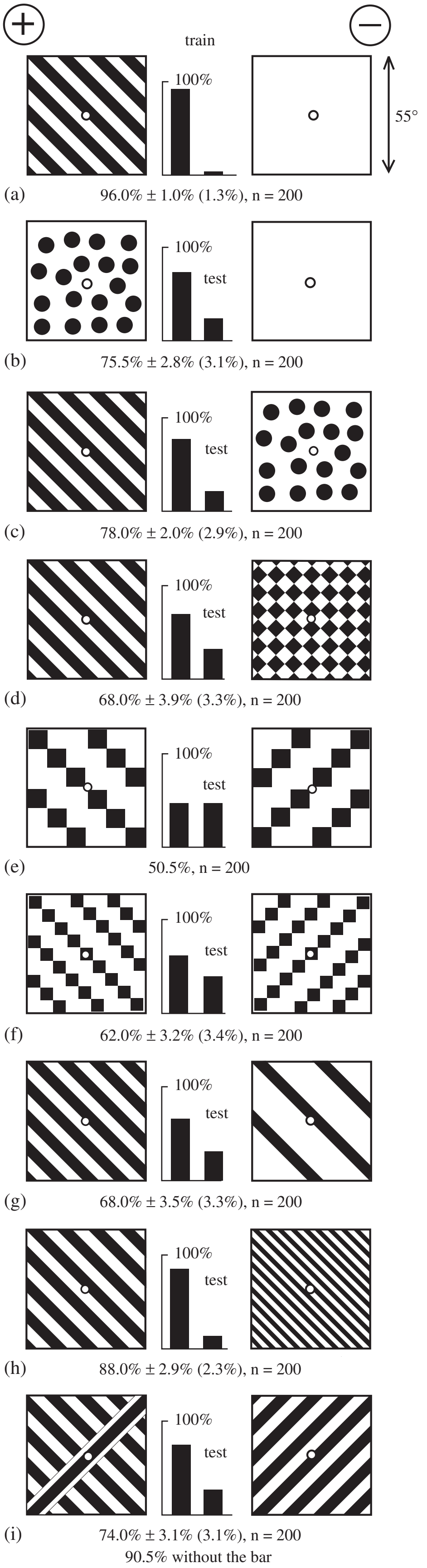


Fig. 4. When trained on an oblique grating versus a white target the bees learned the orientation and modulation. (a) The training targets. (b) A pattern of black spots was discriminated from white target. (c) The training grating was discriminated well from the pattern of black spots. (d) The training grating was discriminated from a checkerboard with the same amount of black. (e) The orthogonal bars with 12° steps were poorly discriminated. (f) The orientation was discriminated with 6° steps. (g) The training grating was discriminated from a similar grating of twice the period. (h) The training grating was discriminated well from a grating of half its period. (i) The training grating was discriminated very well versus the same turned through 90°, and discrimination was reduced by the single bar across it.

52° × 4°) and the other target was plain white (Fig. 5a). The orientation cues were cancelled because the bars were at right angles to each other. The bees were at first reluctant to make a choice, as if cues were scarce, but eventually the score reached 90.5% after 3 h of training.

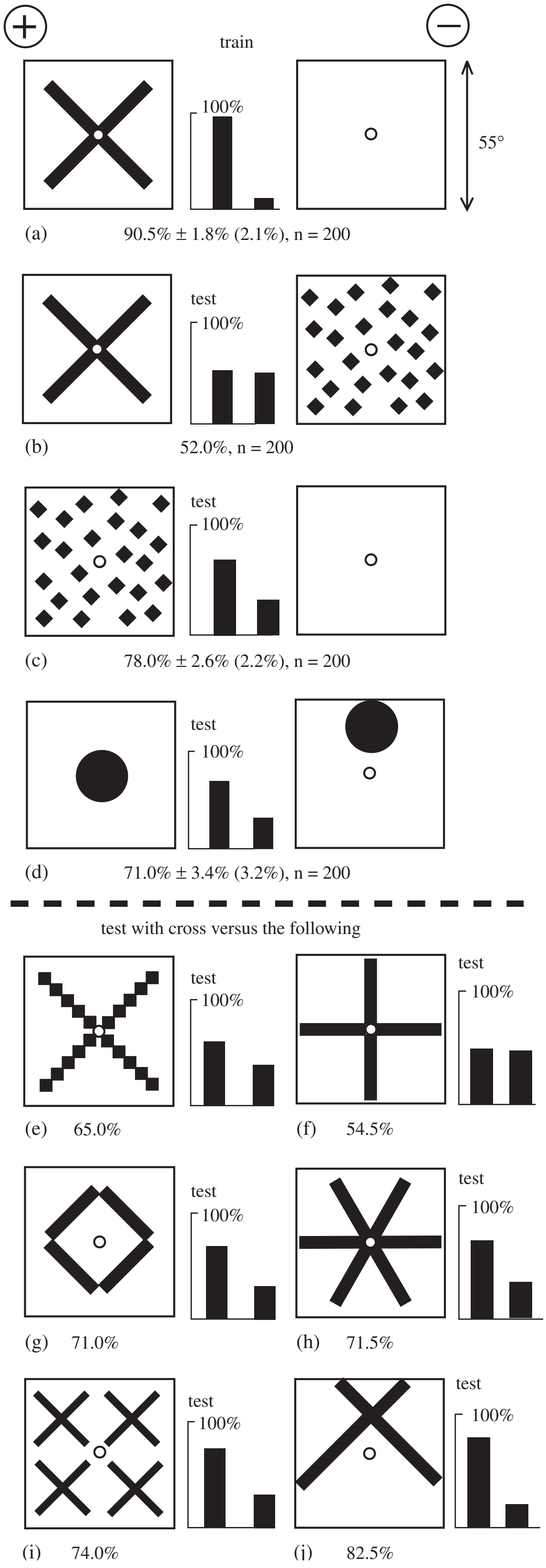
The trained bees were unable to distinguish between the training target and a pattern of 24 small squares of similar total area (Fig. 5b), showing that the cues were equal on the two targets, and therefore the bees had learned nothing about the square cross except perhaps its area, modulation and position of the centre. They were also tested with the pattern of squares versus a white target (Fig. 5c), with a score of 78.0%, which suggested that they had been trained to go to a black and/or modulation cue. The test score was less than the training score, suggesting that there was a further cue.

To demonstrate that the trained bees had learned the position of the centre of the black area of the training cross, they were tested with a black spot at the centre of one target versus the same black spot that was moved to the top of the other target (Fig. 5d). The test score was 71.0%, in favour of the spot at the centre.

