

Pattern discrimination by the honeybee (*Apis mellifera*): training on two pairs of patterns alternately

G.A. Horridge *

Centre for Visual Sciences, Research School of Biological Sciences, Australian National University, GPO Box 475, Canberra, ACT 2601, Australia

Received 1 July 1998; received in revised form 10 August 1998; accepted 21 August 1998

Abstract

Pattern discrimination in the honeybee was studied by training alternately with two different pairs of patterns. Individually marked bees made a forced choice from a fixed distance in a standard Y-choice maze for a reward of sugar solution. Bees were trained, first on one pair of patterns for 10 min then on a second pair, and so on, alternately between the two pairs. The pairs of patterns were selected to test the hypothesis that bees have a limited number of parallel mechanisms for the detection and discrimination of certain generalized global features. If this is so, it might be expected that each channel could process one pair of patterns simultaneously, but two pairs of patterns that are processed by the same channel would interfere with each other during the learning process. Features tested were: average orientation of edges, radial and tangential edges based on a symmetry of three or six, the position of a black spot, and the exchange of black and white. The bees fail to learn when the two alternated pairs of patterns offer the same feature, and they discriminate when the pairs offer two different features. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Honeybee; Vision; Alternate patterns; Filters

1. Introduction

In the study of visual discrimination, a great deal can be learned from the relative performance of an animal in different but related tasks. In the case of bee pattern vision, bees can learn to distinguish some patterns but they confuse others. From their successes and failures we can make inferences about the system that makes the discrimination. To study the learning mechanism, however, the experiment must engage the process of learning, not only the final performance. The experiments presented attempt to do this.

Bees can discriminate between two large targets that differ in the position of areas of black that stay in the same place on the target during the training period, even though the targets are interchanged every 5 min to prevent the bees learning the correct choice by use of landmarks. They must therefore learn the difference between the locations of black in relation to the central reward hole or to the geometry of the apparatus. When presented

with other targets in which the areas of black are displaced, the trained bees sometimes make a choice according to how much the new area of black overlaps with the one on which they were trained (Wehner, 1981, Figs. 60, 86). They can also distinguish between a sector pattern and the same pattern in which black and white are interchanged (Wehner, 1981, Fig. 59). In these tasks, with each target in a fixed angular orientation and subtending 130° at the choice point, the bees respond as if they have learned the position of at least one black area but little more can be said. They respond as if indifferent to the shape of the outline. With these very large black and white targets that are fixed in angular orientation during the training, the resolution of a rotation is excellent. For example, when bees are trained for at least 10 h and the criterion of success is the landing of the bee on the target, they detect a few degrees rotation of a square cross of two bars on a vertical surface if one bar is horizontal. That they can do this shows that they use the direction of gravity and the geometry of the apparatus to stabilize their vision and fixate their attention on the target. The cue is neither the orientation of the actual edges nor the global directions of the bars (Wehner,

* Fax: + 61-2-6249-3808; E-mail: horridge@rsbs.anu.edu.au

1967) but the locations of the ends of the bars (Horridge, 1996b). In general, the mechanisms of discrimination of location of areas of black are unknown.

However, if the pattern subtends less than about 40° at the point of choice, the bees cannot be trained to discriminate a black cross of two bars at right angles on a white background from the same pattern rotated by 45° , although similar rotation of a single bar of the same angular size is easily discriminated (Srinivasan et al., 1994). When presented with a pattern composed of several bars, also subtending less than about 40° at the point of choice, bees behave as if they fail to discriminate the locations or angular orientations of the separate bars. There are many simple patterns composed of edges or bars that are confused when the targets subtend less than 50° at the choice point (Horridge, 1996a). This evidence, and the inability to discriminate the shapes of closed contours, shows that in targets of this size, in forward vision, there cannot be a photographic memory that is compared with each newly presented image.

A second type of visual processing is demonstrated when the locations of edges and areas on the targets are shuffled during the training process.

Bees can learn the average angular orientation of bars or a grating, although the positions of the bars are randomized during learning. This result, together with the failure to discriminate the rotation of a 40° square cross, led to the proposal that the angular orientation of straight edges, averaged over quite large areas, is detected and discriminated by a family of filters. The proposed filters have different axes of angular orientation, are broadly tuned for average angular orientation of edges, and have relatively large fields (Srinivasan et al., 1994). The large fields explain why the individual bars in a cross or other combinations of bars are not separated from each other and why the edges can be shuffled in location without spoiling the discrimination of a feature that is kept constant during training.

