Review

Generalization in visual recognition by the honeybee (*Apis mellifera*) A review and explanation[☆]

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ABSTRACT

During a century of studies on honeybee vision, generalization was the word for the acceptance of an unfamiliar pattern in the place of the training pattern, or the ability to learn a common factor in a group of related patterns. The ideas that bees generalize one pattern for another, detect similarity and differences, or form categories, were derived from the use of the same terms in the human cognitive sciences. Recent work now reveals a mechanistic explanation for bees. Small groups of ommatidia converge upon feature detectors that respond selectively to certain parameters that are in the pattern: modulation in the receptors, edge orientations, or to areas of black or colour. Within each local region of the eye the responses of each type of feature detector are summed to form a cue. The cues are therefore not in the pattern, but are local totals in the bee. Each cue has a quality, a quantity and a position on the eye, like a neuron response. This summation of edge detector responses destroys the local pattern based on edge orientation but preserves a coarse, sparse and simplified version of the panorama. In order of preference, the cues are: local receptor modulation, positions of well-separated black areas, a small black spot, colour and positions of the centres of each cue, radial edges, the averaged edge orientation and tangential edges. A pattern is always accepted by a trained bee that detects the expected cues in the expected places and no unexpected cues. The actual patterns are irrelevant. Therefore we have an explanation of generalization that is based on experimental testing of trained bees, not by analogy with other animals.

Historically, generalization appeared when the training patterns were regularly interchanged to make the bees examine them. This strategy forced the bees to ignore parameters outside the training pattern, so that learning was restricted to one local eye region. This in turn limited the memory to one cue of each type, so that recognition was ambiguous because the cues were insufficient to distinguish all patterns. On the other hand, bees trained on very large targets, or by landing on the pattern, learned cues in several eye regions, and were able to recognize the coarse configural layout.

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Contents

"... it's death if the biggest sense the reader gets from a critical essay is that the narrator's a very critical person ... Hence the importance of being just as critical about oneself as one is about the stuff/people one's being critical of". "Maybe the root challenge here is to form and honor a fairly rigorous contract with the reader, one that involves honesty and unblinkingness"... "so that the reader gets the impression that here's a narrator who's primarily engaged in trying to tell the truth" (David Foster Wallace, 2008).

1. Introduction

The idea of generalization appeared in insect vision in the 1920s, when bees were first trained simultaneously with several patterns that displayed a factor in common (called 'generalization during training'), and were then tested with other patterns. The factor could be as simple as an area of black, or more specific. For example, wasps trained simultaneously with several different equilateral triangles could distinguish other triangles from squares, from which it was inferred that the trained wasps had a concept of 'triangularity' (Verlaine, 1927). The successful performance was observed, but the intuitive conclusion was made by analogy with human cognition.

At the time, there were efforts to find so-called *parameters*, which were defined as real features *displayed in the patterns* that were recognized and measurable, such as the total area, length of contour, ratio of black to white, and so on, by which the patterns could be subsequently recognized. Parameters were detected by humans. Verlaine's data was probably reliable, but his conclusion was not accepted because the wasps may have learned a parameter that was common to the training and test patterns. It was obvious, for example, that the relation of edge length to area was different for squares and triangles.

Indeed, later it was confirmed that bees learned to discriminate any member of a group of triangles from any member of a group of squares of similar size, but the trained bees failed to distinguish an unfamiliar triangle from an unfamiliar square (Anderson, 1977). This failure showed that the bees had not formed a concept of triangularity, and for the time being proved the point, but it was only the rejection of an error. Unfortunately, there were no tests of how the bees had actually made the discriminations in the training.

For human vision, in the early 20th century, it was thought that a spatial representation of the training pattern was laid out in the brain and then compared with each new pattern that was encountered. This idea was based on the 'Gestalt' theory that originated in Germany in the late 19th century and was supported by the discovery of the lay-out of the visual image upon the surface of the visual cortex in the primate brain. Evidence that a pattern or shape was recognized as a whole, even if not laid out spatially, also came from the 'top-down' effect, as illustrated in human visual search for a known object. These ideas influenced the interpreta-

tion of all experiments on the vision of bees until the end of the century, and still persist.

Extensive training and testing of bees on a flat white table by Mathilde Hertz in the 1920s showed that they recognized whether a pattern was spotty, circular or radial in character, or whether an area was textured or smooth, irrespective of the exact shape, so Hertz (1933) concluded that they distinguished a 'Gestalt' or type of pattern as a global feature (three columns in Fig. 1). However, some patterns of similar size and edge length, that look quite different to humans, were hopelessly confused by the bees in training, and trained bees accepted some patterns that seemed to have no relation to their training patterns (Fig. 2), so no comprehensive theory emerged.
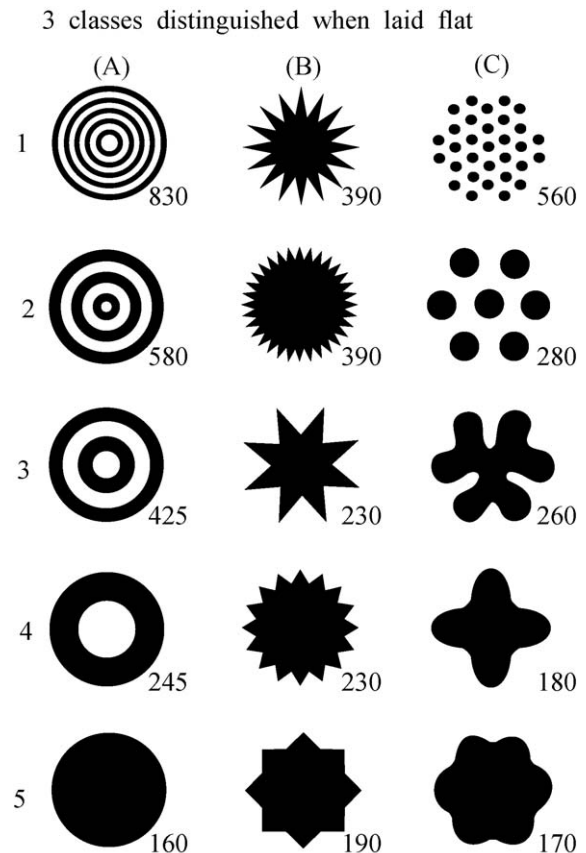
Fig. 1. Early evidence for differences in figure quality and for a parameter based on edge length. The bees distinguished three classes of shapes of similar size that were laid flat on a white table: circles, stars and blobs. Because the upper patterns generated more modulation, the shapes in each column were distinguished more easily from each other the further apart their rows. Bees trained on a pattern usually accepted the adjacent pattern in the same vertical column. Numbers represent edge lengths (after Hertz, 1933).

Fig. 2. An example of an early experiment that defied interpretation at the time. Bees discriminate between the patterns in these pairs [*They used the modulation, radial or circular cues, not the shapes*]. However, bees trained on (a) did not distinguish between (a) and (b), and bees trained on (e) did not distinguish between (c) and (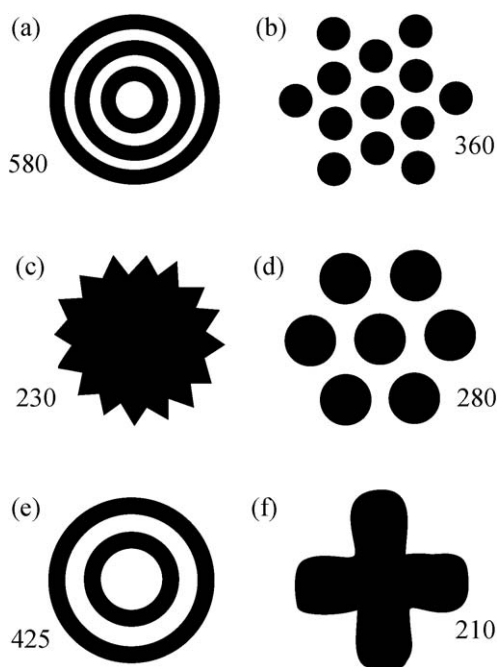d) [*They had learned the modulation and/or area*]. When trained on (b, d, or f) they avoided (a) and (e) [*They avoided circles unless trained on them*]. The results could not be interpreted at the time because the bees learned a different cue in each training experiment (after Carthy, 1958, from Hertz, 1933).