To demonstrate that the trained bees recognized an unfamiliar cue that was not in the training pattern, they were tested with the square cross versus patterns of similar area, modulation and position, that contained other cues known to be effective in training patterns. With the cross versus a stepped cross (Fig. 5e), the same bars in the form of a square (Fig. 5g), six spokes (Fig. 5h), or four small crosses (Fig. 5i), there were moderate scores of 65–75%. The bees detected something in each of these unfamiliar patterns although they did not recognize the training pattern (Fig. 5b). When tested versus the cross-rotated by 45° (Fig. 5f), however, there was no discrimination because there was no unfamiliar cue.

Finally, the trained bees were tested with the cross-centred on the reward hole versus the same cross that had been moved up on the target (Fig. 5j). The test score, 82.5%, showed that in a forced choice between two similar targets, they clearly recognized the difference in positions of the centres, even though the average orientation cue was cancelled out and they could not recognize the cross they were trained on (Fig. 5b, f).

It was concluded from this experiment that the label on the square cross was composed of area, modulation and position of the centre, and that the bees recognized and tended to avoid the unfamiliar cues that they had not expected to detect.



(a) 90.5% ± 1.8% (2.1%), n = 200

(b) 52.0%, n = 200

(c) 78.0% ± 2.6% (2.2%), n = 200

(d) 71.0% ± 3.4% (3.2%), n = 200

(e) 65.0% (f) 54.5%

(g) 71.0% (h) 71.5%

(i) 74.0% (j) 82.5%

Fig. 5. The bees learned the position of the centre a square cross, and to avoid the white target. (a) The training targets. (b) The square cross was not discriminated from a pattern of black squares of similar area. (c) The black squares were discriminated from a white target. (d) A large central black spot was discriminated from the same spot moved up on the other target. (e–j) The square cross was tested versus the following six patterns. (e, f) A stepped cross and a rotated cross were weakly discriminated. (g–i) A hollow square, six spokes and a pattern of four crosses were better discriminated. (j) The square cross was discriminated well from the same cross moved up on the other target.

4.5. Training with a stepped cross versus a white target

Although the stepped cross had been used as a test pattern (Wehner, 1967; Horridge, 2000a), there was no information about it as a training pattern. The question remained whether the edge orientations in the arms of the smooth cross were essential for detection of the position of the centre. Therefore the bees were trained on the stepped square cross versus a white white target (Fig. 6a). This was an easy task, with a score of 95% after 2 h training and 98% between tests during the next 2 days.

The trained bees could not distinguish between a stepped cross of this size and a pattern of the same 20 squares scattered on a white target (Fig. 6b), or the same cross rotated by 22.5° (Fig. 6c), suggesting that they had learned nothing about the lay-out of black on the target or the shape of the cross. They could, however, discriminate a little between the stepped cross and a filled black square of the same area with less modulation (Fig. 6d).

When the trained bees were tested with the stepped cross versus the same with the centre moved upwards on the target (Fig. 6e), there was some discrimination, as there was also when they were tested with the smooth square cross versus the same with the centre moved upwards (Fig. 6f). The difference that the bees detected in Fig. 6e was not attributed to the difference in distribution of black around the reward hole, as shown by the failure to notice a large difference in Fig. 6g.

This experiment showed that the stepped cross-displayed cues of area of black and modulation, with a weak memory of the position of the centre. The trained bees would go to any similar modulation of black centred at the expected place.

4.6. No preference for a square cross

To demonstrate in another way that the bees had no preference for the shape or orientation of a square cross, a group was trained with a rewarded square cross of thin bars versus an unrewarded symmetrical pattern of six thin spokes of the same total area of black (Fig. 7a). As shown in previous work, the angular orientations of the spokes were cues, together with the black area and the modulation. The label also included the hexagonal symmetry, with a hub at the centre (Horridge, 1999, 2000b, 2006a). Learning was slow and reached only 63% correct after 4 h training and 75% by the end of the day.

The trained bees could not distinguish between the square cross and a pattern of nine black squares of the same total area scattered on a white target (Fig. 7b), showing that they had learned little about the lay-out of black, the orientations of edges, or the shape of the cross. In fact, they appeared to ignore the square cross.

They discriminated, however, between the small squares and the six spokes with a test score almost as high as in the

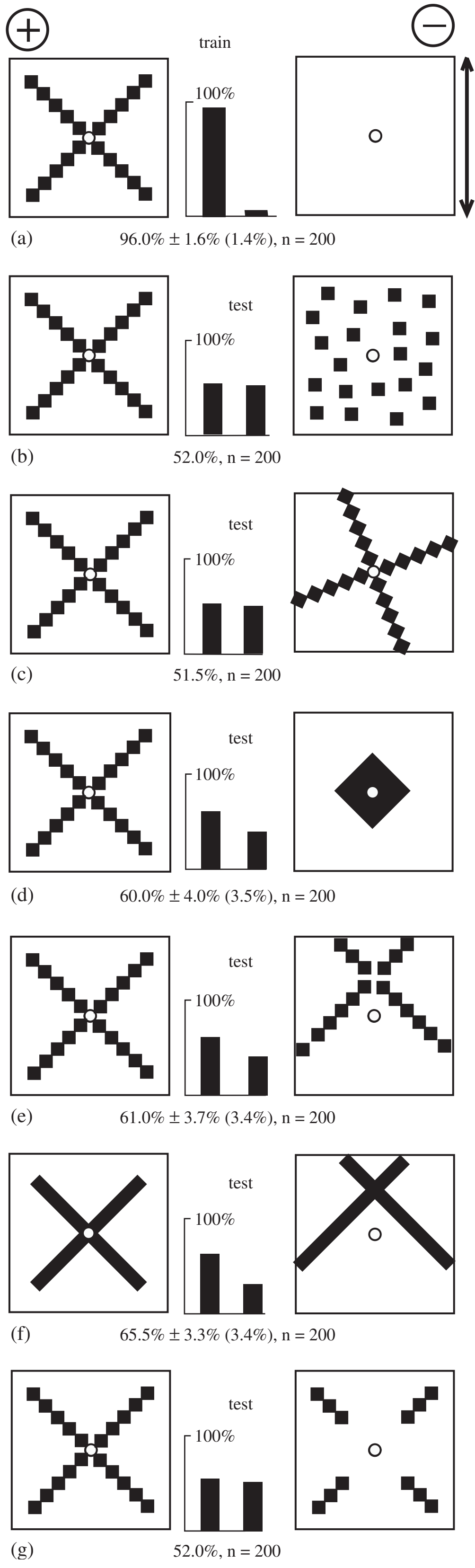


Fig. 6. The bees learned the position of the centre of a stepped square cross, and to avoid the white target. (a) The training targets. (b) The stepped square cross was not discriminated from a pattern of black squares of similar area. (c) The stepped square cross was not discriminated from the same rotated. (d–e) The stepped square cross was weakly discriminated from a black square of the same area and from the stepped cross moved up on the other target. (f) A smooth square cross was discriminated well from the same cross moved up on the other target. (g) Discrimination did not depend on black near the reward hole.