Bees can be trained to discriminate circular from radial patterns, although areas of black, numbers of sectors and sizes of circles are all randomized during the training. The trained bees transfer their training to unfamiliar patterns containing these cues and distinguish them from other patterns not containing these cues, showing that bees learn radial and tangential cues as generalized features (Horridge and Zhang, 1995). To account for these results, filters with large fields and a radial structure and other filters with a circular structure were proposed (Horridge, 1994; Fletcher et al., submitted), analogous to those for orientation. When bees are trained to come to a neutral grey or check pattern, then presented with a varied choice of patterns that they have not seen before, they spontaneously avoid concentric patterns but prefer others with a radial structure (Lehrer et al., 1995). In this case there was no memory of a pattern, so the filters are innate. Such filters would detect a region of

radial or tangential edges but would confuse cues of the same kind within their field. In all this work, the cues are edges irrespective of the exchange of black and white, the spatial resolution is excellent and the bee fixates its attention in relation to the geometry of the apparatus.

There are therefore two quite distinct types of discriminations of black and white patterns: those that are dependent on the exact location of a large area in relation to the geometry of the apparatus, and those in which a limited number of global filters detect various angular orientations of edges. In the former, reversal of contrast causes a reversal of the bees' choice. In the latter, the cues can be shuffled in location because the filters have large fields. Also, black and white can be exchanged during the training or tests, as if the input to the filters is the power in the contrast at edges, as in most visual systems, rather than intensity. The present paper tests some of the implications of this analysis.

As in the transmission of light or information, a filter is defined as a component in the visual system which accepts and lets through a part of the signal. The output of a filter reveals only that the field contained the appropriate feature of the image but no information about the origin or number of simultaneous stimuli, so that two features of the same kind in one field cannot be separated by that filter, or further centrally, unless there is additional information in another channel. With an unknown number or variety of parallel pathways, however, it is no easy task to determine the number of filters and their individual properties. The following procedure is a way to tackle this puzzle.

The selection of patterns in the following experiments is based on trials with various combinations. First, I had the idea from the types of patterns that are useful as successive cues for bees in a simple maze (Zhang et al., 1998). If they can be learned in succession, perhaps they can be learned simultaneously. Second, there are the distinct types of pattern that can be discriminated when they are shuffled or rotated so that locations of edges and areas are useless as cues. Third, there are patterns differing in location of an area of black.

2. Materials and methods

The bees came from a local hive within 50 m of the experimental apparatus and could return to it in 5 min. The experiments were done in the Y-choice apparatus (Fig. 1), with baffles and a circular entrance hole 5 cm in diameter that helps to keep out newly recruited bees. The apparatus was situated under a roof with an open front 3 m wide and 3 m high, with the targets facing the open sky. The walls of the apparatus are of white card, the top is of clear Perspex. The baffles, of transparent 'Artistcare Drawfilm', 0.13 mm thick, are set in a card-

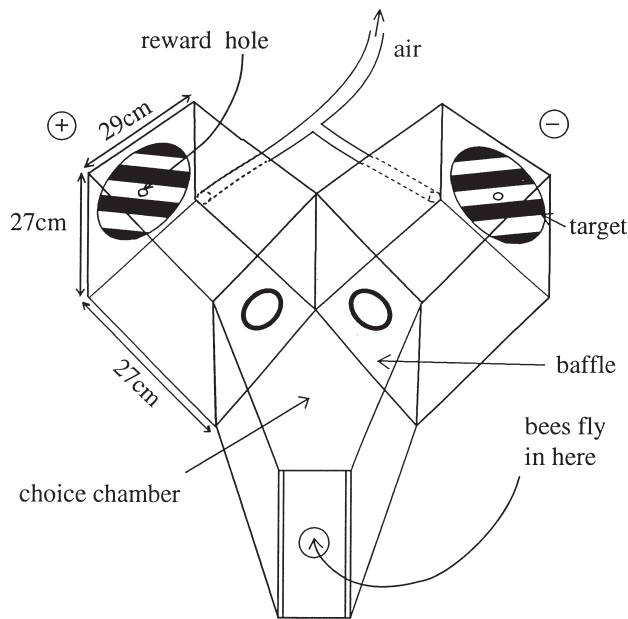


Fig. 1. The modified Y-choice apparatus, which stands outside on a table under a roof. The top is transparent Perspex; the sides are lined with white paper. The bees enter through a hole 5 cm diameter in the front to a choice chamber from which they can see both targets. They enter one side or the other through one of the baffle orifices 5 cm wide. The targets and the reward change sides every 5 min to prevent the bees from learning which side to go to. The air pipes extract odours.

