Discrimination of single bars by the honeybee (*Apis mellifera*)

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Abstract

The bees learn to come for a reward to a very simple pattern, a black bar in a fixed position on a white background, in a Y-choice apparatus, with the targets presented in the vertical plane at a fixed range. They were trained on a number of different arrangements of a single bar on one or both targets. The trained bees were then given appropriate tests to discover what cues they had learned. A cue is an essential parameter that is recognized, not the whole pattern. At the choice point they learn exactly which way to look for consistent cues. After training on a single broad bar versus a blank target, they respond in tests to any area of black where they expect to see it, and are less able to detect it the more it has been displaced from the training position. They are more sensitive to vertical than to horizontal displacement of the bar. The cue is anything black of the right size. They do not recognize the shape or orientation of the bar. When trained to discriminate between two bars at right angles to each other, centred on the reward hole, the cue is the edge orientation at the expected places on the targets, and the bees are less able to discriminate the orientation cues the more they are displaced. When trained on a pair of broad black bars in different positions, the cues are the vertical positions of the centres. Division of the bar into squares, or making the edges stepped, removes the orientation cue but not the position cue. Addition of a large black spot or a checkerboard background to the original bar prevents discrimination, as if the spatial reference frame is disturbed. In training, or testing trained bees, parallax does not assist the discrimination of orientation.
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Keywords: Honeybee vision; Learning; Single bar; Filters

1. Introduction

To understand how visual processing systems function, we must first discover the cues that are detected by the visual system. A cue is a constant feature, much less than the pattern, that is detected in many types of patterns. We then consider the required properties of the filters, which are neurons or combinations of neurons, that detect these cues. In the primates the effort is still at the peripheral processing level, but insects offer a much simpler system. Because honey bees learn to come to some patterns for food, we can search for the actual cues used by the bee in pattern perception, beginning with the simplest.

Let us start with a fixed black bar on a white background. A fixed bar is one that stays in the same place relative to the horizontal and vertical axes at the point of choice of the bees during the training. The position of choice of the bees during the training. The position of the bees' point of choice depends on the design of the apparatus. In earlier experiments the bees were trained to a single very large fixed black bar (subtending an angle of 120° in length from the point of choice) versus a blank white target (Wehner, 1969). When the bees were trained to come to a wide bar, they would prefer it to a narrow bar, but when trained to a narrow bar, they could not discriminate it from a wide one, showing that there was something significant about the area of the bar. The trained bees also discriminated a fixed wide bar from a similar bar at a different angle. The results were related to the differences in position on the target, not to the orientations of the edges. The orientations are the directions on the vertical white targets.

Cruse (1972) used data from Wehner and others and found for a restricted number of patterns that the bees respond to two parameters; one was the mismatch in the overlap of the areas when the training shape was superimposed on the test shape, the other was the difference in the lengths of the edges of the two shapes. The relation between the responses and the mismatch of the shapes for certain classes of patterns led to the idea that

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the bees remember the training shape, but the actual experiments showed only that they remembered something about the area and the edge length. The orientation of the bars was not a factor, and other cues were not investigated.

Anderson (1977) trained bees to come to a single broad black vertical bar (subtending an angle of 100° from the point of choice), versus a blank white target, and then tested them with the original bar versus a variety of black shapes which lay within the outline of the training bar and were divided to various extents into smaller bars. The success rate in the tests corresponded to the product of the total length of edge and the area of the test shape. These quantitative results implied that the bees measure the lengths of edges and the areas; they certainly did not demonstrate that the bees learned anything about the shapes, orientations, or linear heights or widths of the bars. The above results were all obtained by training with a single bar versus a blank target.

In more recent work, without reference to the above, interest shifted to the discrimination between a fixed black bar in one position versus a similar bar at right angles on another target. Although a single bar is a very simple pattern, it is impossible to harmonize the results in the earlier and later literature. In discrimination experiments after 1990, it has been assumed, usually without testing alternatives, that when bees discriminate between a fixed horizontal and a fixed vertical bar, the cue is the difference in the orientation (Chandra et al., 1998; Zhang, Srinivasan, & Collett, 1995). Yet others had inferred the cue to be the difference in the positions of two very large bars (Giger & Srinivasan, 1995) or the ends of large bars (Horridge, 1996a). Recent researchers with single bars have all ignored the discrepancies between their own conclusions and the earlier results (for reviews, see Horridge, 1999, 2000a, 2000b; Srinivasan, 1994). One might conclude that the difference in training arrangements produces different results. However, when bees are trained to come to a single fixed bar, or when they learn a difference between two fixed bars, only some of the cues have been identified. It is possible that all are correct when the full story is uncovered. The present task is to resolve the conflicts in this topic.

For example, two main groups and several subgroups of parallel pathways to the visual memory of the honeybee have been distinguished in a recent model (Horridge, 2000b). The detection of edge orientation and radial/tangential edges depends only on inputs via the green receptors, and is therefore colour blind. On the other hand, the discrimination between the sizes or positions of at least two areas of colour or black depends on other inputs that measure photon flux in the green and in the blue receptors (Horridge, 2000b, 2000c). The discrimination between two broad fixed bars could be done by either or both of these pathways, in different proportions depending on the experimental arrangement.

When the bees are trained on a fixed pattern, one way to infer what they learn is to test them with a large number of carefully selected probe patterns, and then infer the cue in each family of patterns by logical deduction from the failures and successes of the trained bees. A cue is a feature, much less than the pattern, that is detected, in many types of patterns. Known cues that are detected in parallel are:- colour, size, position on the target, average orientation, radial/tangential edges, disruption (spatial frequency) and symmetry (Horridge, 2000b). Because the cues actually used depend on the training patterns, several different training configurations must be used, each requiring a number of appropriate tests, all done in the same apparatus, with controls to prevent the bees from learning during the tests. This is the approach used here.

2. Materials and methods

The experiments are done in indirect sunlight under a roof with an open front 3 m wide and 3 m high. The top of the Y-choice apparatus (Srinivasan & Lehrer, 1988) is of clear Perspex, the walls are of white card (Fig. 1). A circular entrance hole 5 cm in diameter allows in one bee at a time. The baffles, of transparent 'Artistcare Drawfilm', 0.13 mm thick, are set in a cardboard frame 1 cm wide. The baffles force the bees to pause and make their choice in the choice chamber. They control the angle subtended by the pattern at the bees' decision point and allow the observer to make a sharp decision at each
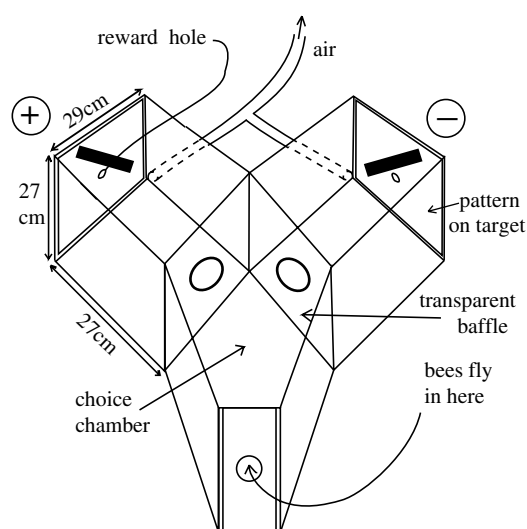

Fig. 1. The Y-choice apparatus. The bees enter through the hole 5 cm diameter into a choice chamber from which they can see both targets. They decide to enter through one of the baffle orifices 5 cm wide. To make the bees look which side to go, the rewarded target with the reward changes sides every 5 min. Odours are extracted by the air pipe.

choice. The bees return the way they came or can pass through slots along the tops of the baffles. The reward, a sucrose solution of appropriate strength to keep the bees coming without attracting recruits, is in a movable black box which they access through the reward hole.

The targets carry the patterns on cards which can be rotated. During training the target that displays the positive pattern and the reward with it is interchanged with the non-rewarded (negative) target every 5 min to prevent the bees from learning which arm of the apparatus to choose. In the illustrations the rewarded pattern is always shown on the left (labelled + at the top).