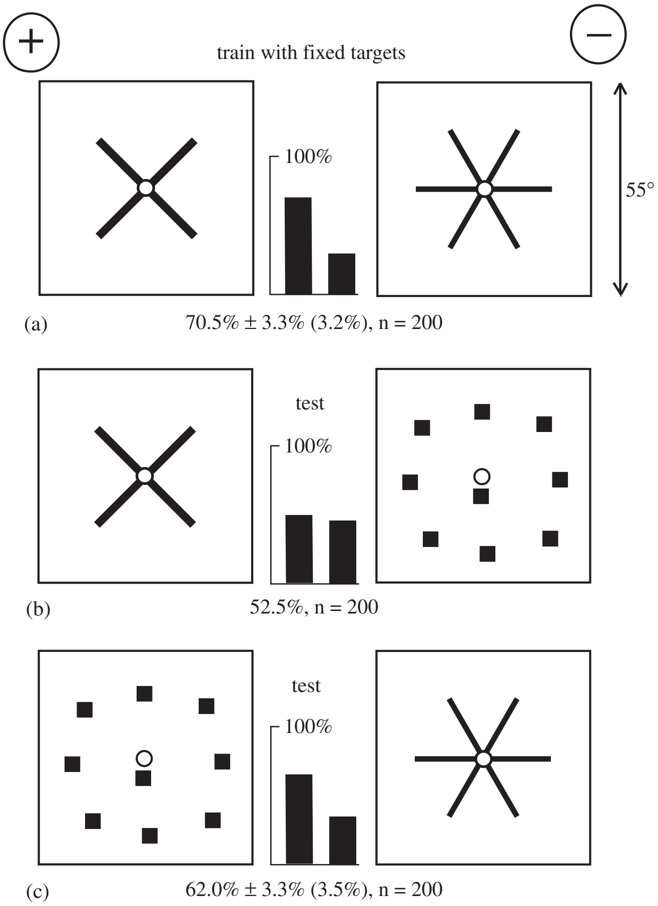


Fig. 7. Six spokes were remembered but the square cross was ignored. (a) Training 4 spokes versus 6 spokes, both centred. (b) The square cross was not discriminated from a pattern of black squares of similar area. (c) The black squares were discriminated from the 6 spokes.

training (Fig. 7c), showing that the learning had concentrated on reducing the attraction of the six spokes on the unrewarded target.

4.7. Training with six spokes versus a white target

In contrast to the results with a square cross, bees trained with six spokes versus a white target (Fig. 8a) detected edge orientation in the rewarded pattern, although they did not necessarily learn anything about the spatial lay-out of black on the target. The score reached 85% after 2 h training, and 100% at times during the training in the following 3 days between tests.

When tested with the rewarded pattern versus a scattering of small squares of the same total area (Fig. 8b), the trained bees discriminated quite well with a test score of 67.5%, and when tested with the small squares versus a white target (Fig. 8c), the test score was 85.0%. These results showed that although there were edge orientation cues available, they had also learned to go to black and they distinguished the six spokes from the pattern of squares (compare Fig. 5b).

When trained against a white target, however, the trained bees had not learned much about the positions of the areas of black. When tested with a stepped version of the training pattern versus the same rotated by 30° (Fig. 8d), the score was only 55.5%. The trained bees recognized the six spokes, as demonstrated by a score of 68.5% in a test with the training pattern versus the square cross (Fig. 8e).

When the trained bees were tested with a large central black spot versus the same moved to the top of the target (Fig. 8f), the score was 68.5%, showing that they remembered the position of the centre, although there was no necessity for them to have learned this cue.

Similarly, with the training pattern (Fig. 8a) versus the same moved upwards (Fig. 8g), or downwards on the target (Fig. 8h), the trained bees recognized the training position of the centre. They also recognized the six spokes from the same six spokes with stepped arms (Fig. 8i), or from a circle of the same area (Fig. 8j). In most of these tests (Fig. 8b, e–j), the test scores were similar, presumably because the bees had learned the orientations of the edges at angles of 60°, together with the position of the centre.

4.8. Training with a single 20° black spot versus a white target

A round black spot is one of the simplest possible landmarks and it is difficult to see what features of a spot the bees could possibly fail to learn. It is already known that bees learn the absolute size of a spot (Horridge et al., 1992). After 2 h of training with a black spot the score reached 80% correct (Fig. 9a), but was reduced to 61.5% in a test with the spot moved up on the target, versus the white target (Fig. 9b), showing that the trained bees had learned the position of the spot.

When tested with the training pattern versus four smaller spots of the same total area, in the form of a square (Fig. 9c) or a line (Fig. 9d), however, the trained bees could not detect the difference. They remembered nothing about the lay-out of black. However, in a test with the training pattern versus 84 smaller spots of the same total area, the score was as high as in the training (Fig. 9e) because the bees detected and avoided the intense modulation that was not in the training target.

The detection of a shift in the position of the spot was measured in a series of tests with different upward displacements (Fig. 9f, g). The minimum detectable shift was about 8°. When the spot was displaced more than 20°, it was no longer confused with the training spot.

The label for a large spot as a landmark was therefore a measure of area and position, with no memory of shape or lay-out of the black area, but the bees remembered that they had been trained on a pattern with little modulation (Fig. 9e).

4.9. Training with a single small black spot

A small black spot (subtending 8°) was an even simpler landmark because in having a smaller area, the position was less well remembered. The score reached 86% after 2 h of training (Fig. 10a), and was only reduced to 81.5% in a test with the spot moved down on the target versus the white target (Fig. 10b), showing that the spot was salient and the trained bees had a poor memory of its position. When tested with the training pattern versus the same with the spot moved down (Fig. 10c), the score was only 61.0%, again showing salience and that the position was not well remembered (contrast Fig. 9b, f).