board frame 1 cm wide. They control the angle subtended by the target at the bees' decision point, and allow the observer to make a sharp decision about the success or failure of the first choice. The 5 cm diameter hole at the centre of each baffle is surrounded by a black annulus 0.5 cm wide. The bees can also exit by walking over the baffle. The targets have a hole 2 cm in diameter at the centre, in positive ones for access to the reward and in negative ones leading to a blind tube. With a blank target, the bees can see this hole from behind the baffle and they usually fly directly towards it.

The reward is a fresh aqueous solution of sucrose sufficiently concentrated to keep the marked bees making regular visits without recruiting too many unmarked bees. The patterns are printed in black on white paper of constant quality. The positive and negative targets change sides every 5 min to prevent the bees from learning which arm of the apparatus to choose, but in the figures the rewarded pattern (labelled ' + ' in the illustrations) is always shown on the left. The bees were trained on one pair of patterns for 10 min (5 min on each side), and then the patterns were exchanged for the alternate pair for 10 min. The targets with radial or tangential cues were rotated at random every 5 min to make the locations of edges and black areas useless as cues. When possible, instead of interchanging the positive and negative targets after 5 min on one side, they were both rotated and the reward was moved to the other arm of the apparatus. This strategy means that the bees have

less chance of using cues, such as odours or accidental details in one target and not in the other, that are not relevant to the experiment.

With the baffle at a distance of 27 cm, the targets of 25 cm diameter subtend an angle of about 50° at the point of choice. The bees are individually marked with one of five colours on the thorax and on the abdomen, and a record is kept of the first choice of each bee in each 5 min period. The group of bees makes a total of 5–15 visits between each change of pattern. The bees require 20 or so visits to build up a memory of a single pattern. There were no tests on unfamiliar patterns.

After an initial training period of 2 h, the number of correct first choices was counted in each block of 10 choices, while training continued. The results from each pair of patterns were recorded separately. The numbers of correct choices in each block of 20–40 blocks are used to calculate the means and the standard deviations. The results are tested by a χ^2 test for a difference from a chance probability (0.5) and then converted to percentages. For a count of 300 choices, a performance of 60% is always statistically significant when the standard deviation is 4% or less. Actually, the statistics are unnecessary because the bees either could or could not learn these combinations of patterns. The results are shown in the figures.

In each experiment the aim was to see whether the bees can do the task or not after a reasonable period of training. By watching the bees in the choice chamber, one can frequently see whether they look at the targets and decide quickly or whether they spend a long time examining first one target and then the other. When the task is impossible they sometimes go at once to one side and then to the other if the first is unsuccessful.

3. Results

3.1. Discrimination between a pair of patterns

Honeybees are readily trained to discriminate between the selected patterns (Fig. 2), most of which have been used in previous work.

The angular orientation of a grating (Fig. 2(a–c)) is discriminated irrespective of the number or positions of the bars. The widths and positions of the bars can be randomized during training and the black and white areas can be interchanged without spoiling the discrimination. To discriminate all the possible angular orientations of a bar or grating there must be a minimum of three broadly tuned filters with widely separated axes of orientation (Srinivasan et al., 1994).