1.1. Parameters

Following Hertz, several authors found that a large difference in the length of edge was correlated with an easy training to discriminate between two patterns (Fig. 1), but there was no explanation why some patterns of similar size, colour and edge length were discriminated and others were not. When bees were trained to discriminate a difference in edge length, their scores in tests with unfamiliar patterns of similar area (different rows in Fig. 1) were also correlated with the difference in edge length, irrespective of pattern. However, it was not explained why this applied only to some patterns. There were no tests whether the bees actually detected the edge length. There was similar evidence for some other parameters, notably colour, pattern size and radial symmetry, and bees avoided circles unless trained to go to them, but further parameters were not suggested at the time.

In these early experiments, the question was never asked how large was the area within which the total edge length or other parameter was measured. The bees obviously did not measure the parameters over the whole compound eye, only the relevant area. Apparently, it was thought that the bee first detected an object or shape, then remembered its edge length. This implied an initial recognition of shape or at least of a closed contour, but there were no investigations of how that might be accomplished.

In an interesting example that looked like generalization, Friedlaender (1931) found that bees that had been trained to discriminate between a black square cross and a black square of similar size on vertical targets were able to discriminate between the same patterns when both were rotated by 45°. It appeared that the shapes were recognized irrespective of their rotation, but at the time it was not realized that the orientations of edges at right angles on the cross and on the square were cancelled, so these patterns can be freely rotated with no change to the bees. To discriminate between the cross and the square, the bees had used the four radial spokes on one and the tangential edges on the other.

In all the previous works, conceptual advance was inhibited by the belief that the bees saw the patterns. Naming the performance of the bees as a generalization was of no help in explaining why some patterns were generalized but others were not. It was even suggested that generalization was the explanation of the bees' behaviour, when in fact it was a just a word for a successful performance.

1.2. Generalization after exchange of white for black

In a series of influential experiments aimed at generalization in the test situation (Wehner, 1971), the patterns subtended a very large angle of about 130° at the eye. The bees were trained to discriminate between a large black bar inclined at 45° to the vertical (Fig. 3a) and two other targets that were blank white, presented vertically. The trained bees then discriminated between the training bar at 45° versus a similar bar at 135° with 97% correct choices (Fig. 3b). To anyone who thought the bees saw the patterns this was not surprising, but the trained bees also discriminated between similar bars that were white on a black background, with 68% correct choices (Fig. 3c). It was inferred that the "particular training parameter" was displayed in black bars on white as well as white bars on black, but this was not an explanation, only a restatement of the result. Today, we know that the bees learn the edge orientation and they ignore which side of the edge is black because the detectors of edge orientation are bilaterally symmetrical (Fig. 4c–e).
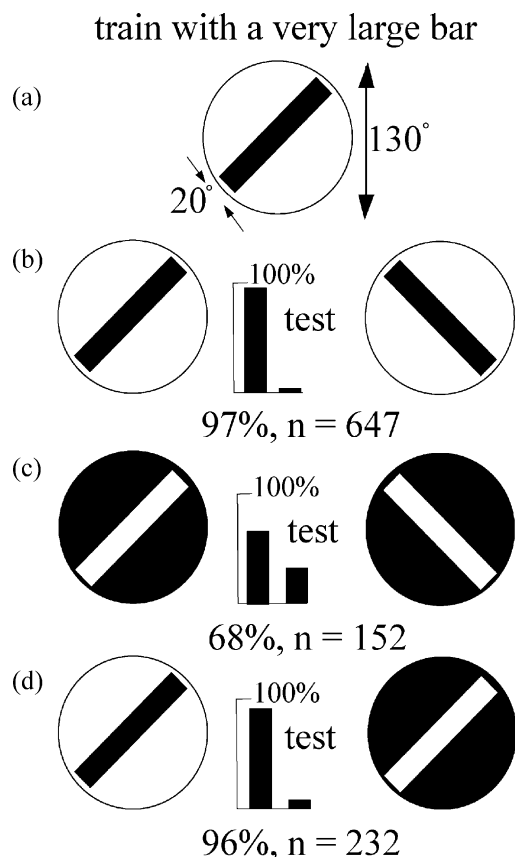
Fig. 3. Learning two available cues. (a) Bees were trained on a single target displaying a black bar. (b) The trained bees discriminated something, either the edge orientations or the positions of black, or both. (c) With black and white interchanged, some edge orientation was discriminated. (d) The trained bees distinguished the training pattern from that with reversed contrast, confirming that the edge orientation was not the only cue (illustration after Wehner, 1971).

Fig. 4. The structure of the feature detectors and cues. (a) The receptor array, with angular separation of axes by 1°. (b) The modulation detector with centre/surround structure making it insensitive to uniform flicker. (c, d and e) The bilaterally symmetrical feature detectors for edge orientation, and also receptor modulation. They respond to movement across an edge or to flicker if standing on an edge. (f) The orientation cue in a local eye region is the sum of the coincident responses of 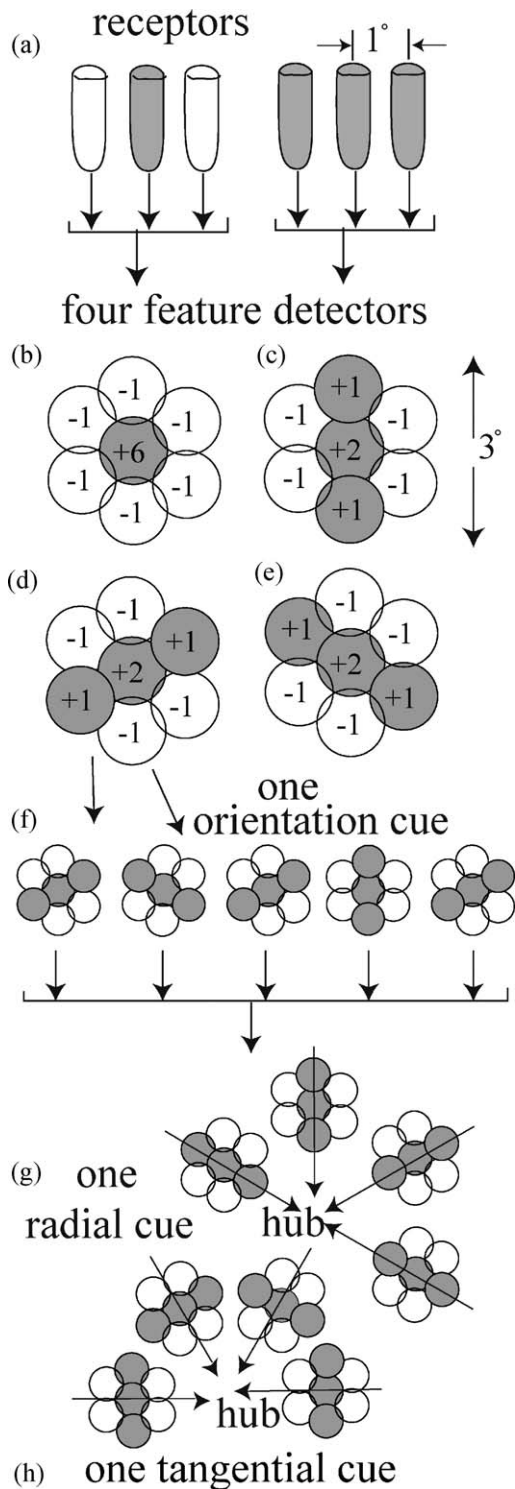the edge detectors. (g and h) Radial and tangential cues are detected by the formation of a hub by the coincidence of the responses of edge detectors in the appropriate orientations over the local region.

In the second set of tests (Fig. 3d), the trained bees were tested with the black bar at 45°, as in the training, versus the white bar on black also at 45°, with the predictable result of 96% correct choices. Therefore it was concluded that "the information about the

direction" is "an invariant information irrespective of the actual contrast condition", which again is a rephrasing of the result in Fig. 3c. Today, we know that the bees can learn the position of the black bar as well as the edge orientation (Horridge, 2003a).

Wehner concluded, however, that the bees "are able to gather some more generalized information" that "can be transferred later on to other stimulus configurations, which never occurred during training", and that "generalization processes are clearly proved in bees". This last phrase shows that generalization was regarded as the recognition of the similarity of the bar shape after the pattern was perceived. Once we know the bees use two independent cues, these verbal efforts are no longer useful.

In the third test (Fig. 3d), the bees distinguished between the training pattern and the most similar of the test patterns. This test was intended to guard against the possibility that the bees were successful in Fig. 3c because they could not tell the difference between training patterns and test patterns. This proviso was aimed at similar work on the wasp (Jander et al., 1970) where the insects failed in a test like Fig. 3d, and it persisted in the literature as part of the definition of generalization (Benard et al., 2006). But it is not valid. For example, if you learn to distinguish between a sheep and a goat, and then distinguish a different sheep from another goat, you have demonstrated generalization. The success is worth little if the two sheep were indistinguishable from each other, but it is generalization in either case, whether or not the sheep look alike to you. A sheep breeder might judge differently. For bee vision, for no obvious reason, it was claimed that generalization required that the bees could distinguish the test patterns from the training patterns. If the test patterns differed from the training patterns but displayed no new cues, the bees would not distinguish them, but clearly they would still generalize them, as illustrated later (Fig. 7).