The trained bees were able to discriminate the small spot from a larger spot at the corresponding position (Fig. 10d), and from other patterns of the same total area that displayed at least one of the previously identified cues (Fig. 10e–g). They discriminated between the small spot and a ring (Fig. 10g), but not between the round ring and six spokes of the same area (Fig. 10h) because neither pattern was in the training.

The label for a small spot as a landmark was therefore a measure of its area, with poor memory of position, and the bees remembered that they had been trained on a pattern with no other cues.

4.10. *Training with several spots versus a white target*

We have seen that the modulation was a strongly preferred cue that was frequently included in the label. To confirm that the modulation was learned quantitatively and to test the salience of modulation, a new group of bees was trained to a pattern of 6 black spots, each subtending 9° versus a white target (Fig. 11a). The score reached 90% correct after 2 h of training, so the label was obvious. In previous work there never has been any evidence that the bees detect the spots separately (see Fig. 9c, d).

The trained bees were tested with the training spots moved down on the target versus the white target (Fig. 11b). The score was 75.5%, showing the salience of the modulated pattern and that the position of the pattern was not a strong cue. The trained bees were also tested with the training spots versus the same with the spots moved down on the target (Fig. 11c). The score was now 61.0%, again showing that the position of the label was not well remembered.

The trained bees were tested with the pattern of 6 spots versus a pattern of 12 black spots, each subtending 6.4°, of the same total area (Fig. 11d). The score, of 71.0%, showed that the difference in modulation was detected. The trained bees were also tested with the pattern of 6 spots versus a pattern of 3 black spots, each subtending 12.7°, of the same total area (Fig. 11e). The score, of 69.5%, again showed that the difference was discriminated although we know that the bees do not remember the shape or number of spots (Fig. 9c, d).

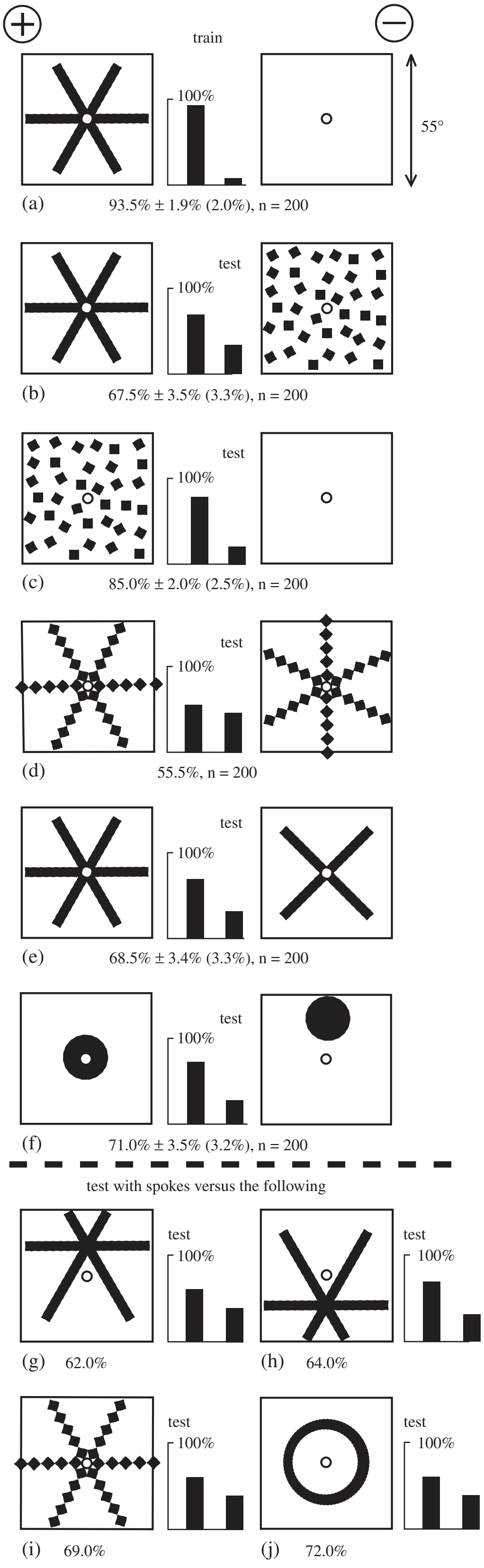


Fig. 8. In a pattern of six spokes the bees learned the edge orientations, the radial cue, the position of the centre and to go to black. (a) Training with six spokes versus a white target. (b) The six spokes were discriminated from a pattern of black squares of similar area. (c) The black squares were preferred to a white target. (d) Six stepped spokes were scarcely discriminated from the same rotated by 30°. (e) Six spokes were discriminated from the square cross. (f) A central spot was discriminated from a higher spot. (g–j) The six spokes were discriminated from the following patterns. (g) Six spokes shifted up. (h) The same shifted down. (i) Six stepped spokes at the centre. (j) A ring.

The trained bees were also tested with the pattern of 3 large spots versus a white target (Fig. 11f) and with the pattern of 12 small spots versus a white target (Fig. 11g). The scores were less than those in the training, showing that the bees recognized the difference although the white target was unchanged.