Bees discriminate the rotation of six radially arranged thin bars, one rotated by half the interbar angle relative to the other (Fig. 2(d)), but not between similar patterns with four, five or seven bars (Horridge, 1997). This

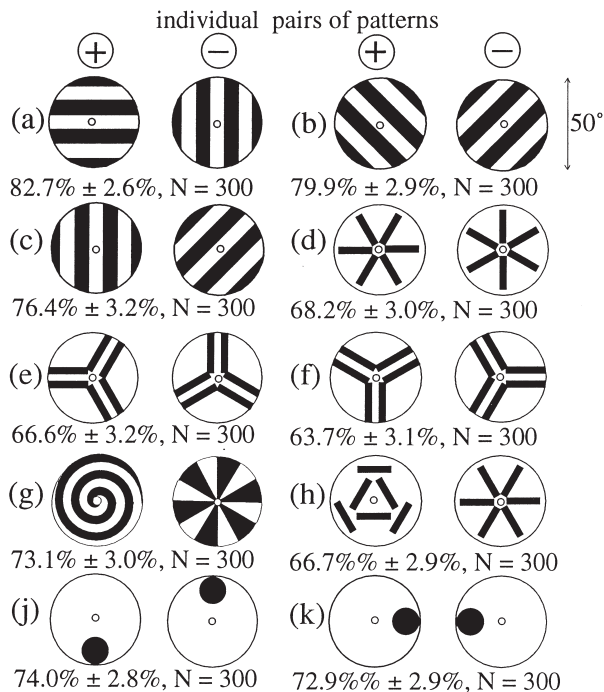


Fig. 2. Discrimination of individual pairs of patterns of the following types: (a–c) parallel gratings, identical apart from angular orientation; the bars can be shuffled in position; (d) two six-ray stars composed of identical bars, one rotated by 30° relative to the other; (e,f) patterns with threefold symmetry, in four positions that are discriminated from each other, fixed in angular orientation during the training; (g) spiral versus six sectors, both 50% black, rotated during training; (h) tangential versus radial patterns of six equal bars, rotated during training; (j,k) four different locations of a single spot that subtends 16° at the point of choice, fixed in position during the training. All discriminations are statistically significant.

result led to the hypothesis that the filters are restricted to radial symmetries based on three and six. Targets with a radial symmetry of three are discriminated in four separate positions (Fig. 2(e,f)), leading to the hypothesis of several filters with a radial symmetry of three, with different axes of orientation. These patterns are necessarily held in the same angular orientation during training. Numerous experiments with two or four bars show that the separate locations or angular orientations of the individual bars are not discriminated (Horridge, 1996a).

A spiral and a sector pattern (Fig. 2(g)), both with 50% black and 50% white, are readily discriminated although both patterns are rotated every 5 min during training. Similar radial and tangential patterns composed of six bars of equal size (Fig. 2(h)) are discriminated, although randomly rotated every 5 min during the training. Previous work has shown that tangential and radial cues are separately discriminated from a neutral pattern such as a checkerboard (Horridge and Zhang, 1995). This result led to the proposal of separate filters for radial and tangential edges.

Turning now to a difference in the position of an area of black, a vertical or horizontal difference in position

of a large black spot can be discriminated (Fig. 2(j,k)). This is quite a different type of behaviour which does not depend solely on the arrangement of edges. The centre of gravity of the black area must be constant in position during the training period but the shape of the outline is of no interest to the bee.

Performances for these separate discriminations are given in Fig. 2.

3.2. Alternations of pattern pairs that prove difficult

In these experiments a group of bees was trained for 10 min first on one pair of patterns then on a second pair for 10 min, and so on, repeated alternately with the two pairs. The following experiments were designed to force the bee to use a single type of filter for both pairs of patterns to see whether the two tasks could be kept separate.

The following refers to discriminations that prove difficult to learn (Fig. 3):

(a) one pair has a horizontal versus a vertical grating and the other pair has a $+45^\circ$ versus -45° gratings, all of the same period, 15° . These patterns were fixed in constant angular orientations during the training.

