10

Visual Discrimination by the Honeybee (*Apis mellifera*)

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> '"I see" said the blind man, but he couldn't see at all.'
> He saw enlightenment in his mind's eye.
> What is the mind's eye? Does a bee have a mind's eye?

Despite the expert piloting and recognition of flowers and places, a bee can never see the surrounding panorama in the detail that humans do. The impasse is not caused by the resolution or structure of the eye, which has an array of receptors like a camera or a human eye (see below, Figures 10.4 and 10.5), but by the large number of interactions required to make sense of an image that is divided into separate pixels by the numerous photoreceptors in the retina, each with its own continuous separate signal. In humans, after interactions in primary visual cortex to detect the most primitive features in the image such as edges, numerous neighbouring parallel channels collaborate to detect useful significant combinations before recognition begins. To "see" something as we do requires a long process of unconsciously learning what is significant, followed by the assembly of shapes and objects from the variety of edges, color patches, and the spatial layout of the meaningful part of the input. The processing occupies a large part of a huge brain and is directed by memory. The bee, on the other hand, tells us that a much simpler and faster visual system, sufficient for piloting in flight and recognition of a place, really exists, so that anything we learn from it is likely to be useful to make seeing machines.

Bees occur worldwide, and experiments cost little but time and ingenuity. Using vision, bees learn to come repeatedly to the same place for a feed of sugar syrup. As a result, they can be trained to fly into an apparatus (Figure 10.1). Here, they choose between two patterns that are displayed on targets, one of which provides a reward to increase the bees' relative preference for it. Between continued training sessions, the trained bees are offered test patterns that are designed to reveal in progressively finer detail exactly what they have learned. The resulting map of the relationships in the visual processing establishes the kind of system, not the neuronal activity. For further details and explanations, see Horridge (2009b).

THE PROBLEM AND ITS SOLUTION

Let us first consider how to analyze the mechanism of recognition of targets subtending 40 to 50 degrees at the eye of the bees at the moment when they make their choice. In the Y-choice maze (Figure 10.1), bees quickly learned to distinguish, for example, between a black disc and a triangle of similar area (Figure 10.2A). At first sight, the bees saw the disc and learned to go to it, rather than to the triangle. How easy it is to believe that the bees see what we see, but how wrong we are! When the trained bees were tested with the disc versus a random pattern of spots, they scarcely recognized the difference (Figure 10.2B). When tested with the spots versus the triangle, however, they avoided the triangle (Figure 10.2C). They did not recognize the disc, but they had learned to avoid the unrewarded target (Horridge, 2006a).

Next, the trained bees were tested with only the outlines of the shapes (Figure 10.2D), and they still avoided the triangle (but only 60% correct). When tested with an inverted black triangle versus the original unrewarded triangle, however, they showed no preference (Figure 10.2E). Therefore, they had learned something about the triangle, but they did

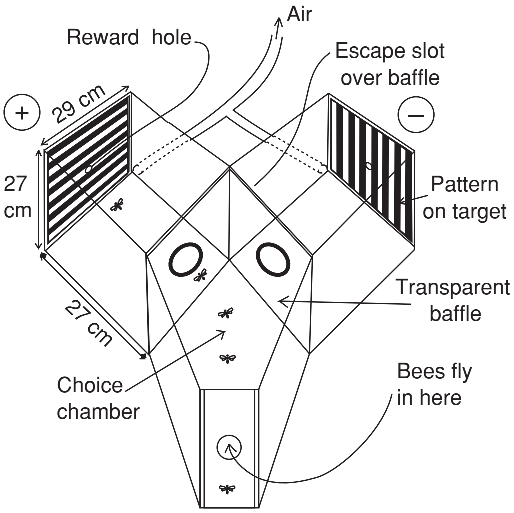

FIGURE 10.1 The Y-choice apparatus in which the flying bees choose between two targets of known angular size, one of which is rewarded. The walls are lined with plain white paper, the top and baffles are transparent. The bees enter one at a time by the front entrance and exit toward the light by the same route. The escape slot releases trapped bees. The targets, together with the reward, are interchanged every 5 min to make the bees look at them. After Srinivasan and Lehrer (1988); baffles after Horridge (1996b) redrawn with corrections.