With the baffles at a distance of 27 cm, the square targets subtend an angle of about 55° at the point of choice. A small group of 10–15 bees are individually marked with spots of fabric paint and other bees excluded. In our conditions, this number ensures a reasonable spacing of the arrivals. A new group of bees is used for each experiment. They require 20 or so visits to build up a discrimination between the two patterns. On the recording sheet, each individual bee has a column, and each horizontal line across the page represents a 5 min period. The criterion for the score is when the bee passes through the hole in one baffle or the other. The criterion without the baffles is the crossing of the line where the baffle would be. After an initial training period of 2–3 h, while training continued, each first choice of each individual bee in each 5 min period was recorded, not the first choice of each arrival. This prevents two choices within each 5 min period if the bee flies back out and enters again. These results are labelled "train" and, with the training patterns, they appear first in the illustrations. All that is required is to have a sample of trained bees, and then find whether they can or cannot do the tests.

Next, a different pair of patterns was substituted for those in the training, and the bees' first choices towards these were recorded in each period of 5 min as before. These are labelled "test". The tests must be carefully controlled. It is essential to give a reward, which can be at random, otherwise the bees continue to search in the Y-maze, and will not go away, but there must be precautions so that the bees do not learn the test patterns. Our apparatus has a narrow entrance which allows only one bee at a time to fly through. If another bee follows, it is easily waved off and made to wait outside the apparatus. Tests with different patterns were interleaved between continued periods of training, so the trained bees do not become familiar with any one test. In the tests the bees get a reward after they have made their only choice in that 5 min period, and when they return the patterns have changed and the side may have changed. In some of the tests the bees fail to discriminate, so they learn nothing from the tests. Tests for 5 min were alternated with 20 min periods of continued training, so filling up each bee's individual column as the hours passed. From

the score sheet, it is easy to observe the performance of each bee individually, for example, to see when they learn the task, and that they do not change their performance in successive tests. Many experiments have been done in previous years to show that the bees do not learn from the test patterns if different tests are interleaved and if the reward is given first to one test pattern and then at another time to the other test pattern. Any one test is not repeated until at least an hour has passed. The scores on the test patterns are compared with scores taken within a short time on the training patterns.

In most of the tests the bees fail anyway, and clearly can learn nothing from them. When the bees fail in a test it is not because they have been rewarded at different times on both targets. If they fail, they fail from the start of the tests. This is easily seen on the protocol sheets for each bee; the scores do not go towards 50%. It is a matter of observation that the results for a given test pattern do not change in a consistent way over time.

The patterns on the targets are made of white, grey, black or coloured papers. The grey and black patterns are made by a Hewlett Packard Laserjet 4M printer. The coloured papers, Nos 384 fawn and 595 light blue, are supplied by Canson Australia Pty, 17 Metropolitan Ave., Nunawading, Vic., Australia. The reflectance spectra of the papers were measured as photon flux with a PC 1000 Fiber Optic Spectrometer, near noon and again in the mid afternoon with the normal ambient illumination of the experiments. The detector, which has a spot field, was placed at the choice point of the bees and the papers at their usual place in the training and tests. The measurements covered a range from 290 to 830 nm, spanning 1035 data points with a resolution of 0.52 nm on average. In the conditions of the experiments, in indirect light, there is negligible reflection of ultraviolet from these papers and the bees' ultraviolet receptors cannot be implicated.

The calibration equipment generated digitized values which were multiplied at 10 nm intervals with the known spectral sensitivity curves of the bee receptor types, over the range from 380 to 620 nm, exactly as done by Giger and Srinivasan (1996). The products were summed to give the relative receptor excitation of the blue and green receptors, for each paper. From these values the relative modulations were calculated for the edge where the papers meet. The Canson fawn 384/light blue 595 combination gives poor contrast to the green receptors (Horridge, 2000c).

The point of all the experiments is to identify the cues that the bees use, not to show how the scores are related quantitatively to the patterns. Performance with most pairs of patterns improves if training is continued for several days, and larger numbers of counts always give a greater statistical significance, but short experiments are more realistic. Training for 2–3 h begins each morning and the experiment was repeated on other days, with

counts of 200 or more choices accumulated over many repetitions of each test. The main requirement is a decision whether the bees can or cannot discriminate in the tests, which is usually obvious, and statistical tests are scarcely necessary.

Two statistical calculations are made. In the first, the number of correct choices is counted in each block of 20 choices. The standard deviation (s.d.) between blocks, for up to 20 of these blocks is calculated, together with the total number of choices. The percentage of correct choices and the value of the s.d. is placed after each significant score.

In the second method (van Hateren, Srinivasan, & Wait, 1990), a minimum estimate of the s.d. is the value of $\sqrt{[p(1-p)/n]}$ where p is the fraction of correct choices and n is the total number of choices. This method assumes that there are no trends, that the individual choices are independent and they have a binomial distribution about the mean. The (s.d.) estimated from this formula is given in brackets after each significant score. By this method a score of 57% based on 200 choices is twice the estimated standard deviation away from the null (random) hypothesis of 50%. The second method usually gives smaller values of the s.d. than the first method.

3. Results

3.1. Training with a single bar versus a blank

A single vertical black bar (subtending 36° by 8°) in the centre of a white background is easily discriminated from a blank white target (Fig. 2a). After 2 h training, the score was 71.0% ± 3.8% (3.2%) correct, $n = 200$ and scores later reached over 80%. Several tests were interleaved over the next 2 days. When the bar was moved 20° to the left and tested against the blank target, the result was 62.5% ± 3.9% (3.4%) correct, $n = 200$, showing that the bees have some memory of the position in the horizontal direction.

In the next test, the bar was turned through 90° about its centre, and tested against the blank target. The result was 60.7% ± 2.9% (3.2%), $n = 240$. The 90° change in orientation or the non-overlap of training and test areas, or both, reduces but does not entirely spoil the discrimination, so the bees do not rely on these cues. The bar in its original place was also tested against an identical bar moved on the target 20° to the left. The result was 51.5% correct, $n = 200$. The bees fail to detect the difference between the original bar and the bar that is displaced horizontally, so the position in the horizontal direction is a weak cue. When tested with a horizontal versus a vertical black and white grating of period 16°, the bees were completely lost, with a score of 49.0%, $n = 200$. There is no sign from any of these tests that the bar orientation was learned.
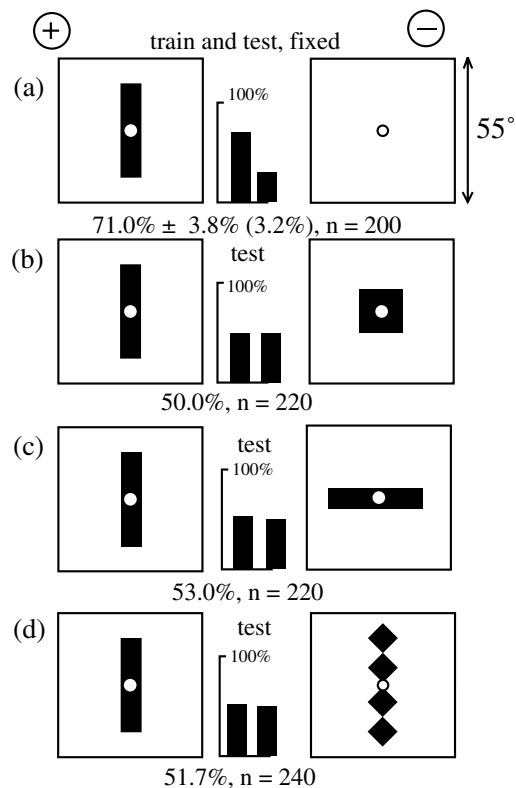

Fig. 2. Training on a single fixed vertical bar versus a blank white target. (a) The training targets. (b) Test with the bar versus a square. (c) Test with the bar versus the bar rotated by 90°. (d) Test with the training bar versus a similar shape without the edge orientation. The bees learn only that there is something black.

Three other tests were made with the original bar versus another shape centred upon the reward hole, all with no discrimination. The trained bees are not able to distinguish the training bar from a square of the same area (Fig. 2b) or from the same bar rotated by 90° (Fig. 2c), or from a vertical row of diamonds (Fig. 2d). They are excellent in the training task, and clearly they have learned to go to a black area, but nothing about shape or edge orientation.