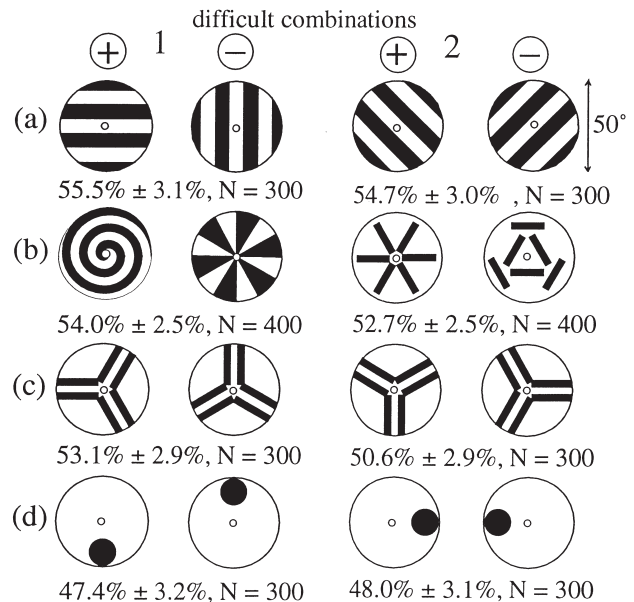


Fig. 3. Patterns that bees do not discriminate when trained alternately on pairs 1 and 2: (a) horizontal versus vertical gratings, and $+45^\circ$ versus -45° ; these patterns were fixed in position during the training; (b) a spiral of period 8° versus 12 sectors, and six radial versus six tangential bars; these patterns were randomized by rotation during the training; (c) two positions of bar patterns based on symmetry of three, and two other positions of the same pattern; these patterns were fixed in position during the training; (d) a spot (subtense 16° at the point of choice) at the top of the pattern versus the same spot at the bottom, and the same spot at right versus at left. None of these discriminations are statistically significant.

The bees do not learn these two different tasks simultaneously;

(b) one pair has a spiral of period 8° versus 12° sectors, and the other pair has six radial versus six equal tangential bars. These four patterns were individually randomized by rotation of each one during the training. The bees do not learn these two tasks, although the patterns look very different to us;

(c) one pair has two positions of bar patterns based on symmetry of three, and the other pair has two other positions of the same pattern. These patterns were all fixed in angular orientation during the training. The bees do not learn the two tasks. This result suggests that the four orientations are not represented as separate filters; and

(d) one pair has a spot (subtending 16° at the point of choice) at the top of the target versus the same spot at the bottom, and the other pair has the same spot on the right versus one on the left.

The bees fail when they are faced with two tasks involving the same type of pattern, although all eight of the pairs are readily learned individually (Fig. 2). They do not learn one of the pairs and ignore the other, which would improve their chance of a reward. They behave as if each filter cannot be used for two tasks. It is my view that the alternation of two pairs is teaching them to ignore the main cue, which in Fig. 3(a) is the orientation and in Fig. 3(b) is the difference between radial and tangential. Their failure certainly shows that they have no other cue, although the patterns look different to us.

The positive cue is tangential for the spiral/sector patterns but is radial for the patterns of six bars in Fig. 3(b), so they are being taught not to use the tangential and radial cues, and are left with nothing else. In Fig. 3(a,c) the patterns all look different to human vision but the result again suggests that the cues excite the same set of filters in the bee. The positions of the spots in Fig. 3(d) are all different but the bees are unable to learn that they are positive in two positions and negative in the other two, when they are seen in the same context.

We can infer that the bees do not find a consistent cue in either the positive or in the negative targets. This result is understandable if there is in fact only one available channel of processing for each of these cues, and this channel receives conflicting inputs.

3.3. Easy alternations of pattern pairs

Bees easily learn to discriminate when one alternated pair of patterns is of one type and the other pair is of quite a different type. The following examples of training alternately on pairs 1 and 2 refer to Fig. 4:

(a) one pair has orientations of a regular grating at -45° versus $+45^\circ$ and the other pair has the spiral