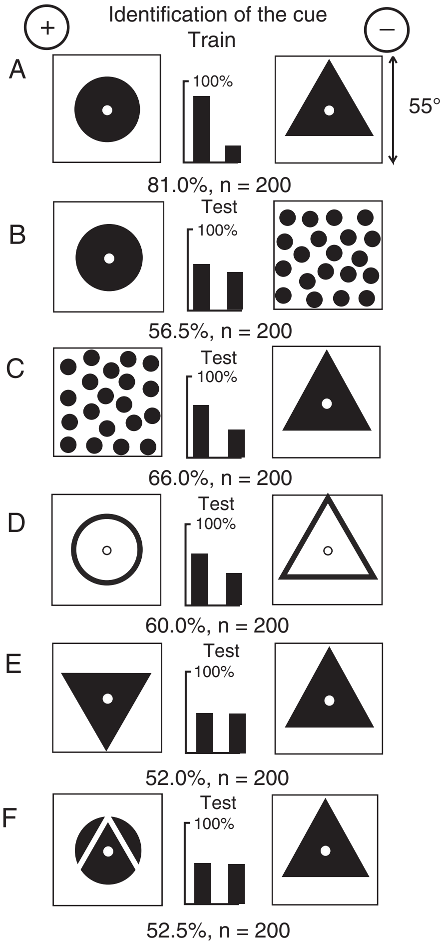

FIGURE 10.2 The search for cues after training to discriminate between two black shapes. **A**: Training patterns. The black disc is rewarded. **B**: A test reveals no preference for the disc versus the spots. **C**: A similar test reveals an avoidance of the triangle. **D**: The cue is related to the edges of the shapes. **E**: The inverted triangle and the triangle at the same center are equally preferred, so the black triangle, or its apex, are not recognized. **F**: When two oblique lines are added to the disc, the equal preference shows that the cue was the oblique edges on the unrewarded shape.

not recognize the original from the training (Figure 10.2A). So, we have now shown that the trained bees recognized neither of the patterns they were trained on, as patterns. What then, did they detect? That is a different question.

Putting these results together, and knowing the parameters that the bees could detect, we devised a critical test by drawing two oblique white lines on the black disc, and tested this against the black triangle (Figure 10.2F). Although the test patterns were quite different, the bees now showed no preference, because the parameter, the vertical average orientation of edges on the two sides of the target, was displayed on both targets. Vertical lines on the circle worked equally well.

As in this case, bees sometimes fail to discriminate because they are equally attracted to the two targets, so the failure is not a proof of the absence of recognition. The cues are shown to exist, however, because when identified, they can be added or omitted at will. There was "absence of proof" that the bees *saw* the whole training shapes or the difference between them, in any sense of the words, but, more importantly, although training continued between the tests, there was a direct demonstration in the tests that the bees did not *remember* the shape of the disc or the triangle, otherwise they would not have consistently failed to recognize the training shapes shown in a variety of tests (Figures 10.2B,E, and F). When the cues are restored, we have positive evidence of their effectiveness. Similar tests, first for the detection of various likely parameters, followed by a proof of dependence on the identified cue, eventually helped to define all the other parameters. There was no "proof of absence" of pattern vision, but there was an observation that it did not appear when called, and the parameters and cues provided a more probable explanation.

Of course, if trained on the two shapes shown in Figure 10.2F, the bees would start afresh to learn a different parameter, such as the difference in modulation or total length of edge, as in Figure 10.3C.

To show that bees recognize the important parameter of edge orientation, we trained a group of bees to discriminate between a pattern of three bars at 45 degrees versus the same at 135 degrees, shuffling the positions of black to remove the bar positions as a parameter (Figure 10.3A). The total positions and areas of black, the modulation, and the edge length, are the same on both targets, so the bees do not learn these parameters. A layman would be forgiven for thinking that the bees remembered the pattern and the lengths of the bars. However, the trained bees showed equal preference for the rewarded training pattern and a pattern of short bars of similar total length, also at 45 degrees (Figure 10.3B), because in the training they had learned only the difference in orientation, not the layout of the patterns.