Whatever the result in Fig. 3d, it would not have affected the conclusion we make today, based on Fig. 3b and c, that the bees had learned something about edge orientation and also the location of black, and could use either cue.

In the same paper, bees were trained to come to a single very large bar versus blank targets and then tested with versions of Fig. 3b with smaller bars in the same positions. The shorter the test bars, the poorer the responses. Because the test patterns differed from the training patterns, it was inferred that the bees had a "generalized information about the direction of visual stimuli". Today, we would say that the bees measured the cues of average edge orientation and the area of black, irrespective of the pattern.

Bees were also trained to come to a very large grating of period 20° and then tested on gratings cut up into rectangles. The more the rectangles resembled squares, the more difficult for the bees to discriminate their orientation. At the time, the bees' acceptance of different patterns was called generalization, but we now see it as the detection of cues whatever the pattern. This example from 1971 illustrates very well that it was difficult at that time to abandon the belief that the bees actually saw the shape of the training pattern, despite the evidence to the contrary.

Later, others found similar examples of acceptance of unfamiliar test patterns by trained bees, and concluded that the different patterns were generalized (Gould, 1985; Ronacher and Duft, 1996; Giurfa et al., 1999, 2001; Dyer et al., 2005). No mechanisms of visual processing were proposed other than the guess that the bees saw the patterns. There were no tests of what the bees actually detected, but re-consideration of each case today suggests that the bees used simple cues.

1.3. Generalization during the training regime

In Canberra, we made use of generalization during the training to identify some real parameters. We trained bees with one

consistent parameter but randomized other aspects of the stimulus during the training. The bees learned the range of a black object irrespective of its absolute size or the angle it subtended (Lehrer et al., 1988). They discriminated between horizontal and vertical black/white gratings irrespective of the width and spacing of the bars (Hateren et al., 1990), and it was later found that they preferred to learn the difference in receptor modulation unless the edges were oblique (Horridge, 2003e). The bees learned the absolute size of a black disc irrespective of range or the angle subtended, and they learned the angle it subtended irrespective of its range or absolute size (Horridge et al., 1992).

The next step in the listing of the parameters and cues in the repertoire of the bees was to generalize during the training by rotating the patterns during the training, removing edge orientation as a parameter but leaving the tangential and radial edges as the consistent differences between the training patterns (Horridge and Zhang, 1995). We found that radial and tangential edges were separate parameters irrespective of the pattern, but there was a pre-existing preference for radial edges (Lehrer et al., 1995; Horridge, 2000b) and avoidance of circles (Hertz, 1933; Horridge, 2006b). Later it was found that the radial and tangential feature detectors that were summed to form the cues were colour blind (Horridge, 1999b), were based on a hexagonal symmetry (Horridge, 2000b) and the same small size (3°) as those for edge orientation (Horridge, 2006b).

We had now recognized four types of feature detectors (Fig. 4), and four cues derived from edges: receptor modulation, edge orientation, radial (spokes) and tangential edges (circles) with their positions. Other cues derived from areas in simple patterns were the total area, colour and the position of the centre in each local area of the eye. The next tasks were to characterize these cues, look for further cues, measure the feature detectors that were the inputs, and search for visual discriminations that could not be explained by the known cues in the bees. These tasks were tackled in a long series of experiments between 1995 and 2006.

2. Improved descriptions of feature detectors and cues

2.1. Definitions

Configural means laid out spatially like a picture.

A *cue* is the sum or a count of the feature detector responses in a local region of the eye. The cues are in the bees, and are inferred from tests of trained bees.

Feature detectors are peripheral neurons or groups of neurons that detect receptor modulation, orientation of edges or small areas of colour or black.

Generalization is the acceptance of an unfamiliar pattern by a trained bee.

A *hub* is the centre of a pattern of radial or tangential edges.

The *image* in the retina is the response of the retina to the pattern.

A *label* on a landmark is a coincidence of cues in a local region of the eye.

The *layout* of the image, features, cues or labels, means the arrangement in space.

Modulation of the receptors is caused by a change in light intensity which in turn is caused by a passing contrast in the pattern.

Orientation is the angle to the vertical on a pattern presented in the vertical plane.

Orthogonal edges are at right angles to each other.

A *parameter* is a part of the pattern seen by humans and related to that detected by the bees.

The *receptors* are the retinula cells in the ommatidia.

A *retinotopic memory* is one that is laid out behind the retina to correspond to the layout of the pattern.

2.2. Modulation

The detector of receptor modulation is smaller than originally suggested by Jander (1964). It now has a single receptor axis surrounded by an antagonistic group of (probably) six receptor axes (Fig. 4b). It responds to a passing contrast (an edge) or to a change in illumination if it stands across an edge. The behavioural evidence for the single central axis is the period of the finest black/white gratings that the bee detects, about 2° (Srinivasan and Lehrer, 1988; Horridge, 2003e). The width of the field of the central receptor has been narrowed by inhibition from the surrounding ones. Receptor modulation is also detected by edge orientation detectors.

The modulation cue is a quantitative estimate (Hertz, 1933) of the number of modulation detectors that respond to the image in each local region of the eye, irrespective of the lay-out of the image (Horridge, 1997a). It is therefore within the eye, not in the pattern. This total is little influenced by the direction of approach as the bees fly over a horizontal pattern. It is the most preferred cue if several are available (Horridge, 2007). There is no evidence that patterns can be distinguished by the lay-out of the modulation within a local region of the eye. When the pattern is rotated or shuffled during the training, the modulation cue persists.

Modulation detection is not colour blind, as shown by experiments with gratings with no green contrast (Srinivasan and Lehrer, 1988). It is not known whether there are separate blue and green modulation detectors, or blue and green channels combined in each modulation detector. Bees discriminate the modulation difference between textured and smooth landmarks in colour (Horridge, 2003e).

2.3. Edge orientation

Orientation detectors respond to a passing edge that is suitably oriented or to a change in illumination if they stand across an edge. They were measured in size by training bees to an orientation cue then testing the trained bees with a large number of equal length parallel edges. The minimum length of edge discriminated was near 3° (Horridge, 2003d). The bees were also tested with lengths of edge that were cut into square equal sized steps to cancel the orientation cue. The steps were then progressively reduced in size until near 3°, when they were no longer resolved by the orientation detectors. Similarly the orientation of a row of black squares was cancelled if the squares were resolved (Horridge, 2000a, 2003c), with maximum separation of the squares near 3°. The feature detectors for orientation are therefore about three ommatidia across (Fig. 4c–e). They act separately and are not strung together to span across gaps.

Orientation detectors are symmetrical about their axis of orientation (Fig. 4c–e), as shown by their failure to distinguish between a white/black and a black/white edge (Fig. 3c). There must be at least three types of them with axes of orientation separated by 120° (Fig. 4c–e), to be able to discriminate all possible orientations (Srinivasan et al., 1994). The resolution of orientation is relatively poor because the detectors are short. A difference of 30° is discriminated with parallel gratings, 45° with single bars. Orientation detectors are green sensitive and colour blind (Giger and Srinivasan, 1996; Horridge, 1999b).

The orientation cue is a sum of the responses of the orientation detectors in each local region of the eye, irrespective of the lay-out of the edges (Horridge, 2000a). The responses of individual orientation detectors with axes at right angles cancel, so only the predominant orientation (Srinivasan et al., 1994) and the

modulation from edges (Hertz, 1933) remain. There must therefore be a count of the responses of detectors at each orientation and an appropriate summation. The orientation cue used by the bee is not obvious from the pattern, and is within the bee.

The size of the eye regions within which summation occurs (about 15°) was measured by training bees to an orientation cue by lateral shuffling a bar during the training. Then an orthogonal bar was added at different angular separations away the first bar and the responses of the trained bees to the resultant of the two orientations were observed. After this mutual cancellation of the different orientations of different edges, there is no way that a pattern could be re-assembled from its edges. As a result of this peculiar summation, the orientation cues are not easily detected by the experimenter (see Figs. 5e, 6e, 7d and 10).

The cues of averaged orientation are kept separate on the two sides of a pattern subtending >45°, as if the bee fixates on the centre (Horridge, 1997b).