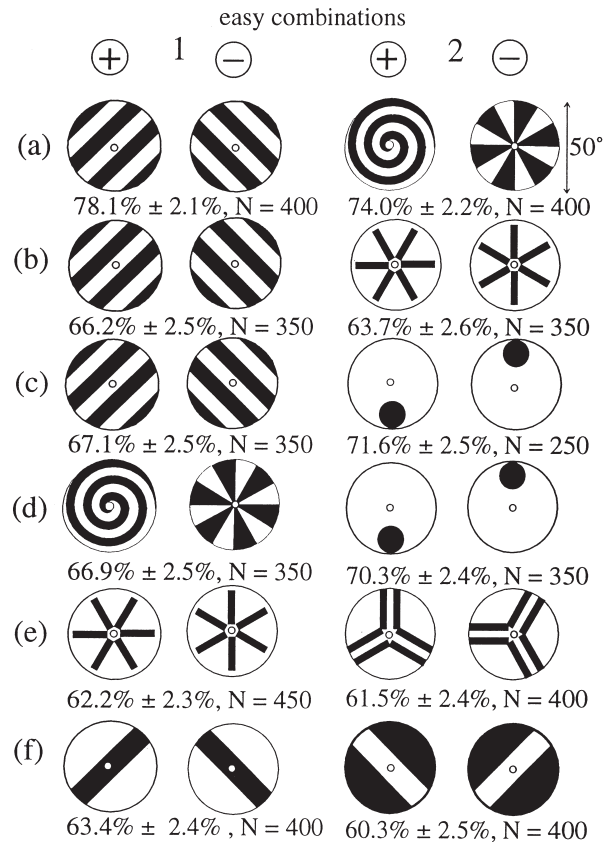


Fig. 4. Patterns that bees easily discriminate when trained alternately on pairs 1 and 2: (a) orientation at -45° versus $+45^\circ$ and spiral versus sectors; (b) orientation at -45° versus $+45^\circ$ and two six-ray stars with different orientation; (c) orientation at -45° versus $+45^\circ$ and two spots, one at top versus one at the bottom; (d) spiral versus sectors (randomly rotated) and two spots, one at top versus one at the bottom; (e) two fixed six-ray stars with different orientation and two fixed three-ray stars with different orientation; (f) single bar at $+45^\circ$ versus -45° and the same bar patterns with black and white interchanged. All discriminations are statistically significant.

versus sectors. The latter are randomized by rotation every 5 min. All patterns are 50% black and 50% white. The performance is over 70% for each pair. This agrees with the proposal of separate processing of angular orientation of straight edges and tangential/radial edges;

(b) one pair has orientations at -45° versus one at $+45^\circ$ and the other pair has two six-ray stars with different axes of angular orientation. As already known from other types of experiment (Horridge, 1996a), this result agrees with the idea of global filters that sum the separate angular orientations of edges over large fields;

(c) one pair has orientations at -45° versus one at $+45^\circ$ and the other pair has two spots, one at the top versus one at the bottom. Angular orientation discrimination is unrelated to the memory of the location of a spot. With the bees' landing on the target as the criterion, Giger and Srinivasan (1995)

showed that an angular orientation of edges and a location of an area of black can be learned simultaneously from the same pair of patterns;

(d) one pair has a randomly rotated spiral versus sectors and the other pair has two spots, one at the top versus one at the bottom. Tangential/radial discrimination does not interfere with the memory of spot location;

(e) one pair has two six-ray stars with different axes of orientation and the other pair has two three-ray stars. If we take into account that the bees do not use locations or orientations of individual bars as cues (Horridge, 1996a), the result agrees with the proposal of separate filters for symmetries based on three and six in radial coordinates (Fletcher et al., submitted); and

(f) one pair has a single bar at $+45^\circ$ versus one at -45° and the other pair has the same bar patterns with black and white interchanged. At first sight, these two pairs teach the bees to ignore the main cue, the orientation, but in this case there are other possible cues. The patterns are stationary during the training and there are large areas of black. The bees may have used the fact that the positive target always has black in the top right hand and bottom left hand quadrants. It is less likely that the bees learn to prefer one orientation in a dark target and the opposite one in a light target. This example illustrates the difficulty of designing suitable tasks that separate parallel mechanisms.

Needless to say, these results rule out the idea of a retinotopic copy of the image. These results are compatible with the hypothesis of a limited number of separate parallel pathways. The bees succeed in learning the discrimination when the two tasks involve different types of the proposed filters. If two tasks are being learned at the same time, there is a restriction caused by the limited variety of processing pathways.

3.4. Three pairs of patterns

Although it is not clear what can be gained by using three pairs of patterns, one experiment was tried with pattern pairs (b), (e) and (j) in Fig. 2, training for periods of 10 min each for 2 h, before counting the score for the next 4 h while training continued. The separated results for the pairs in the combined training were: (b) $59.6\% \pm 2.8\%$, $N = 300$, (e) $63.2\% \pm 2.8\%$, $N = 300$ and (j) $55.6\% \pm 2.9\%$, $N = 300$. The bees learn (b) and (e), but they hardly learn (j) in this time. It may or may not be informative that they perform badly with the spot position as a cue, although they could learn the same difference in spot positions either alone or in alternation with either of the other pairs taken separately.