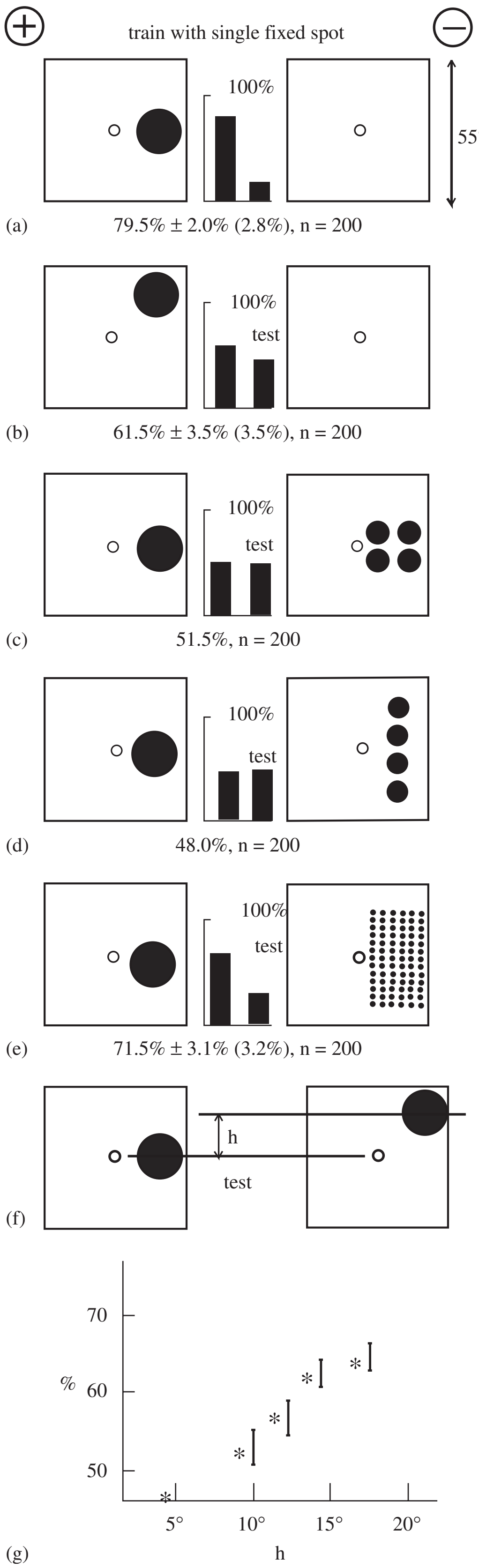


Fig. 9. The label for a large black spot included its position and modulation but not its shape. (a) The training patterns. (b) Moving the spot on the training target reduced the score. (c, d) The single large spot was not distinguished from four small spots. (e) The spot was clearly discriminated from a highly modulated pattern of the same total area. (f) The training spot was tested versus the same spot that was moved through a height h. (g) Results from (f) with vertical bars showing the calculated sds.

In conclusion, something related to the modulation, such as the length of edge, was measured, but its position on the target was not well remembered. The large field of the modulation detector would make it more effective in a search for a familiar label.

4.11. *Training with a thick black ring versus a white target*

Although bees did not discriminate the shape of a ring in earlier experiments, they detected the area of black and the position of the centre (Horridge, 2006a). A ring was distinguished from a square cross or a large spot of similar area because it lacked a black region around the reward hole (Horridge, 2006b). A ring should therefore be as effective as other patterns as a landmark. As in the previous experiments, the bees rapidly reached a high score when trained on a thick black ring (ID 18°; OD 33°) versus a white target (Fig. 12a). When tested on the training pattern versus an irregular pattern of black spots (Fig. 12b), the trained bees could not tell the difference. When tested on the irregular pattern of black spots versus a white target (Fig. 12c), the test score was 75.0%, showing that a large part of the learning could be attributed to attraction to black or modulation and avoidance of the white target, none of which are specific for a ring.

However, when tested on a black spot at the centre versus the same spot at the top of the target (Fig. 12c), the test score was 65.5%, revealing a memory of the position of the centre although the ring had no black centre. The label on the ring included the area, modulation and position of a hub. As a landmark therefore, a thick ring would be about as effective as a square cross or a large black spot but would be distinguished from them with difficulty.

5. Discussion

5.1. *Low preference for edge orientation as a cue*

Although a memory of average orientation has been demonstrated in many experiments, and the length of the unit edge detector is about 3° (Horridge, 2003c), the new results showed that edge orientation was not used when the single target displayed a fixed broad black bar (Fig. 2), a square cross (Fig. 5), or a ring (Fig. 12). Instead, the cues were the area, modulation, positions of the black areas and position of the centre. This anti-intuitive result has a long and curious history.

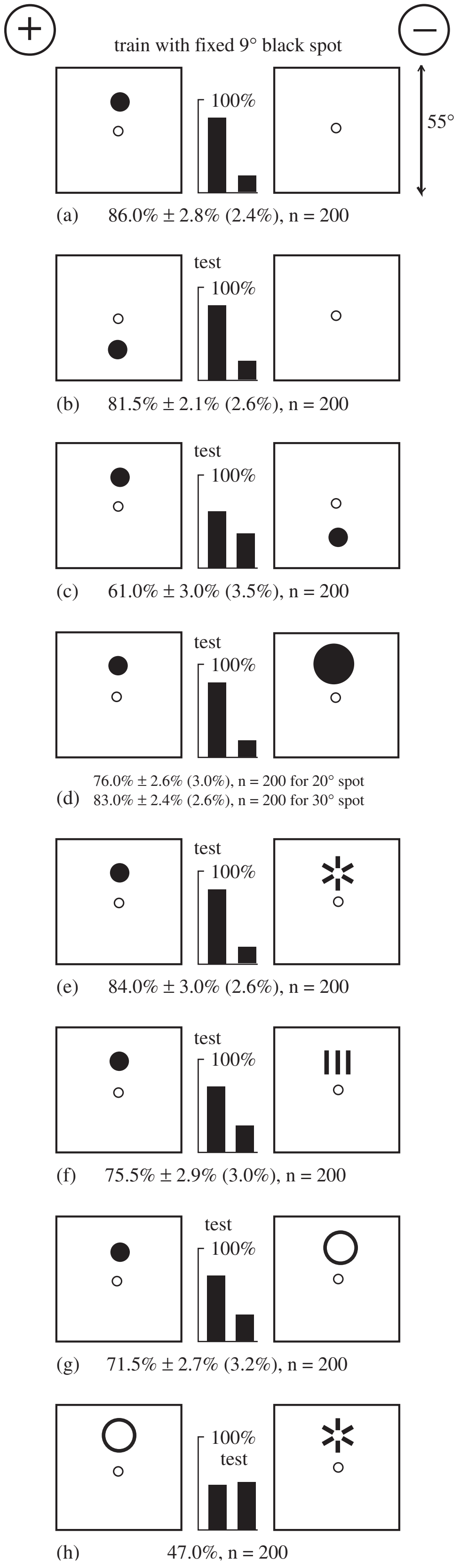


Fig. 10. The label for a small black spot was a measure of its size, with poor memory of position, but the bees remembered that they had been trained on a pattern with no other cues. (a) The training patterns. (b) Lowering the training spot on the target scarcely reduced the score at all. (c) The rewarded spot was poorly discriminated from the same moved down. (d) The spot was discriminated well from a larger spot. (e–g) The spot was discriminated very well from patterns of similar area that displayed an obvious cue. (h) The trained bees were not attracted to a circular shape.