The training was repeated with a new group of bees, this time with the bar placed horizontally across the centre, versus a blank target (Fig. 3a). Again this is an easy task, with a score of 77.5% ± 3.3% (2.9%) correct, $n = 200$, after 3 h training. As before, several tests were interleaved over the next 2 days (Fig. 3). When the bar was moved 10° down and tested against the blank target, the result was 61.5% ± 4.0% (3.4%) correct, $n = 200$, and when it was moved 20° down, the result was 54.5% ± 3.7% (3.5%) correct, $n = 200$ (Fig. 3b), so moving the bar down has a strong effect on the discrimination. Moving the bar upward in the same steps has a smaller effect. Although there is no overlap of the training and test positions, the bar was still detected.

When the horizontal bar is tested against an identical bar moved down by 20° (Fig. 3c), the result was
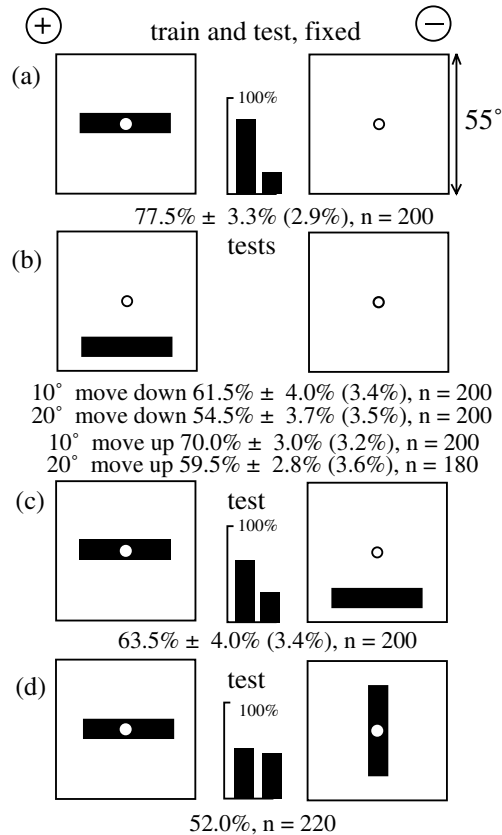
Fig. 3. Training on a single fixed horizontal bar versus a blank white target. (a) The training targets. (b) Tests with the bar moved in the vertical direction. (c) Discrimination between the training bar and the same bar moved down. (d) Test with the training bar versus the same bar rotated by 90°. The bees have learned only the position of something black near the correct vertical level.

$63.5\% \pm 4.0\%$ (3.4%) correct, $n = 200$, which shows that the trained bees discriminate well between the two positions 20° apart in the vertical direction. They know where to look, which is not the case in the horizontal direction for a vertical bar (Fig. 2).

The trained bees are excellent in the training task, and they can distinguish the horizontal bar from the same bar moved in the vertical direction by 20°, but they cannot discriminate it from the square in Fig. 2b or from different shapes of similar size. In particular, they do not distinguish between horizontal and vertical bars centred on the reward hole (Fig. 3d).

In summary, when trained with a single bar versus a blank target in this apparatus, the bees learn the position of a black area in the vertical direction quite well, the position in the horizontal direction less well, but nothing about edge orientation, linear height, or shape.

3.2. Differences between fixed and shuffled oblique bars

In the past the orientation cue has been isolated and the position cue eliminated by shuffling the position of several bars on the target during the training (van Hateren et al., 1990). The results are unexpected when the training is done with single bars.

The bees were trained to discriminate between two targets, each displaying an oblique fixed broad black bar above the reward hole (Fig. 4a). The baffles were omitted for the sake of comparison with earlier work. The bars are at right angles to each other, of equal vertical height and have their centres at equal heights relative to the reward holes. This is not a difficult task. After 3 h training the performance was $69.0\% \pm 4.0\%$ (3.3%) correct, $n = 200$, and continued to improve with further training. Without baffles, the bees fly in without pausing in flight.

On the other hand, with new bees, and with the bars moved on the target every 5 or 10 min during the training without change of orientation (Fig. 4a and b), the result was 53.8%, $n = 1320$, counting all afternoon after 5 h training. If broad black bars are moved during the training, the bees do not learn. This observation suggests that with fixed broad bars the bees learn the positions of the black areas, and shows that they do not
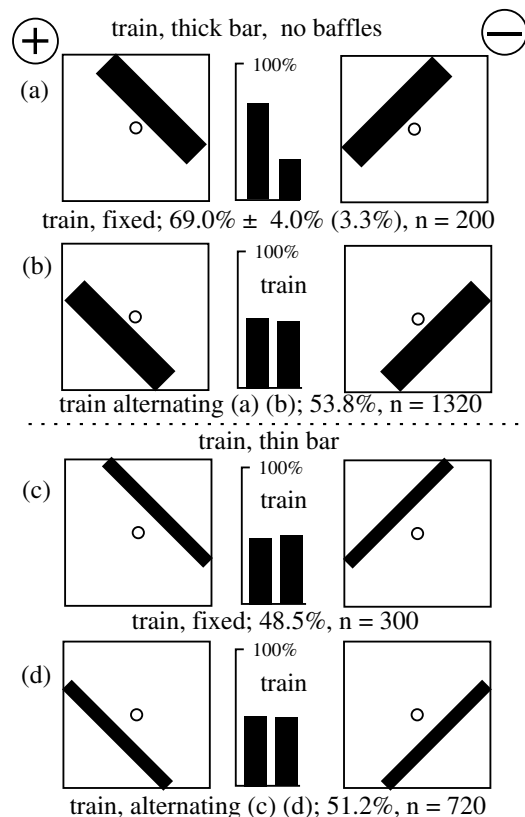

Fig. 4. Fixed and shuffled bars (a) with thick bars (8° by 36°) fixed in different orientations on the two targets, the bees learn to discriminate. (a and b) When the thick bars are alternated between positions (a) and (b) every 5 min they fail to learn. (c) Training with a fixed thin bar (4° by 54°) similarly offset, with baffles, there is no discrimination. (c and d) Training with the thin bar alternating between positions (c) and (d) there is also no discrimination.

look for the bars, otherwise they would follow them as they moved.

There are also unexpected results with thin bars. A new group of bees failed to learn to discriminate from a distance between orthogonal single long thin bars (subtending 55° by 4°) even though they were fixed in position (Fig. 4c). In this case the training result was 48.5%, $n = 300$, after training all day. The explanation is that the thin bar has insufficient area for its location to be learned, and the orientation cues are not in corresponding positions on the two targets, so the edge orientation cannot be learned (Horridge, 1998). Similarly, the single long thin bars are not discriminated from a distance when alternated in location (Fig. 4c and d). The result was 51.2% correct, $n = 720$, training and counting all afternoon.

On the other hand, even when shuffled in position, bars provide an orientation cue when they are presented in corresponding positions during the training (Fig. 5a). The correspondence in position of several edges on the two targets places the orientation cues where the bees learn to look for them on either target (Horridge, 1998).

To investigate the recognition of the orientation cue irrespective of position, a new group of bees was trained with two black oblique bars 4° wide on each target, with no baffles. The bar positions were shuffled by rotating the targets by 180° every 5 min (Fig. 5a and b), keeping the orientation cues in corresponding positions. After 3 h training the result was 75.5% ± 3.7% (3.0%), $n = 200$. Shuffling the location of the bars during the training has the effect that the bees learn the cue within the range of places where it was found during the training.