4. Discussion

Any theory of bee pattern vision has to incorporate the fact that some pairs of simple patterns that subtend less than 50° at the choice point are discriminated after 2 h of training but others are always confused. This fact alone rules out a photographic memory of the image. A limited number of mechanisms must lie in parallel, but not sufficient to discriminate all patterns. Comparing the results in Fig. 3 with those in Fig. 4 now shows that some combinations of pairs of patterns can be learned when alternated but others cannot. This result and the strategy of training on alternate pairs again show that bees do not learn a copy of the image. We can turn, however, to the mechanisms that have already been proposed to explain a large number of known failures and successes of honeybee pattern discrimination.

First and foremost, bees have a mechanism that can discriminate the position of the centre of gravity of at least one area of black or colour in relation to a centre of fixation or to the spatial coordinates that are laid down by the geometry of the apparatus. This mechanism can only function when the targets are fixed in location during the training period. Possibly more than one location of black can be learned in a single pattern but the outlines of closed contours are ignored. The present results throw no light on the properties or mechanisms of this kind of discrimination, but they are in agreement with the proposal that a separate channel is involved.

Second, several broadly tuned global filters with large spatial fields have been proposed (Horridge, 1994; Fletcher et al., submitted). The hypothesis, illustrated in Fig. 5, is that modulation of the receptors passes to the lamina, where contrast is selectively amplified but the background level of intensity is adapted away. At the next stage, in the medulla, edges and their axes of orientation are detected. These local units have been inferred in the bee (Yang and Maddess, 1997) and recorded in the locust (James and Osorio, 1996). Families of these small-field units with a single common angular orientation axis feed into a number of large-field units (Fig. 5(a–c)) that have broad tuning, perhaps as wide as 90° at the 50% sensitivity level. These orientation detectors retain the orientation axes but are insensitive to the polarity of the edges or their location in the image (Yang and Maddess, 1997). Other large-field units collect families of local edge detectors that are orientated radially from the centre of fixation (Fig. 5(e,f,h,i)), and others collect families that are orientated tangentially (Fig. 5(d,g,k,l)). These two groups have several representatives with different angular orientations in radial coordinates. These filters are all essentially innate detectors of arrangements of edges, with high spatial resolution. Also there must be two or three filters that are circular (Fig. 5(j)), in different sizes, that in cooperation are able to estimate the angular size of fixated targets.

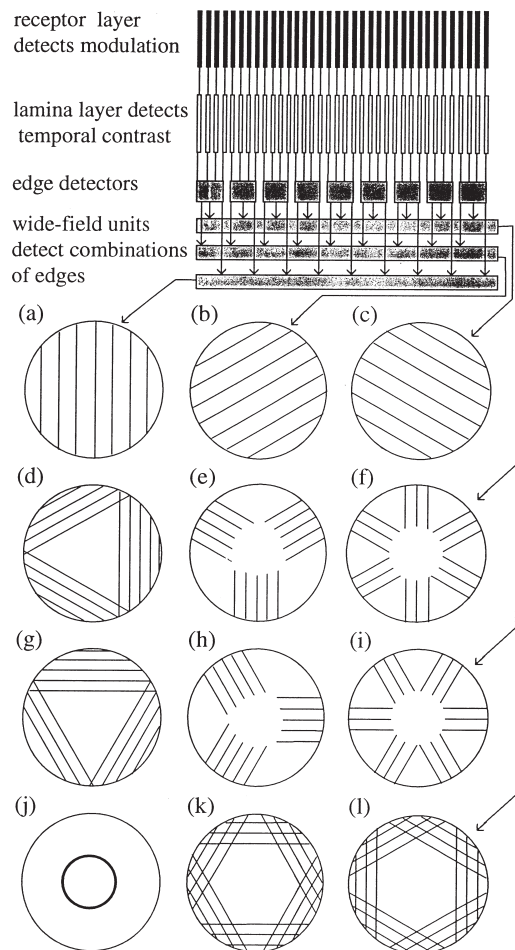


Fig. 5. A representation of the filters that detect generalized features in large fields. The inputs to these filters are large numbers of unit edge detectors in the appropriate arrays. The outputs of these filters are parallel pathways to memory. They can be active simultaneously, but each can learn only one cue at a time. Together they could code the differences between numerous two-dimensional patterns that contain various mixtures of the features to which they are sensitive (modified from Fletcher et al., submitted).