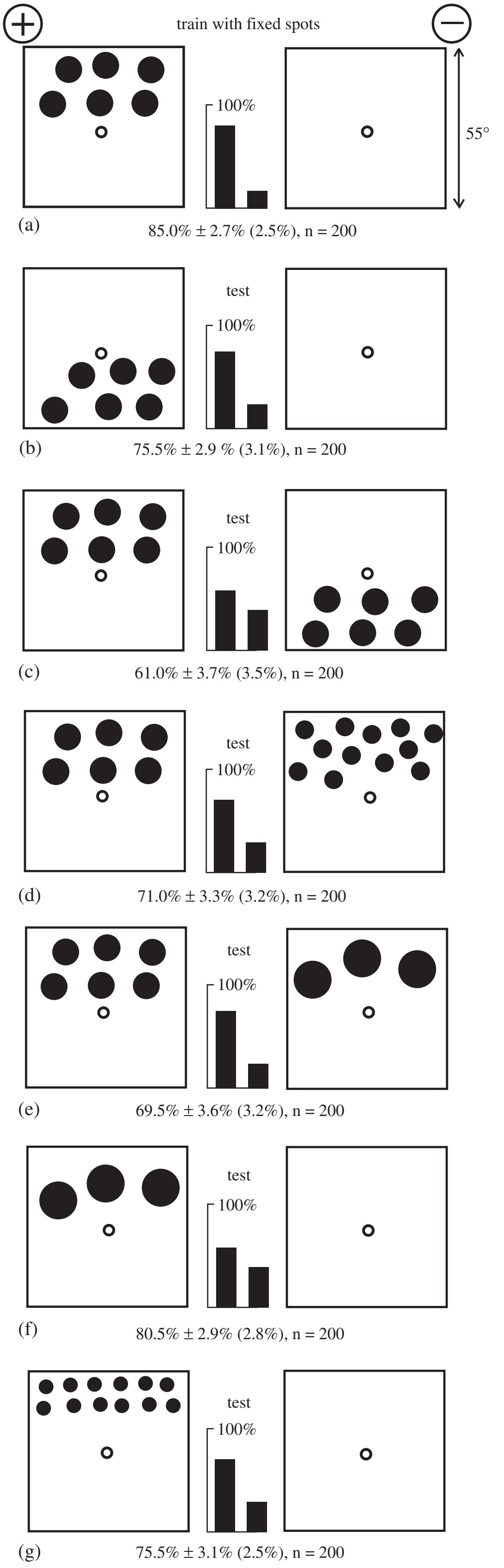
Turner (1911) showed that bees discriminate between a coarse vertical grating versus a similar horizontal one on the vertical faces of two small boxes. The criterion of success was the landing on the reward hole in the centre of the correct pattern. Wiechert (1938) demonstrated discrimination between a long thin vertical bar and a similar but inclined bar on a vertical surface. There were no tests of what the bees remembered, but for different reasons in each case it was probably a difference in edge orientation. The results were not mentioned in the literature for 60 years.

In the experiments of Wehner and Lindauer (1966) the bees were trained to discriminate a square cross subtending 130° presented *side by side* with the same cross rotated by 45°, and a remarkable threshold difference in angle of only 4° was discriminated in tests. They also tested with the arms of the cross cut into square steps subtending nearly 20°, so there would be no net edge orientation, and found that "The stripe contours may be dissected in a sawtooth-like pattern without affecting the orientation to the inclination of the long axes of the black stripes". The bees detected and remembered the positions of black areas irrespective of the edge orientations.

This result is of interest because it was flatly contradicted by Srinivasan et al. (1994) who found, using the Y-choice maze with simultaneous viewing (Fig. 1), that a square cross subtending 40° was not discriminated from the same cross rotated by 45°. On this result Srinivasan et al. based a theory that local orientation detectors were coarsely tuned, and were integrated into large fields within which orientation cues from neighbouring edges at right angles were cancelled. In a re-investigation of this disagreement, also with simultaneous viewing, it was found that the rotation of a very large cross subtending more than 100° could be discriminated from the same cross rotated by 45°, by the well-separated positions of the black areas or edges at the tips of the bars (Horridge, 1996b).

Wehner and Lindauer (1966) also trained bees on a single bar 2 cm × 18 cm at a range of 5 cm, or on a regular grating of five of these bars, side by side with a similar pattern turned through 90°. The criterion of success was the landing on the reward hole at the centre of the rewarded pattern. The trained bees were tested with the rewarded training pattern versus the same pattern that had been rotated. In view of later work, the first interesting result was that the test score as a function of the angle of rotation was similar for a single bar, a regular grating and a square cross (when the scores were reduced to percentages).

A difference in angle of 10° was discriminated, and the response was already saturated by a rotation of 45°. The problem was to explain the results if the cue was not the edge orientation. No mechanism was suggested but the result was re-stated in other words “The most important parameter for measuring the angle of stripes is the