As an example of the inability to re-assemble the bar from its parts, the trained bees were tested with the bars cut up into squares each subtending 4° by 4° with gaps of 4° between the squares (Fig. 5c). The result of the test was 51.7%, $n = 300$. Each black square gives no average orientation cue and the global orientation of the whole pattern is not recognized.
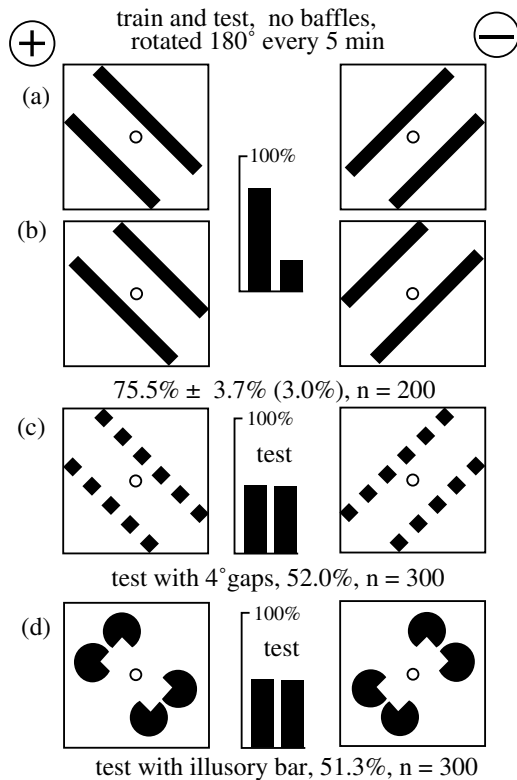

Fig. 5. The orientation cue. (a and b) Training with two bars on each target, alternating between positions (a) and (b) every 5 min. (c) Test with rows of squares; there is no discrimination. (d) Test with an illusory bar; there is no discrimination.
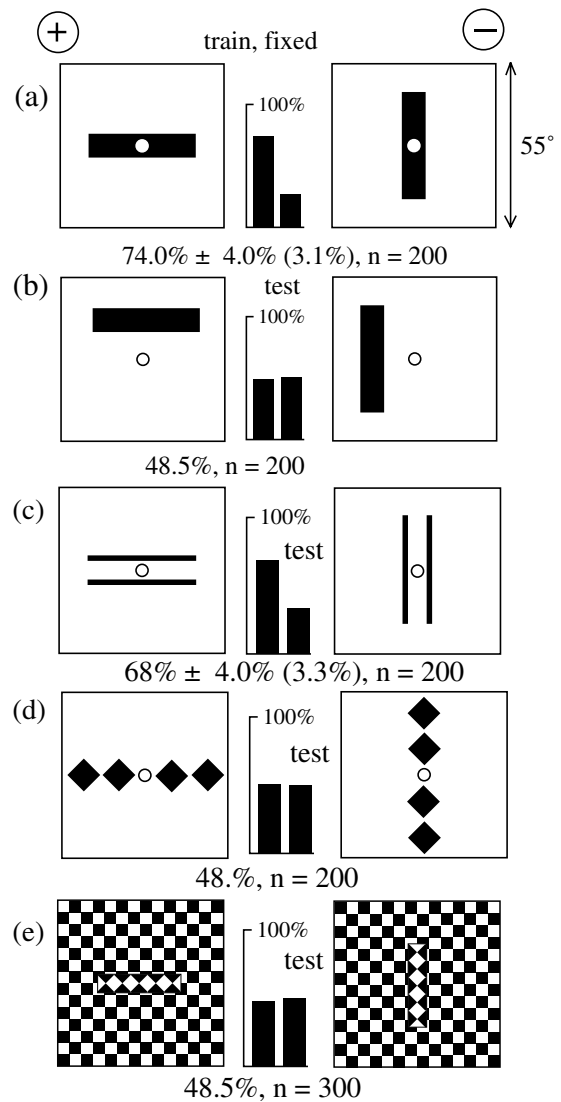

Fig. 6. Training on centrally located horizontal versus vertical fixed black bars, each 36° by 8°. (a) Training patterns. (b) The bars shifted to new positions. (c) Test with only the edges represented by thin bars. (d) The bars are broken into diamonds to spoil the orientation cue. (e) Test with chequered bars raised 6 cm above a checkerboard background. Only the orientation cue in the expected place is detected.

The bees trained to look for an orientation cue anywhere on the target (Fig. 5a and b), were tested with a pattern that might be detected as an illusory bar (Fig. 5d), but they fail to discriminate. The result was 51.0%, $n = 200$. Each black patch on the targets provides no average orientation cue and we infer that the global pattern is not re-assembled. With patterns such as these, with different fixed positions of black areas, however, the bees soon learn the test if it is repeated with one pattern consistently rewarded.

The bees trained to look for the orientation cue anywhere on the target (Fig. 5a and b) were tested with identical oblique black bars on a background of black and white checkerboard (period 8°) but they fail to discriminate. The result was 51.5%, $n = 200$. They were also tested with the black bars raised 6 cm above the checkerboard background, to offer a parallax cue, but with no success. The bees in the choice chamber look repeatedly at the targets and are slow to make a choice at all. When close to the target they fail to find the reward hole on the squared background. Tests of bar orientation on a checkerboard background are inappropriate after training with black bars on a white background (see also Figs. 6e and 11).

In conclusion, when trained on bars with shuffled locations but in corresponding positions on the two targets, the bees learn the orientation cue in its range of places during the training, but the addition of a chequered background spoils the discrimination.

3.3. Training with horizontal versus vertical centred bars

We now turn to discriminations with a fixed bar on each target, first with both bars centred on the reward hole. A group of bees was trained, with baffles, to discriminate between a horizontal black bar 36° by 8° (positive) and a similar vertical black bar (negative), both placed across the centre and of differing vertical dimensions (Fig. 6a). The horizontal bar was the rewarded one to overcome a preference for vertical edges. Learning was slow. After 6 h of training the result was $64.3\% \pm 4.0\%$ (2.8%), $n = 300$, but reached $74.0\% \pm 3.5\%$ (3.1%), $n = 200$ on the next day.

When tested with the bars moved 20° (Fig. 6b), the trained bees failed to discriminate them in their new locations. This result, 48.5%, $n = 200$, shows that the bees do not search for the bar, or look at the bar in isolation, otherwise they would discriminate it when it is moved.

When the trained bees were tested with black squares (8° by 8°) which replace the ends of the bars, there was a negligible preference of 54.5%, $n = 200$ for the horizontal arrangement. The squares convey no orientation cue and are not large enough to act as cues of position. This result also shows that the heights and widths of the patterns are not a significant cue.

When tested with bars that are composed of a checkerboard of small squares (each subtending 4°), there was a small preference of $58.0\% \pm 3.5\%$ (2.8%), $n = 320$ for the horizontal arrangement,. The cue is inferred to be the unchanged general position of black because the cue from the edge orientation has been reduced by breaking the bar into squares (see Fig. 5c). The trained bees were also tested with black exchanged for white but they fail to discriminate.

When the bees trained on centred bars (Fig. 6a) were tested for orientation with two thin black lines (Fig. 6c), discrimination was $68.0\% \pm 4.0\%$ (3.3%), $n = 200$, and with single thin black lines it was $66.0\% \pm 3.5\%$ (3.3%), $n = 200$, which shows that the bees find the orientation cue when it is at the right place. The cue is the edge orientation in the expected place. This conclusion is supported by their poor discrimination of a row of diamonds at the right place but with incorrect edge orientation (Fig. 6d). The result was 48.0%, $n = 200$, which again shows that the edge orientation is essential but the vertical dimension of the bar and the shape or general distribution of black is not the cue. The trained bees must first identify the right place to look for the cue, and are confused when the targets differ strongly from the training targets. For example, when tested with a pair of coarse black and white gratings, the bees fail.

The bees trained on horizontal versus vertical centred bars were also tested with checkerboard bars raised 6 cm above checkerboard backgrounds (Fig. 6e). To the human eye, the bars are very obvious as seen by parallax generated by head movements, but the bees fail completely to discriminate them. The result was 48.5%, $n = 300$. When presented with these targets, the trained bees refuse to make a choice for several minutes, and it is clear that this is not a suitable test for bees trained with black bars on a white background. When the same test is frequently repeated, rewarding the horizontal bar each time, the bees eventually find a cue, possibly the shadows of edges.

The bees trained on centred black bars (Fig. 6a) were also tested with two black spots subtending 12° added to the training targets. The result was 54.0%, $n = 200$. The bees fail to discriminate. The bars themselves are unchanged, so the added spots must make the bees look in the wrong place. When they approach the reward hole, the bees fly towards the spot, as if it interferes with the direction in which they look for the cue.

3.4. No green contrast

To remove the orientation cue, the bees trained on the horizontal (positive) and vertical (negative) fixed black bars (Fig. 6a) were also tested with bars made of fawn paper (Canson 384) in the same positions on a blue (Canson 595) background, giving no contrast to the green receptors. To the blue receptors, the fawn bars

look dark on a light background, as in the training, but the bees fail to discriminate. The result was 50.5%, $n = 200$. There is no transfer of the discrimination because the lack of green contrast deprives the bees of the orientation cue.