The results presented here are compatible with the hypothesis that these filters act in independent parallel pathways and that learning is hindered when one filter becomes engaged in two incompatible tasks. The bees cannot learn whether a cue is positive or negative according to the rest of the pattern that contains it. They detect the cue or not. They do not learn one of the alternate pairs and ignore the other. The result may be different if the bees are trained first on one pair and then on another in a different context, for example, in a maze with successive choices (Zhang et al., 1998), but that remains to be seen. With successful alternate training (Fig. 4) they behave as if each channel learns simultaneously, progressively and independently. In principle, the method will test whether any postulated filters act independently during the learning process. The strategy

reminds us that to study the learning process, the experiment must bear upon it, not on the final performance.

When bees learn most ordinary tasks, presumably each channel can process only one type of cue, and some patterns are confused because channels are limited in variety. Even so, the filters act in parallel, so that, given sufficient contrast, the bees can discriminate between many patterns but not all, just as three types of cones in the human eye can collaborate together in each small region of the image to allow many mixtures of wavelengths, but not all, to be distinguished.

Acknowledgements

I am much obliged to Edyta Kucharska for many hours of patient counting of bee choices during the course of these experiments, and to Professor Neville Fletcher and an unknown referee for helpful comments on the manuscript.

References

- Fletcher, N.H., Horridge, G.A., Greentree, A.D., submitted. Spatial filters and insect vision.
- Giger, A., Srinivasan, M.V., 1995. Pattern recognition in honeybees: eidetic imagery and orientation discrimination. *Journal of Comparative Physiology A176*, 791–795.
- Horridge, G.A., 1994. Bee vision of pattern and 3D. *Bioessays* 16, 877–884.
- Horridge, G.A., 1996a. Vision of the honeybee *Apis mellifera* for patterns with two pairs of equal orthogonal bars. *Journal of Insect Physiology* 42, 131–138.
- Horridge, G.A., 1996b. Pattern vision of the honeybee (*Apis mellifera*): the significance of the angle subtended by the target. *Journal of Insect Physiology* 42, 693–703.
- Horridge, G.A., 1997. Spatial and non-spatial coding of patterns by the honeybee. In: Srinivasan, M.V., Venkatesh, S. (Eds.), *From Living Eyes to Seeing Machines*. Oxford University Press, Oxford, pp. 52–79.
- Horridge, G.A., Zhang, S.W., 1995. Pattern vision of bees: flower-like patterns with no predominant orientation. *Journal of Insect Physiology* 41, 681–688.
- James, A.C., Osorio, D., 1996. Characterization of columnar neurons and visual signal processing in the medulla of the locust optic lobe by system identification techniques. *Journal of Comparative Physiology A178*, 183–199.
- Lehrer, M., Horridge, G.A., Zhang, S.W., Gadagkar, R., 1995. Pattern vision in bees: preference for radial patterns. *Philosophical Transactions of the Royal Society of London B347*, 123–137.
- Srinivasan, M.V., Zhang, S.W., Witney, K., 1994. Visual discrimination of pattern orientation by honeybees. *Philosophical Transactions of the Royal Society of London B343*, 199–210.
- Wehner, R., 1967. Pattern recognition in bees. *Nature (London)* 215, 1244–1248.
- Wehner, R., 1981. Spatial vision in arthropods. In: Autrum, H. (Ed.), *Vision in Invertebrates, Handbook of Sensory Physiology, Vol. VII/6C*. Springer, Berlin, Heidelberg, New York, pp. 287–616.
- Yang, E.-C., Maddess, T., 1997. Orientation-sensitive neurons in the brain of the honey bee (*Apis mellifera*). *Journal of Insect Physiology* 43, 329–336.
- Zhang, S.W., Lehrer, M., Srinivasan, M.V., 1998. Stimulus-conditioned sequence learning in honeybees. *Proceedings of the 26th Göttingen Neurobiology Conference*. Georg Thieme, Stuttgart, New York, p. 519.