2.4. Cues from areas

The cue of area is a count of the number of receptor responses in a local region of the eye, irrespective of the lay-out of the image. The resolution of area depends on the light intensity. The position of the centre of the area is also a cue. When there are two or more spots within a 12°–15° local region of the eye, they are not recognized as separate but are counted as one, and the position of their common centre is remembered (Horridge, 2003b). The cue for an area has a colour, a position and a quantity, but there is no information about its edge or shape. An area of modulation, for example a checkerboard, also has a measure of the area, but the pattern is lost.

The patterns must be fixed, i.e., not shuffled laterally if the bees are expected to learn cues from areas. If the areas are moved after training, the learning starts again afresh.

2.5. Radial and circular symmetrical patterns

For decades it was thought that radially symmetrical patterns were detected globally as whole (Hertz, 1933; Horridge, 1994, 2000b). However, it was impossible to imagine global filters with which a bee could detect circles or radial patterns of all sizes, and also be able to distinguish between the two halves of a single circle or radial pattern. Therefore a different mechanism was sought.

The detection of radial and tangential cues and the position of their hubs relative to the reward hole is done by a distributed mechanism, irrespective of the lay-out of the image (Horridge, 1997c). Each orientation detector (Fig. 4) sends an R signal along its axis of bilateral symmetry and a T signal at right angles to the axis (Fig. 4g and h). Where these signals point to a hub (a multiple cross-over point) irrespective of the lay-out of the image, they identify the centre of spokes or a ring (Horridge, 2006b). The positions of the hubs of the tangential and radial cues lie where the R or T signals have the most dense coincidences (Fig. 4g and h). The R and T signals could be carried by axon arborizations of the edge orientation detector neurons. The nature of the pattern, tangential or radial, and the positions of the hubs, are identified, but the actual pattern is obliterated in the summation, just as happens with an orientation cue (Fig. 4f).

There was therefore no need for a large selection of special templates for radial or circular symmetry, and such templates are ruled out by the ability of the bees to discriminate one half of these patterns from the other half. Unlike the orientation cue, a tangential or radial cue learned by one eye is transferred to the other eye. The mechanism has been demonstrated only when the bees fixate and use the front of the eye, so there is probably a single forward-looking system.

2.6. Full utilization of the feature detector responses

An interesting feature of the bee visual processing is the way that the responses of a very small variety of feature detectors are summed in the local region of the eye to produce cues that each have a quality, a quantity and a position of their centre. The spatial lay-out of the parameters in the local part of the pattern is replaced by a check list of cues at a higher level in the bee, converting a part of the pattern into signals in a few lines, so avoiding the complex processing required for re-assembly of the image. Each cue has an identity (e.g., an orientation), a quantity and a position on the eye, just as a high level neuron has a line-labelled identity, a response strength and a position. The bee cannot see the pattern, but derives several cues from it. The experimenter cannot see the cues but can infer them by giving the trained bees numerous and varied tests.

When trained on a single pattern subtending 40°, or on two different patterns one of which is rewarded, the bees learn one cue of each type (Horridge, 1999a) and their positions, in order of preference starting with modulation and the position of black. If the bees are trained to choose between two different patterns that are shuffled laterally during training, the bees learn the preferred cues from either pattern in the range of places where they were displayed. In the tests, the bees discriminate the cues only where they expect them. They notice the absence of an expected cue, and also the presence of an unexpected cue, irrespective of other features of the pattern. If the cues are changed during training, the bees start to learn again from the beginning (Horridge, 2003a).

2.7. Preferences for the cues

There is a scale of preference for the cues in the learning and testing process, with the modulation difference the most preferred, then the position of the centre, colour, radial, area, black near the reward hole, orientation, no cue, and then finally they avoid tangential cues (Horridge, 2007). They prefer to use cues that display a large difference. If the preferred cue is on the unrewarded target, the bees learn to avoid it and may learn nothing from the rewarded target (Horridge, 2006b). Bees often learn more than one cue but they tend to ignore details that are low on the preference scale and are the same on both targets, and they prefer to avoid a circular cue (Horridge, 2006c).

2.8. Generalization as a tool to identify cues

The cues and their properties were originally inferred from the training scores with fixed (i.e., not shuffled) patterns of four bars that were arranged in different ways to display orientation, radial or tangential parameters, any combination of these, or none of these (Figs. 5 and 6). In this series in 1996, the cues were inferred from the results of training experiments only, because critical tests could not be done before the cues were identified and listed. Patterns were easily made with the orientation parameter the same on each side of the pattern, or different (Fig. 5e), or absent (Fig. 6), as shown in the illustrations. The areas and the positions of the centres were useless as parameters, because they were the same in each pair of patterns. Orientation parameters were limited in their effect to their own side of the pattern, but radial and tangential ones were not. Many pairs of quite different patterns were found that the bees could not discriminate (Fig. 6), so it was clear that these pairs displayed no difference in the cues. Alternately, the bees could be trained simultaneously on a selection of these patterns that displayed one parameter in common, for example a vertical axis of bilateral symmetry (Horridge, 1996a). The trained bees then detected the cue in unfamiliar patterns, irrespective of the actual pattern.

Bees trained to discriminate between two patterns were able to accept many other patterns producing the same cues in the same
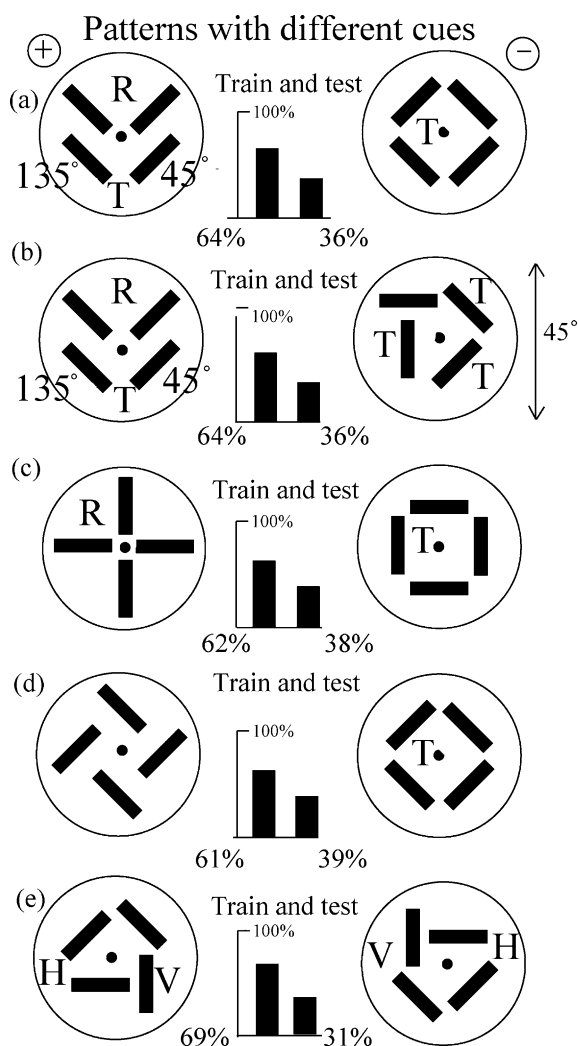
Patterns with different cues

Fig. 5. Pairs of patterns that are discriminated by bees. Bees trained on one member of these pairs subtending 45° at the point of choice will not generalize to the other member of the pair because the cues differ. (a–d) These patterns illustrate radial (R), tangential (T), or edge orientations on each side of the target. (e) Two asymmetrical patterns with contrasting horizontal and vertical summed orientations on the two sides of the target, but no other difference. Compare similar patterns (Figs. 7e and 10) (after Horridge, 1996a).
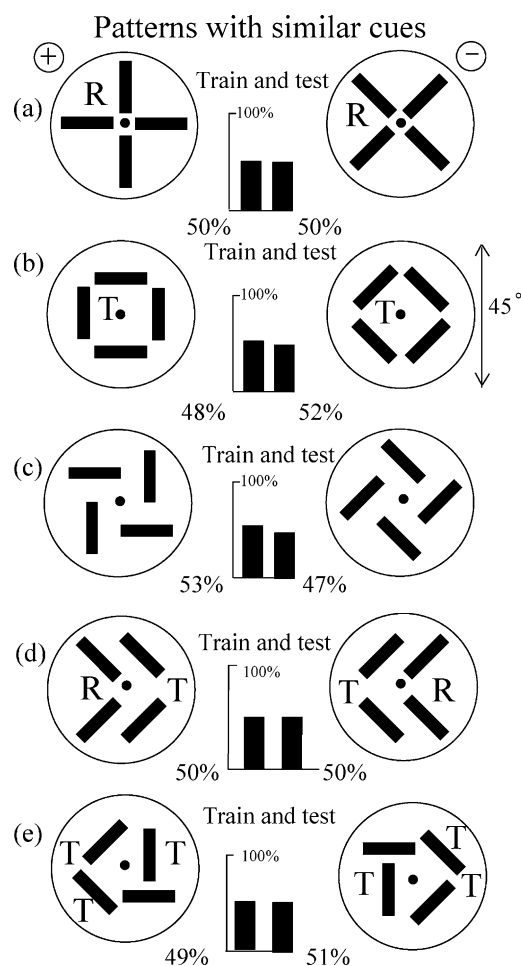
Patterns with similar cues