3.5. Tests with only vertical patterns

A new group of bees was trained to discriminate between a vertical black bar subtending 8° by 36° (positive) and a similar horizontal bar (negative), with both bars centred on the reward hole (Fig. 7a). Learning was rapid; $68.5\% \pm 4.0\%$ (3.3%), $n = 200$ after 6 h of training, with scores over 75% on the next day. In the tests, one target displayed the vertical bar, or a variant of it, and the other target also displayed a variant of the vertical bar.

With the vertical bar in its expected position versus two thin black bars in place of its edges (Fig. 7b), the score was $61.5\% \pm 2.3\%$ (3.5%), $n = 200$ in favour of the original bar, but well below the score during training. The black lines, where the edges are expected to be, have less attraction than the whole bar. With the bar displaced away from the centre versus the two thin black bars, however, the score was 52.0%, $n = 200$. The two targets were not discriminated although the thick bar in its expected place is distinguished from the two black lines, showing again that shape is not a cue and the training bar has no salience.

The trained bees prefer spots in the right place to the orientation cue. With two black spots (subtense 15°)

versus the two thin vertical bars (Fig. 7c), the result was $59.5\% \pm 3.5\%$ (2.5%), $n = 200$ in favour of the spots, not the bars. This is the result of a forced choice between two unfamiliar targets, and is explained by the bees' preference for black spots, especially when they are in the right place.

In summary, when they learn to discriminate between a fixed black orthogonal bars placed across the centre, the bees learn to look only in the right place. They remember the orientation of edges, and something about the location of black. They do not necessarily combine these cues to make an internal image of the bar. They do not recognize the shape of the bar, and when it is moved on the target, or a black spot is added, they do not recognize it.

3.6. Training with bars offset from the centre

In the next experiment the training bars offer different cues because they have their centres at different positions on the targets. A group of bees was trained with baffles to discriminate between a fixed horizontal black bar (positive) and a similar vertical bar (negative) subtending 8° by 36°, with both bars offset from the centre (Fig. 8a). Learning is initially slow, possibly because the bees must first learn to look in two different places, neither of which is at the centre, and the training is against the spontaneous preference. After 4 h of training the result was 55% and after 6 h was $65.0\% \pm 4.0\%$ (3.2%), $n = 220$ rising above 70% on the next day. As before, the trained bees were given a variety of interleaved tests between periods of continued training.

When tested with the bars across the centres of the targets, not overlapping with their former positions, the result was $61.5\% \pm 3.2\%$ (3.4%), $n = 200$, showing that something is recognized. The further the bars are moved from their expected positions, however, the more difficult is the discrimination. When tested with the bars moved to the other side of the reward hole (Fig. 8b), the result was 48.5%, $n = 200$ in favour of the horizontal. From this we can infer that the bees do not look for the bar in isolation, or detect its linear vertical height, and they do not detect the vertical bar from a distance with the aid of horizontal (yaw) movements in flight.

The trained bees were also tested with two black lines (width 1°) in the positions of the edges of the training bars (Fig. 8c). Surprisingly, the result was only 57% correct choices, $n = 200$. Edge orientation is not the major cue that it is when the training bars have their centres at the same place.

When tested with the bars in their training positions but composed of black and white checkerboard of period 8°, the bees discriminated with a result of $61.0\% \pm 3.5\%$ (2.8%), $n = 300$, but they fail to discriminate the checkerboard bars when they lie across the
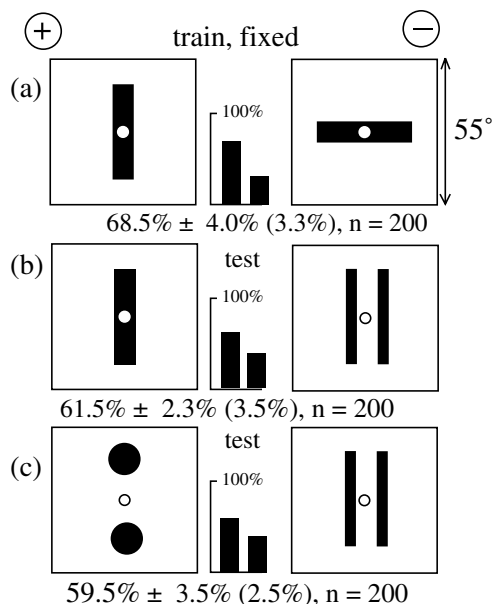

Fig. 7. (a) Train on vertical versus horizontal fixed bars that are centred on the reward hole (the reverse of the targets in Fig. 6a). (b) Test the training bar versus two bars in the positions of the edges. (c) Test with two spots versus two bars.
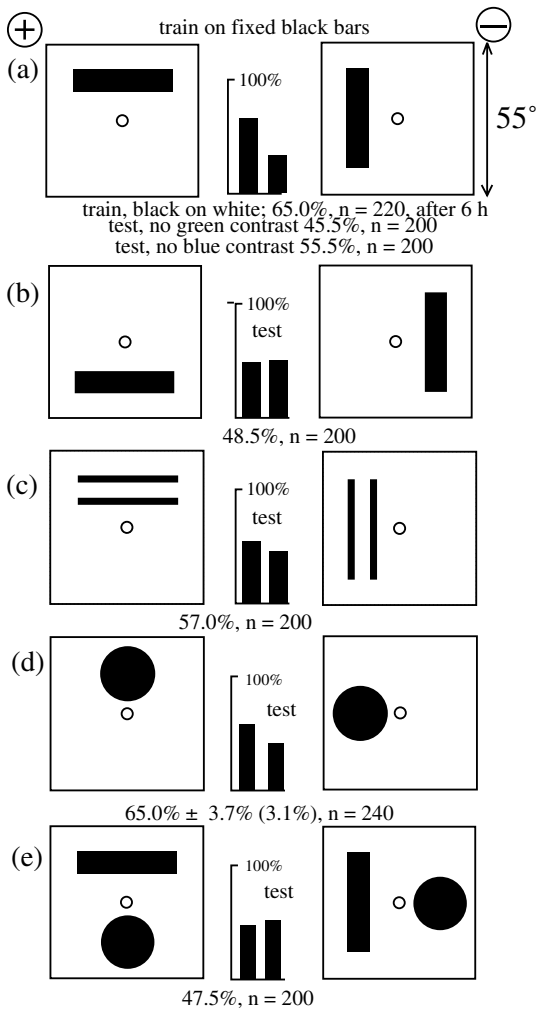
Fig. 8. Training on offset vertical and horizontal single fixed bars. (a)
Training patterns. (b) Test with the bars moved to the opposite sides of
the centre. (c) Test with two thin bars in the positions of the edges. (d)
Test with single spots in the former positions of the bars. (e) Test with
the original bars and an added spot.

centre, in agreement with the finding that the position of
black is the major cue.

In the training situation (Fig. 8a), a possible cue is the
difference in positions of the centres. The trained bees
were therefore tested with each bar replaced by a black
spot subtending 18° (Fig. 8d). The result was 65.0% ±
3.7% (3.1%), $n = 240$ in favour of the correct position. A
similar result was obtained when the trained bees were
tested with two identical oblique bars centred upon the
centres of the training bars. The result was 62.0% ± 4.0%
(3.4%), $n = 200$ in favour of the correct position. These
results show that the position of the centre of the bar is
the cue, the orientation or shape does not matter, and
the vertical dimension of the bar is not a cue.

When tested with the bars in their original positions
with a black spot (subtending 18°) added (Fig. 8e),
discrimination is lost. The result was 47.5%, $n = 200$.

When black was exchanged for white on both targets,
discrimination was reduced to 62.0% ± 3.7% (2.8%),
$n = 300$. These are factors that spoil the direction of
looking.

The trained bees were also tested with each bar in the
training position but rotated by 90° on its centre. The
weak orientation cue is now in opposition to the strong
position cue. The result was 59.0% ± 2.7% (3.5%), $n =
200$, in favour of the correct position.

In conclusion, with the training bars in different pla-
ces, the bees learn the difference in position of the cen-
tres, not the vertical dimensions, shape, or orientations
of edges. An added background or spot spoils the dis-
crimination by interfering with the expected position of
the cue.