To show that bees could recognize a modulation difference, we trained a new group of bees to discriminate between the pattern of three bars at 45 degrees versus the short bars also at 45 degrees (Figure 10.3C). Again, you might suppose that the bees noticed the difference in the patterns or the length of the bars. In a test with all the bars at 135 degrees, the trained bees discriminated the modulation difference (Figure 10.3D), but in another test, they were unable to distinguish between long bars at 45 degrees (the training pattern) versus long bars at 135 degrees (Figure 10.3E). They ignored the orientations in this test because they had been the same on both training targets. However, they could detect the modulation difference in completely different patterns (Figure 10.3F).

The choice of tests in these experiments was the result of a long history of progressive understanding of the way that bee vision works for targets subtending 40–50 degrees at the eye. Once a way was found to define the test set for each pair of patterns that were discriminated, it was possible to test each cue in turn, to discover exactly what the bees had learned. Each example yielded the same general conclusions. They learn to ignore parameters that were the same on both targets, and they remember one or more simple cues in order of preference, but nothing about the layout of the pattern, and clearly the pattern is not reassembled in the memory of the bee (Figures 10.2 and 10.3).

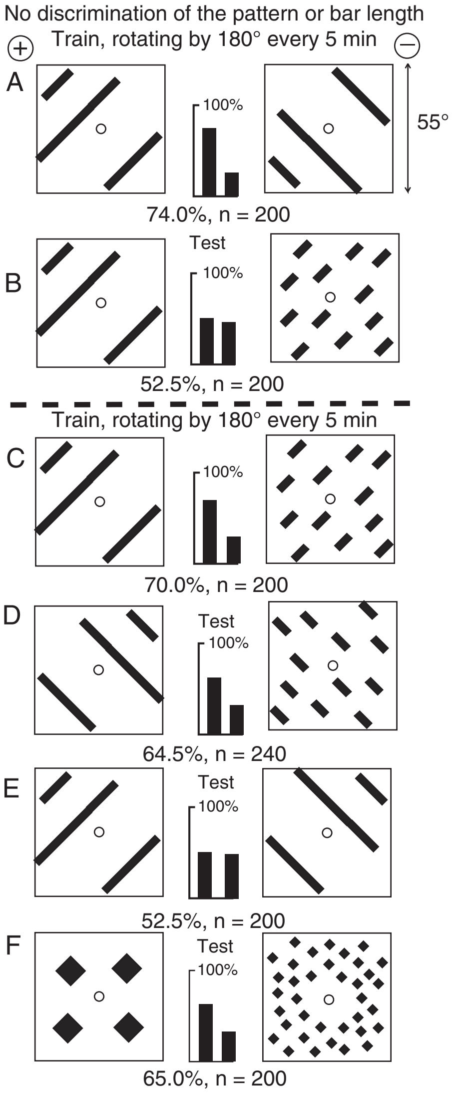

FIGURE 10.3 The distinction between modulation, total edge length, and the lengths of the individual bars. **A**: Training for the orientation cue. **B**: In this test, the bees do not remember the pattern or the lengths of the training bars. **C**: New training patterns with a difference in modulation and bar length but the same orientation and total area. **D**: Recognition of the modulation difference irrespective of orientation. **E**: No preference for the rewarded pattern or the orientation. **F**: A clear preference for the lower modulation in unfamiliar patterns.

Having introduced the problem of pattern discrimination and revealed the method for a general solution, it is time to list a few technical terms.

DEFINITIONS OF TERMS

The *parameters* are outside the eye. The *feature detectors* behind the eye respond to the parameters. A *cue* is the sum or count of the responses of one kind of feature detector in a local region of the eye, and is therefore inside the bee. The *cue* is derived from a part of the *image* in the local region, but the process of summation destroys the local layout. Bees learn retinotopic positions of cues. Some cues are measured quantitatively. There is an order of preference for the known cues. A *landmark* is recognized as the coincidence of the several different cues in a local region of the eye.