Fig. 6. Pairs of patterns that are not discriminated by bees, but bees trained on one member of these pairs subtending 45° will generalize to the other member of the pair because the cues are the same. (a–d) Bees cannot be trained to discriminate these pairs of patterns because the cues are the same in each pair. (e) The radial and tangential cues are not restricted to one side of the target (after Horridge, 1996a).

places as the rewarded pattern, but if presented with the rewarded pattern versus a pattern producing the same cues in the same places, they were not able to tell the difference (Horridge, 2006a). They did not recognize the pattern they had been trained on, only the cues.

When making a generalization (i.e., accept a different pattern in the place of the training pattern), the bees perform, not in a mysterious way, but by use of a simple mechanism based on the order of preference of identified real cues. Now that the cues are known and can be picked out from the patterns, anyone can infer whether or not the trained bees will generalize.

Rule: Trained bees accept an unfamiliar pattern of approximately the expected size in the expected place if it produces most of the expected cues in approximately the expected positions, and no unexpected cues. Nothing that could be called cognition is involved in this very obvious mechanical process.

3. Large and small patterns

3.1. A paradox

For a long time, between 1926 and 1996, bees were trained with patterns of various sizes with little attention to the angular subtense at the eye of the bee. Then, the contrast between two experiments, one published by Wehner (1967) the other by Srinivasan et al. (1994), forced our attention to the difference between large and small patterns, for the bee. In the first, the criterion of success was the bees' landing on the reward hole, so the patterns were huge when the bees made their final choice. Later, about 1968, the angle subtended by the pattern at the point of choice was controlled at about 130°, which is still huge.

The bees were trained to discriminate between a large square cross (subtending 130°) and a blank target, or between a large square cross and the same cross when rotated by 45° (Fig. 7a). The discrimination was unaffected when the trained bees were tested with the same crosses with the edges cut into large square steps to remove the edge orientation (Fig. 7b). The trained bees could detect a rotation of the large cross by as little as 4°, which was too small to be detected by edge orientation detectors but is quite a large lateral shift of the ends of the bars.

From this result it was inferred that the bees compared the spatial lay-out of black in the rewarded pattern with that in the test pattern, in what would now be called a "configural visual discrimination". At the time it was further concluded that the bees remembered an eidetic (=retinotopic) image of the whole training pattern, which they compared with each test pattern. This intuitively reasonable guess became established in the literature, but no one considered why some pairs of obviously different patterns were discriminated but others were not (Fig. 2).

train with very large targets

(a)

130°

(b)   > 90% correct

test

130°

> 90% correct

train in Y-choice apparatus
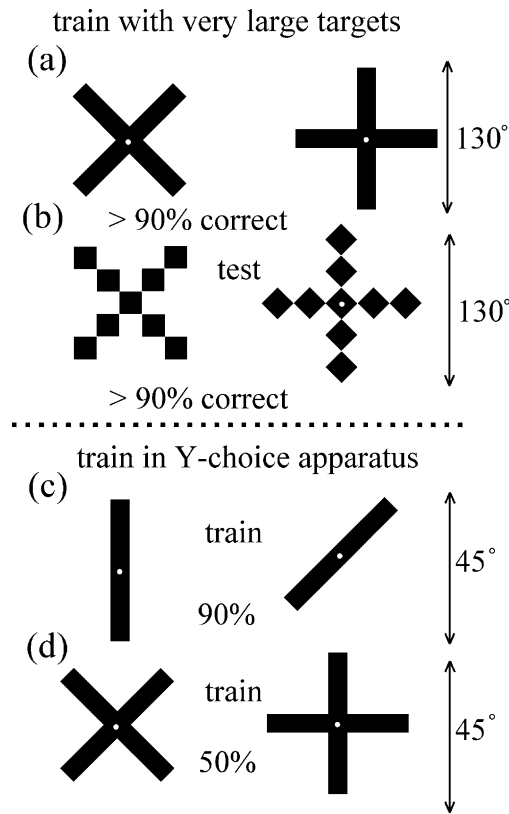
(c)

train

90%

45°

(d)

train

50%

45°

Fig. 7. (a) Discrimination between a very large square cross and the same rotated by 45°. (b) Removing the orientation by cutting the edges into square steps had no effect on the discrimination, so the cues were inferred to be the positions of areas of black (after Wehner, 1967). (c) With targets subtending 45°, rotation of a bar is discriminated but (d) rotation of a cross that is formed by two similar bars is not detected because the orientations at right angles cancel in the local region of the eye (after Srinivasan et al., 1994).

Quite a different result was obtained when the patterns subtended about 40° at the point of choice (Srinivasan et al., 1994). Bees could be easily trained to discriminate between a black bar and the same bar rotated by 45° (Fig. 7c) but not between a square cross and the same square cross when rotated by 45° (Fig. 7d). This result was the basis of an extensive theory in which the orientation detectors were supposed to have very large fields, and at the time Wehner's result was not mentioned. There was obviously a topic here to be investigated.

Later, the supposed large fields of the orientation detectors were replaced by cues that were totals of the responses of many small short edge orientation detectors (Fig. 4).

3.2. Differences between large and small patterns

The effect of the angle subtended by the target was investigated using a choice chamber in which the targets were displayed at a controlled distance from the point of choice (Fig. 8a and b). An asymmetrical pattern of four bars was not distinguished from the same pattern rotated by 180° when it subtended 45°–50° (Fig. 8c), but was easily discriminated when the bees were allowed to land on the reward hole or when the pattern subtended 100° (Fig. 8d and e).

This is an interesting pattern in which the orientation cue is cancelled on each side by the equal lengths of edges at right angles, and which shows that the bees cannot tell which side of the target the tangential edges are displayed. Neither the separate bars nor the whole pattern are discriminated at a subtense of 45°–50° (Figs. 6c and 8c). However, these patterns are easily discriminated when

rotated by 90° because the orientation is then different on the two sides (Fig. 5e).

When the patterns are very large the preferred cue is the difference in the lay-out of black areas (Figs. 8d and e and 9). By controlling the size of the pattern, we now had a means of measuring the size of the local eye region within which each cue was summed, and therefore the resolution of the configural lay-out of the pattern for each cue.