3.7. Training on oblique fixed bars

In the next experiments the two broad black training
bars were oblique and centred at corresponding places
on the targets, so that they have the same vertical di-
mensions and the same position of the centre below the
reward hole. This pair of patterns, with mirror image
symmetry, presents the bees with no difference in mod-
ulation of the receptors (flicker) as the bees in flight scan
the targets. As before, there are cues of position of the
bar ends and edge orientations. The baffles were omitted
so that the results could be compared with previous
work (Chandra et al., 1998; Srinivasan, Zhang, & Rolfe,
1993; Zhang et al., 1995). A new group of bees was
trained to discriminate between a black bar (subtending
35° by 8°) at 45° to the vertical, and the same bar at −45°
(Fig. 9a). After 3 h training the result was 65.0%,
$n = 200$, and later between tests reached 78.0% ± 3.0%
(2.4%), $n = 300$. Over 4 days, between periods of further
training, the trained bees were tested in a variety of
ways. At times, performance between tests was above
80% correct.

In the first test (Fig. 9b), the bars were placed above
the reward hole on both targets, but they are scarcely
discriminated. The result was 56.5% ± 3.2% (3.5%),
$n = 200$, which shows that the bar does not have to
move far for recognition to be lost. Clearly the bees do
not search for the bars.

In the next test (Fig. 9c), the bars in the training lo-
cations were broken into three squares each subtending
8° by 8°. The result was 55.0% correct, $n = 200$, but the
discrimination of the training patterns at this time was
near 80% correct. Although the squares lie in the orig-
inal locations of black, the average orientation cue has
been removed by breaking the bars into squares (see
Figs. 5c and 6d). With the bars above the reward holes
and broken into squares, so that the location is changed
as well as the bar being disrupted, the result was 51.5%
correct, $n = 200$. Therefore the bees rely upon the dif-
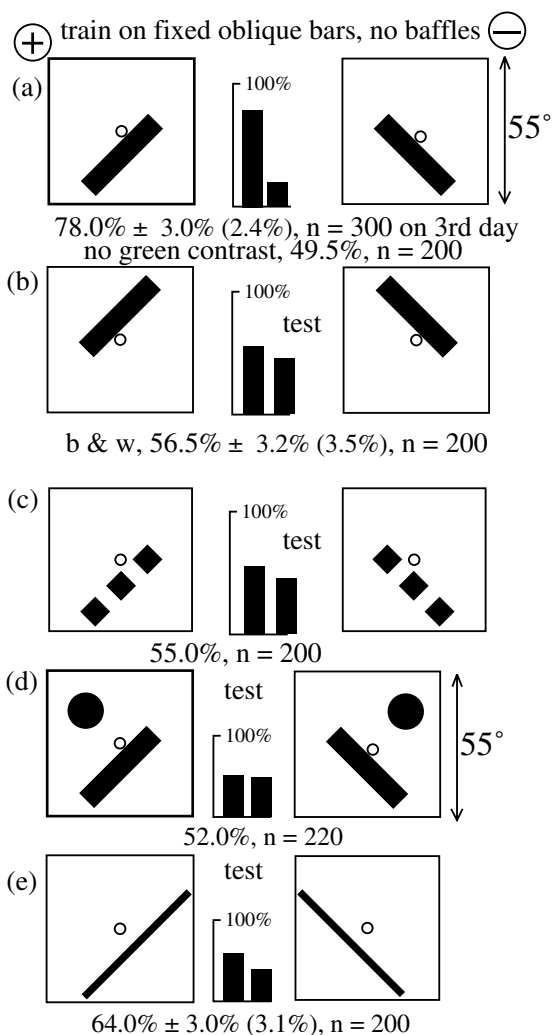ference between edge orientations at the right places.

Fig. 9. Single oblique fixed bars (36° by 8°) below the reward hole. (a) The training situation. (b) Test with the bars moved above the centres. (c) Test with the bars divided into squares each 8° by 8° separated by gaps of 6°. (d) Single spots added to each target spoil the discrimination. (e) Test with thin bars.

When the trained bees were tested with a small but resolvable white gap 4° wide in the centre of the black bar, the performance was reduced from 80% during training to $69.0\% \pm 3.5\%$ (3.3%), $n = 200$. The areas of black are scarcely changed, but the orthogonal edges reduce the average orientation cues.

The trained bees were also tested with bars of blue Canson paper 595 on a background of fawn 384 paper, with the bars in the training positions below the reward hole. The result was 49.5%, $n = 200$. The lack of green contrast means that vision cannot be stabilized and also that the orientation cue is not available.

The bees trained with the fixed oblique bars (Fig. 9a) were given more interleaved tests. In the first, a black spot (subtense 16°) was added to both targets (Fig. 9d). The bees failed to discriminate and they did not improve with repetition of the test with a consistent reward. With

a similar spot, but blue (Canson paper 595), discrimination failed at the first test, but improved steadily over six repeated and suitably rewarded tests, to a performance better than 70% correct. Although the added blue spot is at first a distraction, the bees can learn to ignore it.

When the background is black in the tests and the bars are white, discrimination is poor, with a result of 57.5%. When the trained bees are tested with a checkerboard background to the bars, they are slow to make a choice and behave as if quite lost. The result was 49.5%, $n = 300$. When tested with two regular oblique gratings of period 16°, the bees behaved as if they did not know where to look, and discrimination was reduced to $60.5\% \pm 3.1\%$ (3.5%), $n = 200$. These results again show that discrimination fails when the direction of looking is disturbed.

With a thin bar in the original training position (Fig. 9e), the result was $64.0\% \pm 3.0\%$ (3.1%), $n = 240$, and with the thin bars above the reward hole, the result was $61.5\% \pm 3.0\%$ (3.4%), $n = 200$. These results show that the trained bees recognize an orientation cue only exactly in the correct place.

3.8. Training with a black spot on the target

When it was discovered that a black spot added in the tests spoils the frame of reference for position, a new group of bees was trained (with baffles in place) with a black spot, subtending 12° already in place, above bars subtending 30° by 6° in corresponding positions on the left side of each target (Fig. 10a). After 3 h training the result was $70.0\% \pm 3.5\%$ (3.2%), $n = 200$ over the next 2 h. When these trained bees were tested with the spots removed (Fig. 10b), performance was reduced to 52.0%, $n = 200$, although the bars were unchanged. Again, discrimination of the orientation cue fails when the reference frame is changed after training, although the bar itself is unchanged.

3.9. Tests with the same cue on both targets

We now return to tests to see whether the trained bees can distinguish between the training bar and a different pattern with the same cue (as in Fig. 2b–d). A group of bees was trained (as in Fig. 9a, with baffles) to discriminate between the orthogonal oblique bars (subtending 36° by 8°). The trained bees were tested with a target displaying the original bar versus a target displaying two thin parallel bars (each subtending 36° by 2°), all with the same orientation (Fig. 10c). The performance in the test was 55.0%, $n = 200$ correct, although it was over 75% during the continued training between tests. The trained bees have difficulty in distinguishing between the bar and lines at the edges of the bar, showing that there is nothing special about the bar.
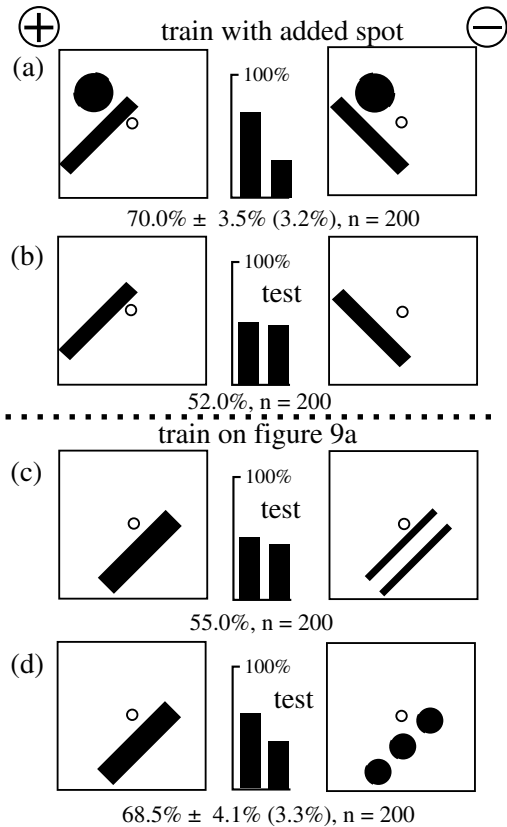
Fig. 10. (a) Train with a spot and a bar on the left side of each target. (b) Test without the spots. (c) After training as in Fig. 9a, test of the training bar versus edges only. (d) After training as in Fig. 9a, test of the training bar versus a row of three spots.