The *feature detectors* are the units of perception of modulation, edge orientation, black, white, or color. They are small, about 3 ommatidia across on the retina, and all respond independently in parallel. The responses of the feature detectors are summed to form cues, and the bee remembers the totals and their averaged positions, not the individual detector responses.

The *field* of a filter or neuron is the region in space and time within which a signal is detected.

A *fixed* pattern, as opposed to a *shuffled* one, has the pattern fixed as seen from the choice point of the bee.

A *generalized parameter* is one that is recognized in a context other than in the training pattern. Originally, it was merely in a different position on the target, but later it was in a different pattern.

The *image* is the pattern of excitation in the array of receptors in the retina.

The *label* is the coincidence of cues in a local region of the eye, by which the bee recognizes a landmark and its position.

The *modulation* of a receptor is the change in the light intensity in the receptor, and the consequent electrical signal. The motion of the eye over *contrasts* generates the modulation of the receptors. The *modulation* of a pattern is roughly equal to the total length of edges in it.

Orientation of an edge is usually the angle to the vertical in a vertical plane. Within the local region of the eye, averaged orientation has a retinotopic position that bees can be trained to remember.

A *parameter* is a scalar or vector measurement of some aspect of the pattern outside the eye; for example, the area, total length of edge or averaged edge orientation.

The *patterns* are displayed on the *targets* during training and tests.

Place for bees is a geocentric term, like the place on a map; *position* and *direction* are usually retinotopic terms for the direction relative to the axes of the head. *Location* or *position* also refers to the position of a parameter on the target, a shift in position of a pattern or a shuffle of the locations of boxes, targets, or bars during training and tests.

Point of choice is the place where the bee detects a cue and makes a choice by moving away or toward the reward or the next target.

A *sign stimulus* is an older and more general term that is not restricted to vision (e.g., the call of a bird). It is the human idea of the essential stimulus *outside* the animal, not the parameter that is eventually identified, and certainly not the cue formed by the feature detector responses *within* the animal.

A *template* is a hypothetical mechanism that detects a fairly complicated pattern that has been identified by the human observer. It may be innate or learned. In vision, a spatial copy is usually implied. Templates are useful in preprogrammed robot vision.

THE MECHANISM

We now turn to each stage of visual processing, the way a place is remembered, and finally to the consequences of this mechanism.

The Retina and Optic Lobe

The honeybee has an array of photoreceptors that act independently of each other, like the cones in our own eyes. With a small overlap at the front, they collect light from the panorama around the head (Figures 10.4A and 10.5), and collectively form a single image that is divided into about 5,500 pixels per eye. Despite early misconceptions that the compound eye produces multiple images, the composite image laid out across the eye is fundamentally similar to that in the vertebrate eye (Figure 10.4B), as inferred by Hooke (1665).

Below the retina, the optic lobe of the brain contains three main regions of synapses: the lamina, medulla, and lobula (Figure 10.4C). The columns of small neurons corresponding to each facet on the eye contain 8–10 neurons in the lamina, about 200 small neurons in the medulla, and about 10 larger ones in the lobula. The columns are similar to each other, but the successive arrays are very different, with progressive summation to larger fields (Figure 10.4D).