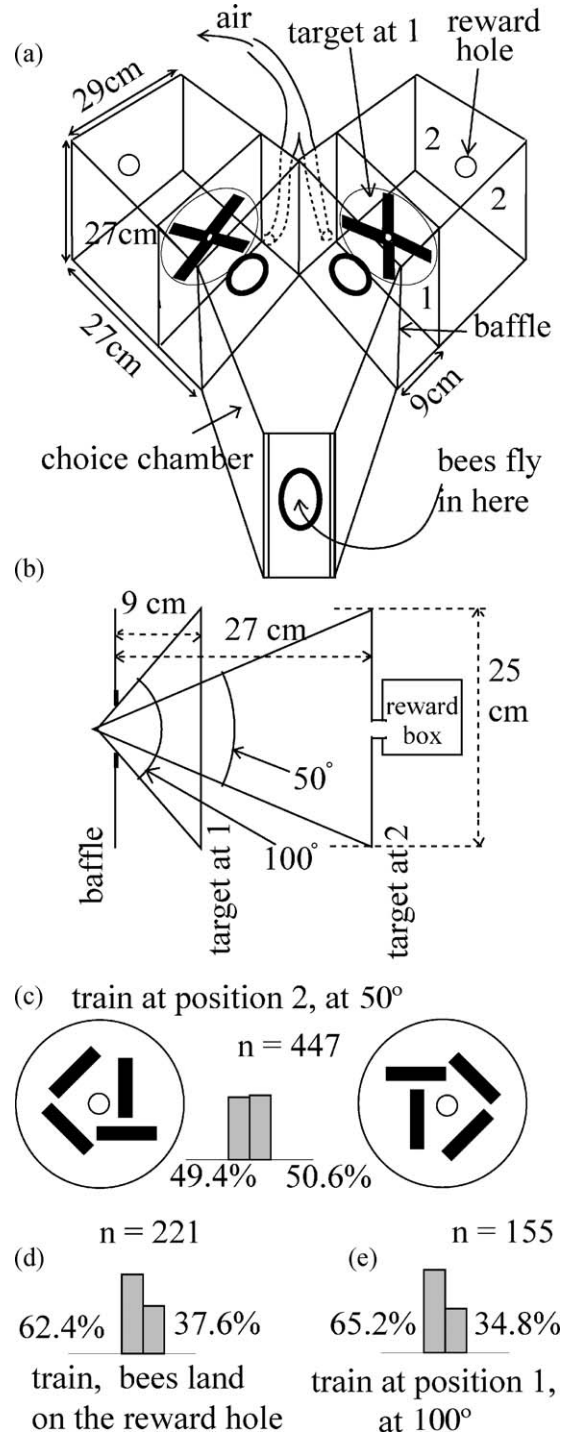

Fig. 8. (a and b) The Y-choice maze, with baffles that slowed down the bees in flight and extended the time taken to make a choice. To control the angular subtense, the targets were placed at positions 1, 2, or 3. (c) Two patterns at 50° subtense that are not discriminated (after Horridge, 1996b). (d and e) The patterns are easily discriminated when the bees land on them, or at 100° subtense.
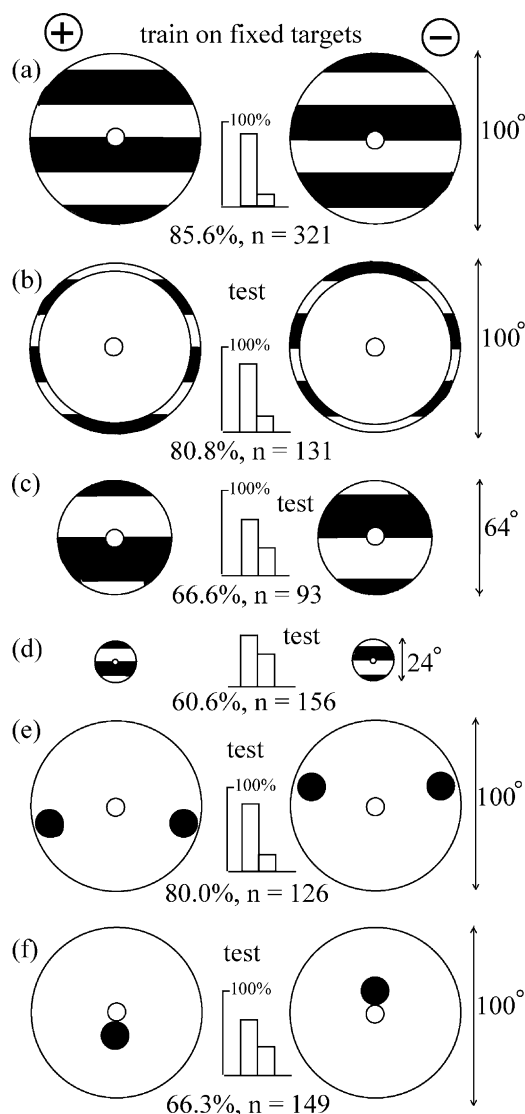
Fig. 9. The bees generalize when they detect either of the two cues: the positions of black in the periphery of a large target, and the presence of black below the reward hole. (a) Fixed training patterns at a visual angle of 100°. (b) The performance is hardly reduced by removing all but the rim 3° wide around the edge. (c) The central part of the targets, 64° in diameter, is also quite effective. (d) The bees still see a cue when the pattern is reduced to an angle of 24°. (e) The position of black provides sufficient cue. (f) A single black spot below the reward hole is a sufficient cue (after Horridge, 1996b).

A pattern of black bars subtending 100° was discriminated from the same pattern moved up by half a period (Fig. 9a) even when the patterns subtended 24° (Fig. 9d). Good discrimination of the peripheral rim alone shows that in the training the bees used the most separated parts of the patterns (Fig. 9b). A black area below the reward hole was also a sufficient parameter (Fig. 9f), or even two black spots in the expected positions (Fig. 9e). Learning of the configural layout of the periphery is not found with targets that subtend angles of 40° or less at the point of choice.

3.3. Patterns with four sectors

In 1992, we set out to discover whether bees could detect the different orientations in four quadrants of a circular pattern, and concluded that they could (Zhang and Horridge, 1992). We were unaware that the responses of edge orientation detectors are summed over each side of the target separately, or that radial and

tangential cues existed at all. Unfortunately our inadequate knowledge of the cues led us and others into confusion.

A fixed (not shuffled) target in the Y-choice maze (Fig. 8) subtending an angle of 40°, was divided into four quadrants with a grating of period 8° differently oriented in each quadrant (Fig. 10a and b). Bees discriminated the rewarded training pattern from a similar pattern with the quadrants re-arranged. Increasing the number of sectors showed that the minimum sectors subtended about 22° at the eye, which was more than 100 facets, or a similar number of unit orientation detectors. This calculation gave "some idea of how an array of numerous templates, each individually ineffective, can collaborate together to make specific ensembles that fit the pattern sufficiently well". We supposed that the templates were within the visual system.

Unknowingly, we had selected patterns with average horizontal on the left and average vertical on the right of the rewarded pattern (compare Figs. 5e, 6e, and 8c with Fig. 10a and b). We never noticed these parameters in Fig. 10a and b, but naturally the bees used them. We also were unaware that the bees learned the cues in the places where they were displayed during the training, and detected them in tests only in the same range of places. Therefore in tests, the bees would tend to respond to the cues in their quadrants and so appear to learn the lay-out of the pattern.

From a variety of experiments, we concluded that "Bees are clearly able to resolve and discriminate between the quadrants of stripes at different angles and they are able to assign some information about these angles to different locations in the pattern." Of course, this rubbish was contrary to subsequent experimental results that revealed the radial and tangential cues and the summation of edge orientation over the local region of the eye.

With similar patterns, Giurfa et al. (1999) allowed the bees to approach close to the targets, so the patterns were very large at the point of choice and the bees were able to separate them into parts and learn the peripheral positions of black (see also Figs. 8e and 9). However, the pattern size was not discussed. Like ours, their rewarded pattern had horizontal bars on one side of the target and vertical bars on the other. Moreover, one pattern had two quadrants of radial bars and the other two quadrants of tangential bars (Fig. 10d). All the test patterns had a quadrant of radial bars and/or tangential bars, but these obvious cues were not mentioned. Probably they were not noticed by the experimenters, although described in the literature (Lehrer et al., 1995; Horridge, 1996a). It was concluded that when trained on one pattern versus a blank, the bees learned the lower half, but when trained on one pattern versus a different one, learning was extended to the whole pattern.

Similar patterns with obvious radial and tangential edges (Fig. 10f) were used to train bees in a Y-choice apparatus. The trained bees were tested with the mirror image or the 180° rotation of the same patterns (Stach and Giurfa, 2001). The trained bees preferred the mirror image and the rotated patterns to an unfamiliar pattern. This result was explained by "matching with a retinotopic template of the trained patterns" or 'matching with a generalized pattern configuration'. "The latter allows for categorization of novel patterns." Bees would "approach a pattern provided a particular quadrant provides a particular orientation." However, this intuitive explanation does not allow for the cancellation of the orientations in different quadrants and provides no details of what was actually detected in the training. The authors failed to mention that their patterns had radial and/or tangential edges that would not be changed in a mirror image or by rotation of the pattern (Fig. 10e and f).