The bees look for the orientations of edges at the correct place on the target (the cue), not for the whole bar (the pattern).

The trained bees were also tested with a target displaying the original bar versus a target displaying a row of three spots with the same global orientation (Fig. 10d). The result was now $68.5\% \pm 4.1\%$ (3.3%), $n = 200$. The bees have no difficulty in distinguishing between the bar and the row of spots, showing that the cue lies in the orientations of the bar edges at the correct place, and not in the distribution of black without the orientation cue.

In conclusion, with equal but orthogonal oblique bars centred at corresponding points on the targets (Fig. 9a), the cue is the difference in orientation at the right place. The cue has no salience, as shown by the failures when the edges are moved from the expected place, or when the frame of reference is disturbed.

3.10. Testing with bars composed of black and white squares

The discovery that equal lengths of edges at right angles cancel out the orientation cue (Srinivasan, Zhang,

& Witney, 1994) implies that when the bars or background are made of black and white squares that are resolved, the orientation cues will be submerged in a mass of conflicting orientations. We have already illustrated examples (Figs. 6e and 9c).

Bees trained without baffles on the fixed oblique bars (Fig. 9a) fail to discriminate when tested (without baffles) with similar bars composed of random squares (pixel size 2° by 2°) 50% black, 50% white on a white background (Fig. 11a). The result was 54.5%, $n = 200$. The bees may know where to look, but the only cue they have, the edge orientation, is spoiled by many lengths of orthogonal edges.

The same bees trained as in Fig. 9a were also tested without baffles with a pattern in three dimensions, with the patterned bars (36° by 8°) raised 6 cm above the patterned background (Fig. 11b). Both bar and background were covered with a pattern of random pixels (50% black, 50% white, pixel size 2° by 2°) to generate a parallax cue as the bees moved in flight. The pixel edges were all horizontal or vertical. The bees refused to respond to this test, but continued to fly about in the choice chamber for a long time. Training to discriminate between the orientations of two fixed black bars on flat white backgrounds is not a suitable training for discrimination of an orientation cue that might be detected by the parallax of a raised bar over a background of resolvable lengths of orthogonal edges. Instead, therefore, it was decided to train with the background already in place.

3.11. A black bar on a random pixel background

On the next day, bees trained on the fixed oblique bars (Fig. 9a) were retrained, again without baffles, with a pair of oblique black bars (36° by 6°) with a white border 3° wide, superimposed flat on patterned targets (Fig. 11c). Both training targets had backgrounds of randomly arranged squares (50% black, 50% white, pixel size 2° by 2°). The bees learn quite quickly to discriminate the orientations of the plain black bars on this background. After 3 h training the result was $62.5\% \pm 3.7\%$ (3.4%), $n = 200$. After 6 h training the result was 66.5%, $n = 200$. The patterned background does not prevent learning. When tested with the plain black bars on a white background (Fig. 9a), the trained bees responded better than in the training, with 82 correct out of 100 choices. Removing the patterned background does not spoil the discrimination of the plain bars.

The bees trained with plain bars on a patterned background (Fig. 11c) were tested with the patterns in three dimensions, with the bars (36° by 8°) raised 6 cm above the background (Fig. 11b). The bars and backgrounds in the tests were covered with a pattern of random pixels (50% black, 50% white, pixel size 2° by
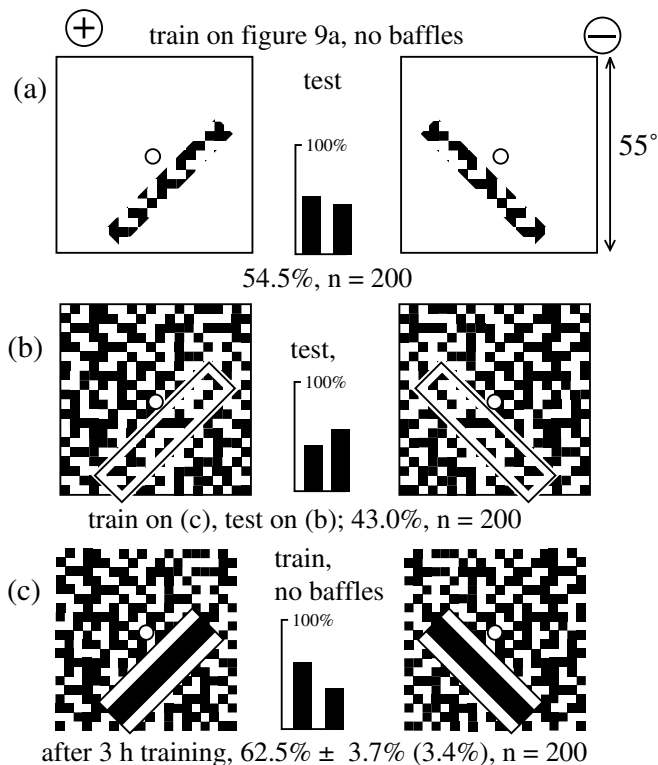
Fig. 11. Textures of random pixels, 50% black, 50% white. (a) The bees were trained on the fixed bars (Fig. 9a) and tested on textured bars (pixel size 2°) on a white background. (b) The same bees were tested with three dimensional patterns with a textured bar raised 6 cm above a textured background. (c) New bees were trained with a black bar flat on a random pixel background (pixel sizes 2°). The bees trained in (c) were tested with the three dimensional pattern in (b). There is no evidence that the bar orientation can be discriminated using the parallax.

2°). The bees are quite hopeless in this test and could not at first find the reward hole. The actual score was 43.0%, $n = 200$. The conclusion is that raised bars of black and white squares on a patterned background are not suitable test patterns when the patches of pixels and edges are large enough to be resolved by the bees. Parallax does not assist the discrimination of the orientation of the bars.

Following from this result, the bees trained on Fig. 11c were also tested with the three dimensional patterns with 4 mm pixels, which each subtend 0.8° and are too small to be resolved by the bees. This pattern is not the same as grey because the pixel patterns are not regular. Care was taken to reduce the formation of shadows. The result of the test was 39.0% correct, $n = 300$. The conclusion is that in three dimensional patterns with a bar raised by 6 cm, and with pixels that are too small to be resolved, bees that are already trained on the black bar on a patterned background (Fig. 11c) do not detect the orientation of the raised bars.

As a final check, the bees trained without baffles to discriminate between two fixed black bars on a white background (Fig. 9a) were tested with a pair of targets made of plain white bars raised 6 cm over plain white backgrounds. The result was 58.5%, $n = 200$, showing that with no black at all on the targets, well trained bees

find sufficient contrast in the shadows to give a weak discrimination between the raised white bars. Therefore, if bees can be trained to discriminate the orientation of a patterned bar raised over a patterned background, it is probable for several reasons that they use some other cue such as shadows, not parallax. Of course, the bees may see the parallax, the problem is that they do not learn or recognize the orientations of the edges of the bars by use of parallax.

4. Discussion

When the patterns are fixed in relation to the choice point of the bees, and discrimination is successful, it is not possible to discover what is remembered by the bees unless a great many carefully designed tests are done to investigate all the probable cues. When the bees fail in a test, one can infer that they do not find the expected cue in the test patterns. In the present work, even with a single bar, a large number of tests have been made, and two cues, position and orientation, can be inferred while several others have been eliminated.

Similar methods have led to the inference of two classes of channels in parallel in the visual discrimination system of the bee (Horridge, 2000b). The first class

retains the position of one, two or a few areas in colour, or the size and location of the centre of a black area, irrespective of shape or orientation. The other class are colour-blind channels that detect the orientations of edges on each side of the target, and the presence of edges that are radial or tangential relative to a centre.