(a) 85.0% ± 2.7% (2.5%), n = 200

(b) 75.5% ± 2.9 % (3.1%), n = 200

(c) 61.0% ± 3.7% (3.5%), n = 200

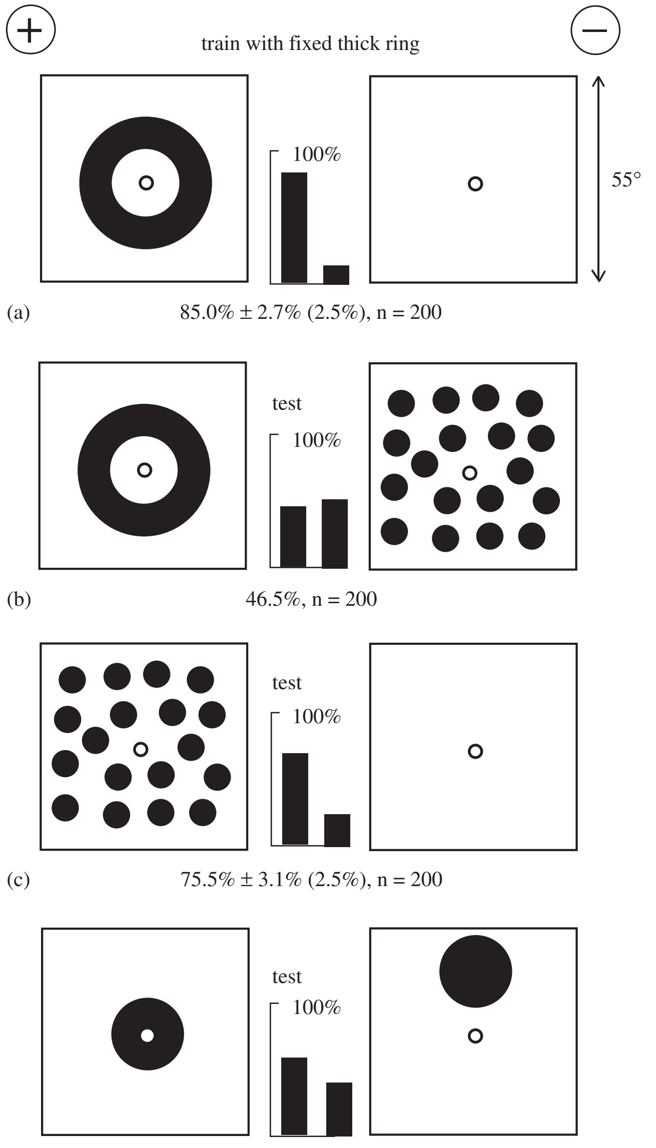
(d) 71.0% ± 3.3% (3.2%), n = 200

(e) 69.5% ± 3.6% (3.2%), n = 200

(f) 80.5% ± 2.9% (2.8%), n = 200

(g) 75.5% ± 3.1% (2.5%), n = 200

Fig. 11. The label for a strongly modulated pattern contained quantitative information about modulation but little about its position. (a) The training patterns. (b) Lowering the spots on the target scarcely reduced the score. (c) The training spots were poorly discriminated from the same spots moved down. (d) The 9° spots were discriminated from 4.5° spots. (e) The 9° spots were discriminated from 18° spots. (f–g) The 18° spots and the 4.5° spots were discriminated from a white target, but with a reduced score.



(a) 85.0% ± 2.7% (2.5%), n = 200

(b) 46.5%, n = 200

(c) 75.5% ± 3.1% (2.5%), n = 200

(d) 65.5% ± 3.9 % (2.7 %), n = 200

Fig. 12. The bees had negative preference for a ring, which was remembered by the coincidence of a black area, modulation and position of the centre. (a) The training patterns. (b) The ring was not distinguished from the pattern of spots. (c) The spots were clearly discriminated from a white target. (d) The position of the centre was remembered.

orientation of the long axes of the black stripes, but not the direction of the black and white contours" (Wehner, 1967).

Almost immediately, Wehner (1969) trained on a single huge black bar, subtending 130° × 50° versus plain white targets, and tested with the training bar versus a similar bar that was rotated through various angles. The results agreed with the idea that the bees detected the changes in the overlap and non-overlap of the black areas (each multiplied by arbitrary constants) if the two patterns were superimposed. It was concluded that the bees remembered the shape of the training pattern and compared it with each test pattern that was presented. Edge orientation was not mentioned as a possible cue.

At the same time, Jander et al. (1970), working in the same Institute, found that wasps could be trained to discriminate the orientation of a vertical bar presented side by side with a similar bar at 45°. The trained animals discriminated these orientations in unfamiliar patterns, even in single white bars on a black background. These striking results were interpreted in terms of strings of local edge detectors with different orientations (Jander, 1964).

Without delay, Wehner (1971) trained bees on a single oblique black bar (subtending 130° × 20°) side by side with white targets, and tested them with the black training bar versus a similar bar at right angles (97% correct), repeating the test with white bars on black backgrounds (68% correct). He simply restated the observed result "the information about the direction of a visual stimulus—is laid down in the central nervous system as an invariant information irrespective of the actual contrast condition". Nowhere does he suggest edge detectors with different orientations.

Twenty years passed. The scene moved to Australia and the use of the Y-choice maze in which the bees could see both targets at the same time. Bees were trained with a forced choice between a grating versus another grating of the same size with randomized widths of the bars, amount of black and numbers of bars, leaving only the orientation difference as the cue (van Hateren et al., 1990). The bees trained on the grating detected the orientation cue in black bars, black/white edges and white bars on a black background, all centred on the reward hole at the centre. As a result, it was accepted that oriented bars were detected by oriented edge detectors and other cues were forgotten.

There followed a number of papers in which the bees were trained on two targets with fixed bars, gratings or crosses, ignoring the position of black areas or other cues, and insufficient tests to rule them out (e.g., Srinivasan et al., 1994; Zhang et al., 1995; Chandra et al., 1998; Horridge 1996a, Fig. 3). In view of the new findings (e.g., Fig. 2), alternative conclusions are more likely. In an improved strategy, the positions of black areas were randomized for all cues except the desired one (Horridge, 1996b, c, 1977). Randomization of the locations of unwanted cues made possible the isolation of individual cues, but fixed patterns were required to demonstrate the retinotopic nature of the cues.

In 1996 the baffles were introduced to define the range at which the choices were made (Fig. 1) but they had the effect of slowing down the bees and allowing them to stabilize in the turning (yaw) plane in flight. This allowed the bees to stabilize the image on the eye. The orientation of a bar was learned only when it was presented in corresponding places on the two targets as seen from the choice point of the bee, i.e., at the same point in eye coordinates (Horridge, 1998). Later it was shown that the orientation cue was lost if the oriented edges were moved on the target in a test (Horridge, 2003a, Fig. 4 therein). The finding that the cues were recognized only in the places where they had been displayed in the training, finally showed that the cue, not the pattern, was retinotopic, but left open the question of what was learned from a single pattern versus a white target.

The new results presented here show that when bees were free to choose the cues presented by a single bar or cross, they preferred the area, the position of the centre and the modulation. The orientations of the edges and the shape or lay-out of the pattern were irrelevant (Figs. 2, 5, 7). With three oblique bars or a grating, however, the orientation cue was detected and the positions of the black areas were less attractive (Figs. 3, 4). When the period of the grating was reduced, the orientation cue disappeared at a period near 3° and the modulation cue near 2° (Horridge, 2003d), but the area of black remained.

5.2. Successive versus simultaneous presentation

In all the earlier work, from von Frisch (1914) to Wehner (1967), in which bees were trained with vertical targets *side by side*, orientation was scarcely mentioned as a cue. The reported cues were the position, the area and length of edge (Cruse, 1972; Anderson, 1977). The situation has been obscured because, without drawing attention to the change in technique, Wehner (1968) switched to training on a single pattern versus a white target, and actually published data showing that the change made no difference to the results with bars. Therefore one must draw the conclusion that in all the work from 1914 to 1987, before the Y-choice maze with simultaneous viewing was introduced (Srinivasan and Lehrer, 1988), the bees could see only one target at a time. For some reason they did not learn orientation, possibly because the orientation cues must be compared in corresponding positions on the two targets (Horridge, 1998). Not surprisingly, with the Y-choice maze from 1988 onwards, orientation was a popular cue. With a single pattern versus a white target, however, the cues were the expected positions of the area of black and the receptor modulation because the forced choice between two patterns was replaced by the preferences of the bees.