More recently, bees were trained with similar quadrant patterns that consistently displayed the four orientations in the four quadrants but with different thickness and positions of the bars versus a similar unrewarded group with a different pattern of

training each pair on fixed patterns

(a)

Z&H, fig 3　　67%　　33%

(b)

Z&H, fig 4　　61%　　39%

(c)

H 1996,
fig 2e　　49.4%　　50.6%

(d)

Giurfa, 1999　　87%　　13%

(e)

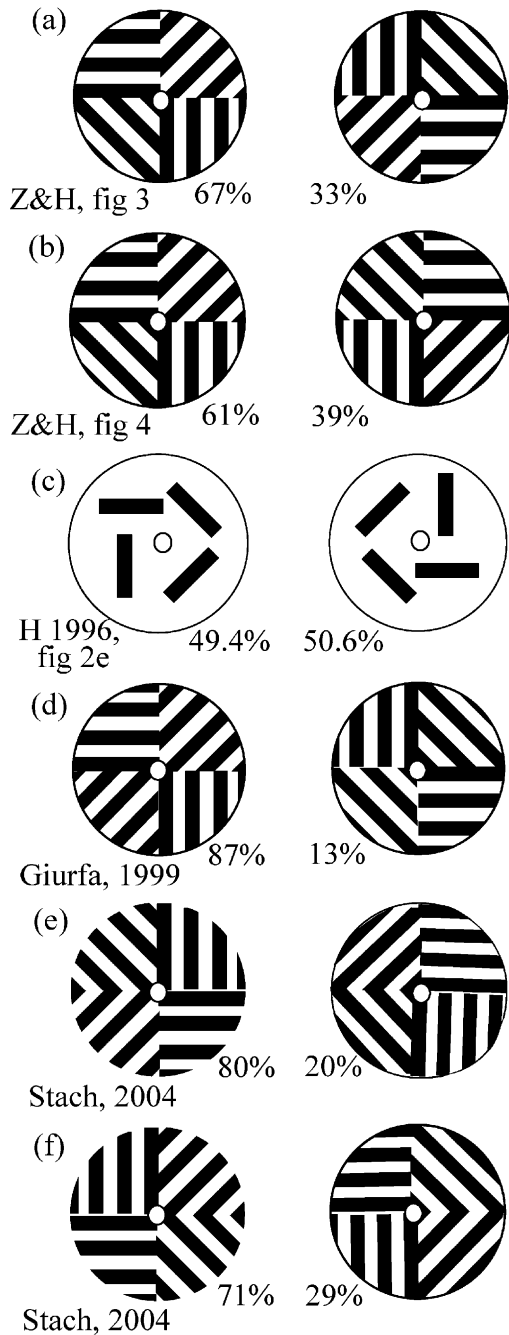Stach, 2004　　80%　　20%

(f)

Stach, 2004　　71%　　29%

Fig. 10. Training with four different orientations in the four quadrants. (a) With radial edges cancelling tangential edges, but with different average edge orientations on the two sides of the targets. (b) As before, but rotation of the right target makes no difference to the cues. (c) Patterns subtending 50° that were not discriminated, so there was no difference in cues between the two patterns. Compare Fig. 8c. (d) Very large patterns with radial versus tangential cues and orientation differences on the two sides. (e and f) 40° patterns with radial versus tangential cues but no orientation differences on the two sides. In all these examples, except (c), it was thought at the time that the bees detected the quadrants separately, and the cues were not mentioned. (a and b) from Zhang and Horridge (1992), (c) from Horridge (1996a), (d) from Giurfa et al. (1999), (e and f) from Stach et al. (2004); Benard et al. (2006).

orientations (Stach et al., 2004; Stach and Giurfa, 2005). Discrimination depended on green contrast, and therefore edges were involved, suggesting orientation, radial or tangential cues. The targets subtended 37° at the point of choice in a Y-choice maze,

so the orientations were summed separately on each side of the target. Again, on the right in the rewarded targets, and in all the tests there were obvious radial or tangential edges that the experimenters did not mention (Fig. 10e and f).

The ability of the bees to discriminate, despite small shifts of the bar positions within each quadrant or loss of some bars, was described as a generalization, and "under such a differential conditioning the bees learn the patterns as a whole, not only their local cues". The obvious cues for the bees' were not noticed by the experimenters and there was no test whether vision was in fact global.

In tests, the trained bees discriminated the orientations when there was only one bar in each quadrant or with black and white reversed, as would be expected because the rad/tan edges remained. It was concluded that the bees "also generalize their response to patterns with fewer correct orientations, depending on their match with the trained layout" but in fact the cues in the training were still available, and the match with the lay-out was not tested. The claim that the bees responded to "the best match between the memorized and the perceived lay-out and thus on the number of coincident edges between layouts" was again a restatement of the experimental result, not an explanation. There were no tests in a search for simple cues or even to identify which edges were involved.

Following Zhang and Horridge (1992), see above, the authors took the view that the "results show that honeybees can recognize visual patterns on the basis of the global layout made from four different orientations, common to a series of different patterns". Actually, there were no tests whether the lay-out had been remembered at all. Furthermore, the data was compatible with the recognition of the radial versus tangential cues by the bees, but not noticed by the experimenters.

The same data was used again by Benard et al. (2006) who intuitively concluded "Besides focusing on a single feature, honeybees were shown to assemble different features to build a generic pattern representation, which could be used to respond appropriately to novel stimuli sharing such a basic layout." and again "Thus, the question of whether bees can extract a configuration common to a group of rewarded patterns, made from four different edge orientations arranged in a specific spatial relationship to each other, was answered positively."

And so on, all intuitive guesswork with no tests whether the inferences were valid, when a mechanistic explanation was available and the radial and tangential edges were displayed for all to see. There was some excuse to mislead the world in 1992, when Zhang and I were unaware of cues that were discovered later, but there was no excuse after the cues and the methods of testing the bees were published.

4. Making use of the whole eye

We can now put together the local regions of the eye to make a whole eye that detects a very coarse representation of the configural lay-out of the panorama or of very large patterns.

4.1. Labels on landmarks

When working with patterns that subtended less than 40° (Figs. 5, 6 and 8c), only one cue of each type was remembered in each side of the pattern, corresponding to a local area of the eye (Horridge, 1999a). The group of cues that was detected by a local region (Fig. 11) was remembered as the label that was recognized irrespective of whether there was a pattern, a single object or several in that local region (Horridge, 2006c). Bees do not see a landmark with a local eye region, they detect a coincidence of cues that they may recognize as a landmark label if rewarded. With the
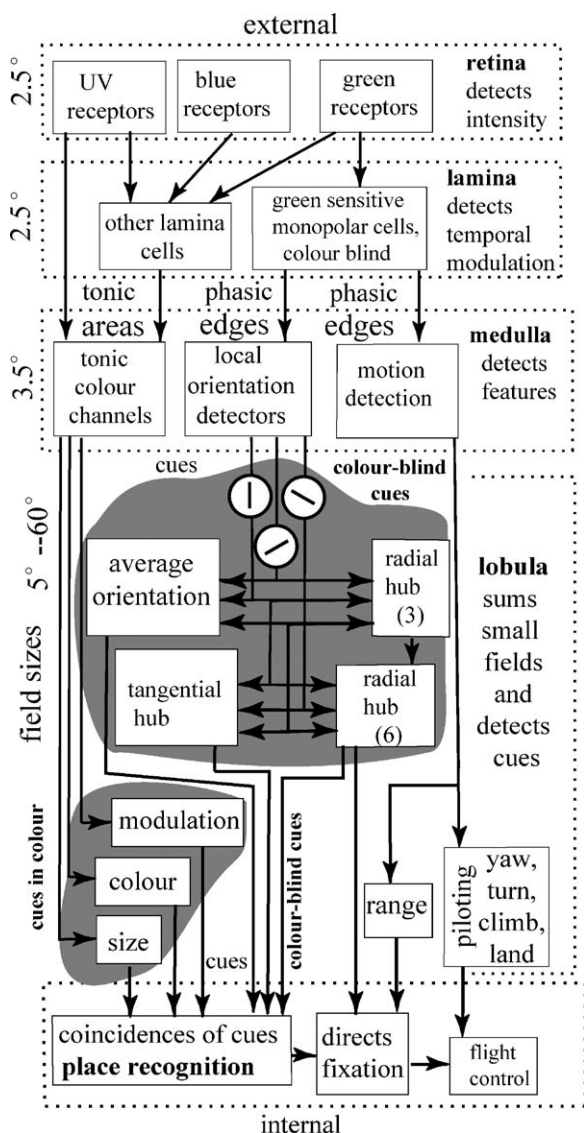
Fig. 11. A map of the interactions that generate the coincidences of cues in each local region of the eye. At the top is an array of very numerous receptors. Below that is an array of very numerous lamina neurons followed by arrays of very numerous feature detectors. In the shaded parts, the responses of the feature detectors are summed to form one cue of each type. The coincidence of cues (bottom left) makes one landmark label (after Horridge, 2006a).
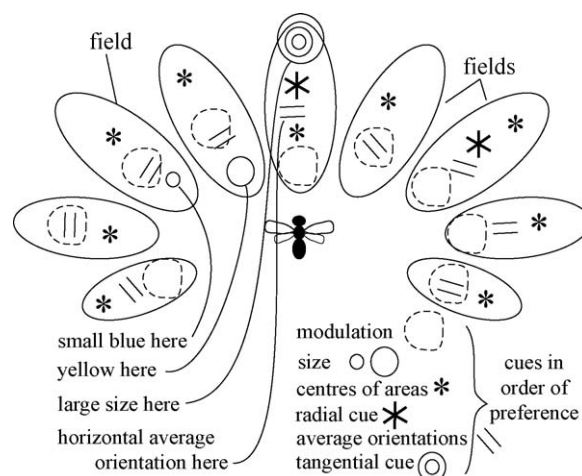