As a result of doing many tests, several points are clarified. The data obtained before 1990 with a single bar versus a blank was reliable, but the failure to discriminate when the bar was moved did not imply that the bees remember the spatial representation (eidetic image) that is laid out upon the eye. The more economical explanation is that the bees learn exactly where to expect the cue, in this case the existence of the black area (Figs. 2 and 3). The training results obtained after 1990 were also reliable. The assumption that the cue is the difference between the edge orientations is correct when the bars are centred at the reward hole on both targets (Figs. 6 and 7). When the bars are centred at different places on the two targets, the bees learn their positions (Fig. 8).

In many earlier experiments, however, tests were made in such a way that the bees could learn the test pattern as the test was repeated. A study of the literature reveals that the training results were correct, but the results of tests with other patterns in fixed positions were sometimes over 60% when they should have been near 50%. When repeated with several different tests interleaved and no consistent reward to any one test pattern, to prevent learning during the tests, only test patterns with the correct cue in the expected place are discriminated. This re-examination harmonizes the old data and the recent training data, all of which are repeatable, but it implies new interpretations of both old and recent work.

4.1. Where to look

The bees are familiar with the geometry of the apparatus before training starts, otherwise they would not arrive for the training. Between experiments, both of the targets in the apparatus (Fig. 1) were blank but sugar syrup was provided at both. The bees arrive at the choice chamber with no indication which side to go. On the morning of the experiment the training patterns are placed on the targets, only one of which is rewarded so that 50% of the choices are at first wrong. The rewarded pattern with the reward changes sides every 5 min so that the bees are obliged to look at the targets to see which side to go. After 2–4 h, depending on the task, the bees are sufficiently trained. At a point in the choice chamber, called the point of choice, they learn to look at the place where they find consistent cues, which could be the position of an area or the orientation of an edge. Probably they learn the most obvious cue first.

Let us first consider the cue provided by the direction of a black area, as seen from the point of choice. The geometry of the apparatus provides several reference points and contrasting edges. The bees' posture in flight allows a measure of the positions of the centres of the black areas in the vertical direction but not so well in the horizontal direction (Figs. 2 and 3). Bees will not learn the orientation of a thick bar that is moved during the training (Fig. 4a and b), and trained bees fail to discriminate orientation in tests in which a broad bar is moved to a new place on the target (Figs. 6b, 8b and 9b), so the bees do not follow the shift of the bar. In other words, neither the bar nor the orientation cue has salience, otherwise the bees would detect them when they are moved.

However, when two or more black bars are shuffled in corresponding positions on the two targets during the training (Fig. 5a and b), the bees learn to ignore the position cue and they expect to find the orientation cue within the range of places where it occurred during the training.

Next, the discrimination is spoiled by the addition of a black spot or a patterned background (Figs. 6e, 8e and 9d), so these additions must alter the expected direction of both position and orientation cues relative to the reference coordinates. The bees can learn the discrimination when the spots or backgrounds are present throughout the training, but the discrimination is then lost if the spot is removed (Fig. 10b), and may be reduced if the background is removed. The position of the cue has not changed, and so the discrimination is lost because the reference coordinates have changed and the bees do not know which way to look.

In the apparatus used here (Fig. 1), the results are the same if the bees make the choices in free flight after the baffles have been removed, or if they pause at the baffles. There is no evidence that they fixate on the reward hole, and there is abundant evidence that they do not follow the movements of the cue or the bar. Instead, at the point of choice they must be making use of reference coordinates from the geometry of the apparatus. Then, based on these coordinates, they learn to look for the consistent cue in exactly the expected place. There is no evidence that they recognize the patterns, only the cue in the right place.

4.2. What to look for

The cue in the experiments with bars is the orientation at the expected place or the position of the centre of the black area. Anything that moves the centres spoils the discrimination, even if the bars are unchanged, but changing the pattern without moving the centres or the cue has no effect (Figs. 2b and c, 3e, 6c, 8d and 10d). A reasonable area of black is necessary for its position to be learned. If the targets are coloured, the bees may use

relative positions of two colours, but there is less data about that (Horridge, 2000c).

When there is no cue from the difference in positions of the centres (Figs. 6a and 9a), the naive bees must find another consistent cue, frequently a difference in edge orientation. The orientation detectors sum together the orientations of edges in the same region in such a way that equal lengths of orthogonal edges cancel the orientation cue (Srinivasan et al., 1994). Again they learn the averaged orientation in the expected position, and if it is not there, the rest of the pattern counts for nothing (Figs. 5c, 6d and e and 9c).

Previous work has revealed two other useful cues. When the bees are trained to a single fixed black shape versus a blank target, they learn something about the area and something about the length of edge in the pattern (Anderson, 1977; Cruse, 1972). The 'area' is related to 'size', and 'edge length' to 'disruption' or 'spatial frequency'. As before, if the pattern is moved on the target for the tests, discrimination fails because these cues are no longer in the expected positions. The qualitative parameter related to the score in the recognition response is the shift in position, not the reduced overlap.

When trained on a single bar versus a blank target, the bees learn nothing about shape, bar height or edge orientation. When the bees are trained with a single fixed broad black bar versus an orthogonal bar centred on the same place, they learn the edge orientation, which must be at the expected place on the target, and little else (Figs. 6 and 9). They do not learn the shapes. When the bees are trained with a bars at two different places on the respective targets, they learn the positions and little else (Figs. 2, 3 and 8). In some situations with fixed shapes in different positions, there is no evidence that the bees remember the orientations of the edges at all, only the difference in positions of the centres (Horridge, 1997b). If there are two or four bars on the targets, the edge orientations are averaged, the bees do not discriminate them separately (Srinivasan et al., 1994), and the pattern is not re-assembled (Horridge, 1996b, 1997a). The formal arrangement of the several parallel pathways that account for these results has been summarized in a model (Horridge, 2000b). The visual system of the bee detects cues in the expected places and processes them separately, but the image is not re-assembled. The vision of the bee distinguishes different classes of cues with reference to a strict local spatial frame of reference, not different shapes irrespective of the surroundings, in the way that human vision does.

4.3. Patterned bars on patterned backgrounds

Bees have difficulty in learning to discriminate between targets that have a background pattern of black and white squares, as if they cannot find a consistent reference position. The equal lengths of edges at right angles in the pattern cancel the orientation cue (Srinivasan et al., 1994).

The cancellation of the orientation cue by equal lengths of edges at right angles means that we have to reconsider the use of checkerboards and randomly arranged square pixels in discriminations of orientation. The only cue so far discovered in a checkerboard is the period of the pattern (Horridge, 1997b). The visual system of the bee does not recognize a global orientation of squares or spots that are separately resolved, and bees trained to the orientation cue do not recognize an orientation cue in a line of squares (Figs. 5c, 6d and 9c), or in other patterns (Figs. 5d and 10d) where the individual parts display no average orientation.

When the bees are trained to discriminate orientation, they fail in tests with raised patterned bars over a patterned background (Fig. 11b), unless there are cues from shadows or the bees learn from repetition of the tests. The patterns of edges at right angles cancel the orientation cue, and also prevent the bees from looking in the right place. With long training, the bees eventually find alternative cues, probably shadows. None of the tests give any indication that parallax assists discrimination of orientation (Fig. 11). On the other hand, even a plain white bar raised by 6 cm over a white background provides sufficient shadow for discrimination. If the orientation of a bar composed of a pattern of black and white squares is discriminated when raised 6 cm over a background with a similar pattern, whether or not the pixels are resolved (Zhang et al., 1995), there must be another cue such as a difference in shading or blurring.

In conclusion, the bees learn a frame of reference, look for each cue in exactly the expected place, and detect the separate cues in parallel. They do not remember the global pattern, only the cues. There is no evidence for, and much against, the idea that a pattern is laid out spatially in memory for measurement of parameters or for recall. These results bring together three principles of how bees recognize patterns; first, the idea that the bees learn exactly where to look from the choice point, secondly, the idea that generalized cues are detected by a limited variety of neural filters that detect the different cues, and thirdly, the idea that each cue is recognized only within the expected range of places. This conjunction of requirements ensures that the bees make a response with minimum processing only to the correct pattern in the right place. In artificial vision or in evolution, by progressively increasing the number of filters in parallel and their corresponding cues, this mechanism of discrimination can be improved to any required level of specificity.

Acknowledgements

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