5.3. Why do they learn more than one cue?

The very high scores obtained when training on a single pattern versus a white target were partly due to the fact that the bees easily detected the one showing some black (and yet they still made some errors). However, this soft option is not validated by the subsequent tests, which showed in every case that the bees learned several cues in parallel, notably the area, the modulation and the position of the centre (Figs. 2d, 9b). High training scores are misleading only at the start of the training, when the bees first learn to go to black. The high scores show that the bees have an easy choice, not that they see the patterns.

The bees soon learned several cues in order of preference, with their positions, which conferred two advantages. Firstly, in the natural situation the coincidence of several cues makes it less likely that they mistake the place. Secondly, the more cues they learn, the more likely they are to find the reward although some part of the scene is changed.

5.4. Cue preferences

Over the past century, the bees usually had no choice about what cues they should learn; the decisions were in the hands of the experimenter. The results progressively revealed the range of cues that could be learned. This strategy, however, gave little information about the preferences of the bees for different cues.

Training on a single pattern versus a white target revealed the relative preferences for what happened to be available. With each example the bees learned the most preferred cues, which were the location of the centre of black and the location of a strong modulation. When these cues were not available, or were similar on the two test targets, the trained bees revealed that they had learned little about orientation, less about the pattern of six spokes. When trained with the square cross or the ring, the bees learned to go to the centre of black and/or modulation, as before, but they had learned nothing about edge orientations or shape.

Because the feature detectors detect cues, not patterns, and because bees have strong preferences, the bees used a small choice of the same preferred cues for each task, in different proportions and locations on the eye, but nothing more, although they appeared to discriminate patterns if only the successful training was considered.(Figs. 2a, 5a, 6a, 7a, 8a, 10a, 11a, 12a).

5.5. Avoidance of cues not in the training

When testing bees trained on a single pattern, it became obvious that the trained bees noticed unfamiliar cues that had been omitted from the training. The bees behaved as if they marked all the boxes in the list of their feature detectors with a tick or a cross depending on whether they were positive or negative. Maybe this idea can be extended to training on two patterns. The unfamiliar cues improved the score in favour of the training pattern (Figs. 5g–j, 8j, 9e, 10e–g, 12b). As a result, a small black spot with few cues was characterized by what was not there (Fig. 10d–g). This decision process makes full use of the available options provided by the repertoire of feature detectors. It increases the variety of labels and therefore of useful landmarks.

5.6. Generalization

Generalization used to mean the recognition of a pattern although it had been moved to an unfamiliar place (Wehner, 1981), but this is no longer applicable to bees because they use localized cues in different directions on the eye to recognize places, irrespective of the patterns. Generalization came to mean the recognition of similarity, so that the training pattern could be replaced by similar test patterns, or by a mirror image, or part of the training pattern (Wehner, 1971). Sometimes by analogy with human vision, generalization was regarded as a sign of a higher cognitive function, and this view persists.

Recently, generalization was defined as a cognitive ability that allows similar stimuli along a given dimension to be treated as equivalents (Stach et al., 2004). In their example, bees were trained to discriminate between two discs with four differently oriented gratings in each quadrant. The same bees recognized patterns with the same orientations, with only a single bar in some or all of the quadrants. Green contrast was essential, so the highest priority cues were the edge orientations. They did not test whether the local features were integrated together, but they concluded that the bees recognized the patterns on the basis of the best match with the global lay-out.

In other examples, bees categorized visual information and mastered abstract inter-relationships such as sameness and difference (Giurfa et al., 2001); they abstracted global regularities, established correspondences among correlated features and generalized feature assemblies (Stach et al., 2004; Stach and Giurfa, 2005). In retrospect, it was attractive to make an anthropomorphic hypothesis that bees had some form of higher visual processing. When successes alone were considered, bee vision was certainly compatible with this hypothesis, but this did not show that indeed the bees had cognitive processing.

Generalization in this sense is a mechanical result of two factors; first, coarsely tuned feature detectors respond to their appropriate cue with tolerance within a field, and secondly, the bees use the same few common cues, so that they easily accept test patterns as equivalent to training patterns (Figs. 2b, c, 3g, h, 5b, f, 6b, c, 7b, 9c, d, 12b). When the cues that they have learned are displayed, bees readily make choices between test patterns, irrespective of the actual pattern (Horridge, 1997). This is the behaviour expected of a recognition mechanism based on the coincidences of responses of localized feature detectors (Hinton et al., 1986), not a proof of intelligent perception.

After the cues had been identified in each example of training, there was no reason to postulate more. We see here a fundamental paradigmatic shift in the replacement of the older, now out-dated, Gestalt/cognitive/global recognition/perceptual organization/object description theories by a mechanistic theory based on several arrays of a few kinds of independent and localized feature detectors, a theory that can guide electrophysiology and computer modelling.

5.7. Centres and hubs as a primitive separation of objects

As shown in detail, bees detect the position of the centre of a single shape, and they discriminate a difference in the vertical positions of two black shapes on different targets (Horridge, 2003b). Using vectors at right angles to the tangents at edges, they also detect the positions of hubs of radially symmetrical patterns irrespective of the centre of black (Horridge, 2006a) and discriminate differences in the positions (Figs. 5d, j, 6f, 8g, h,). In the new work, a centre of black now turns out to be equivalent to a hub (Figs. 5d, 12d). It is of interest, therefore, whether bees can detect the positions of hubs of several shapes simultaneously, and whether this enables them to detect common objects as separate and discrete hubs although they remember nothing about the actual shapes.

6. Conclusion

When trained to a variety of single patterns versus a white target, the labels that the bees learned were all rather similar because the presence of black, the position of the centre of black and the modulation were preferred cues that were adequate for each separate task. If they had been trained to discriminate *between two* patterns, the labels could have included orientation of an isolated edge, radial and tangential edges, bilateral symmetry and the position of the hub of radial or tangential edges.

In retrospect, the conceptual blocks to understanding the use of landmarks were more significant than the lack of experimental data. Bee vision is anti-intuitive, so it was hard to imagine that the mechanism was so simple, and even more difficult to design the right experiments. Finally it was realized that the bees did not remember the patterns or the landmarks as objects; they remembered the label that marked the right place. From that point on, the identification of the cues, and their coincidences in the labels, was relatively rapid. The bees learned first a coincidence of modulation, area and position, then the less preferred cues, and they recognized added cues that were not in the training, but nothing more.

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