Fig. 12. The partition of the panorama by the local regions of the eyes makes possible the configural discrimination of places. Each of the local regions, shown as an oval, locates and measures all of the available cues in parallel in its field of view, as detailed in Fig. 11. In each local region, the coincidences of the cues, as indicated by the symbols, forms a landmark label. The memory of familiar place is the memory of the coincidence of landmark labels at different angles around the eye (after Horridge, 2006a).

regions (Fig. 12). The configural resolution (the separation of eye regions) is not the same for each cue. Evidence of the size of the local regions comes from several sources. Gould (1985) found that a target divided into areas of different colours is discriminated from a similar target with the colours re-arranged if the areas subtend more than about 10°. For horizontal coloured bars, I found the minimum to be 8° (Horridge, 2000c). Gould reckoned that this resolution was the minimum area of the colour, but it is more like to be related to the area over which colour is summed in each local eye region when the average colour is discriminated, because the patches of colour were adjacent.

When two black spots were close together, bees learned the position of their common centre in the vertical direction, but treated them as separate when more than about 15° apart (Horridge, 2003b). Similarly, two edges of equal length at right angles cancelled the orientation cue if close together, but the effect diminished with separations up to about 20°. Each cue was summed over its own local region (solid angle on the eye).

5. The origin of generalization

We are now in a position to explain why generalization in bee vision appeared when trained bees were tested with unfamiliar patterns.

When the interesting black American entomologist, Charles Henry Turner (1867–1923), first trained bees to distinguish between two boxes, one had a reward of sugar inside and displayed horizontal black stripes, the other had vertical stripes and no reward. He exchanged the positions of the boxes at intervals to make the bees look for the rewarded pattern irrespective of the place so that he could control the training and test patterns. This was the break-through in technique that made possible the analysis of the visual system. By shuffling the positions of the boxes, Turner (1911) had broken the nexus between the recognition of the place by the surrounding landmarks, and the recognition of the single landmark label on the box, which was the striped pattern. The technique was copied with various modifications, by all later investigators. von Frisch (1914) used several boxes that were interchanged in position at intervals along a balcony rail. Friedlaender (1931) rotated them on a large vertical wheel. Hertz (1933) laid out black patterns flat on a

whole eye, they do not see the panorama, they detect and recognize a coincidence of several landmark labels that together identify a place, or the rough configural layout of parts of a very large pattern (Fig. 12).

4.2. The separation of local eye regions

As shown by extensive studies of how bees locate a place, the relations between familiar landmarks in the whole panorama are discriminated as a group (Thorpe, 1963; Collett et al., 2002; Fry and Wehner, 2002). The minimum angle of landmark separation in controlled conditions is about 15°. With several landmarks in a coarse configural lay-out, the bee has sufficient information to identify a feeding site without errors, and bees ignore training patterns that are presented in unexpected places. If the place of the reward is moved, the bees no longer recognize it (Forel, 1908).

In my model, the definition of the landmark as a coincidence of cues implies that different landmarks fall into separate local eye

white table and placed a reward of sugar solution next to one of them. She broke the nexus between the pattern on the reward and the surrounding landmarks by shuffling the patterns on the table at intervals to liberate them from one place, and make the bees search. In all the early examples, before 1968, the criterion of success was the landing of the bees on the reward hole or pattern.

For the first time, it was noticed that the bees required a long period of training. Furthermore, when trained they would accept some unfamiliar patterns, a performance called generalization. The bees were either very tolerant or liable to mistakes. In contrast, they returned to a natural place after a single visit and rarely made an error. Very large patterns had to be extremely simple to demonstrate generalization (Figs. 1, 3 and 7b). The claims of retinotopic memory originated from very large patterns, and learning was faster and to higher scores.

Lets explain. When the positions of the patterns were shuffled, the bees were obliged to look for cues within the rewarded pattern. The immediate surroundings of the reward became irrelevant and nearby landmarks outside the rewarded pattern were inconsistent. The bees trained themselves to ignore the nearby landmarks but not the more distant landmarks that indicated the location of the experiment. It is therefore understandable why training took so long, whereas in a fixed natural place the learning was immediate.

The targets were relatively small so the bees could no longer use the whole eye. As they always did, the bees learned one or two cues for that particular task, not for patterns in general. The few cues that the bees learned from a small simple pattern, for example, modulation and positions of peripheral black, were inadequate to distinguish every pattern. Therefore alternating or shuffling the targets limited the memory and caused ambiguity in the recognition process, exposing the bees to errors. It was called generalization.

In contrast, generalization was not observed in the identification of a natural situation where recognition involved the retinotopic detection of a variety of features with the whole eye, and the bees made a reliable fit with cues in their expected places at large angles to each other in the whole scene (Thorpe, 1963; Collett et al., 2002; Fry and Wehner, 2002). There also, the bees were not interested in the pattern or the panorama, only the place of the reward. For a bee, a pattern or a landmark is simply a local group of cues.

6. Discussion

A major difficulty for the newcomer to this subject is the large proportion of publications entitled "Shape perception" "Discrimination of pattern", "The concepts of 'sameness' etc., "Global discrimination" "Cognitive perception", etc. For all my own research career, questions of perception and mechanism have been influenced by the terminology in favour of an anthropomorphic interpretation of the performance, even after the mechanisms were found. In the case of bee vision, the experimenters saw the patterns but not the cues; the bees detected the cues but not the patterns. There was certainly no meeting of minds.

Terms such as 'abstract properties' and 'generalization' were borrowed from authoritative text books because they conveyed what the bees appeared to do, but they said nothing about mechanisms. There was no consideration why some patterns were global or generalized, or some properties abstract, but others not. When trained bees accepted an unfamiliar pattern, it was 'explained' as a generalization, as if the bees saw the patterns, or at least appraised them and detected a similarity. The way forward was blocked by an intuitive inference based on what was thought to be a successful recognition, followed by naming the performance as 'generalization'.

These were explanations for the 19th, not the 20th century. The English empiricist philosopher, John Stuart Mill (1806–1873) would have been horrified at the credulity of serious bee researchers in the 20th century. He would have insisted on numerous observations followed by deduction of the logical consequences, followed by tests to validate the conclusions. In fact, there were no tests whether the bees used only a part of the pattern, as suggested by Carthy (1958), or a cue derived by summation of edge length (Hertz, 1933), or positions of black (Wehner, 1967), or the large fields of orientation detectors (Srinivasan et al., 1994).

The data in the literature has usually been confirmed and the conclusions based on intuition can now be explained in terms of cues in separate eye regions that detect configural layout. Because bees use feature detectors and cues, they necessarily appear to interpolate, detect 'similarity' and 'differences', and discriminate circularity, radial patterns, some shapes and other apparently sophisticated properties of patterns.

The methods of Ethology – to describe performance and think of a function and explanation – are unfortunately unavoidable in most studies of animal behaviour, but they not sufficient for the analysis of visual mechanisms. It is hard for us now to understand why the bees that had been carefully trained with great effort were not thoroughly tested at the time to see what they had learned. Ethologists, in general, were satisfied with descriptions of successful performances that said little about mechanisms (Lehrman, 1953). The idea that the bees generalized was even thought to be an explanation. It was accepted that the bees saw the patterns. Eventually, the right question "What do the bees actually detect?" was answered by testing the trained bees to the limits. The results revealed the cues and gave us the measurements of the resolution by the feature detectors (2°–3°), cues (10°–25°) and landmark labels (15°–40°).

The experimental results were influenced by the technique of training, first the shuffling of patterns to make the bees ignore surrounding cues, and second, the angle subtended by the pattern from the point of choice (Fig. 8). Analysis of these factors led to the discovery of the separation of local eye regions (Fig. 12). Bee vision is counter-intuitive because the feature detector responses are summed in local eye regions to make one cue of each type (Fig. 11). A local coincidence of cues becomes a landmark label if associated with the reward. The bees then identify a place by the coarse configural arrangement of landmark labels using the whole eye. Objects, shapes, patterns and landmarks exist in the human world, but they have no place in the bees' world. Bees detect features and remember coincidences of cues and landmark labels, not patterns, landmarks, or the panorama. 'Generalization' is a word for a particular kind of performance which is a consequence of training with few cues.

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