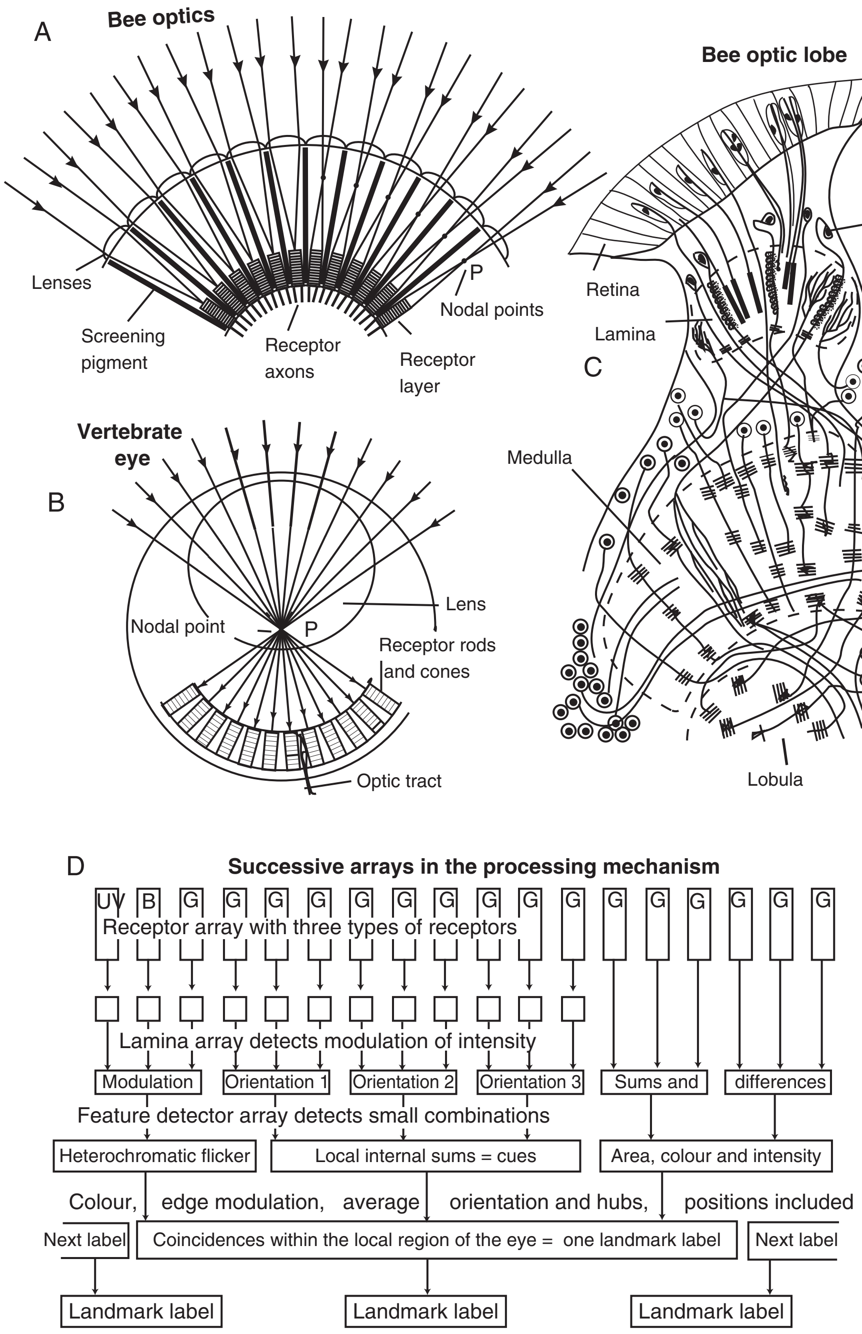

FIGURE 10.4 Simplified optics and visual processing mechanism. **A**: A section through the retina of a compound eye, like that of the bee. An array of small facets, each with its own lens, looks out in each direction. A corresponding array of cones of light fall upon the receptor layer, producing an erect image in the eye as a whole. The optics of each ommatidium can be simplified as (*left*) a parallel beam focused on each receptor tip, or (*right*) the projection of the receptor to the outside through the nodal point of its lens. **B**: A vertebrate eye, which is anatomically different but functionally similar, but with an inverted image. **C**: A section through the optic lobe of the bee with representative neurons, showing that the processing mechanism involves successive arrays of synaptic connections, in the lamina, medulla, and lobula (Cajal & Sanchez, 1915). **D**: A block diagram of the inferred visual processing mechanism, showing the successive summation of the arrays of receptors, feature detectors, and cues into progressively larger fields.

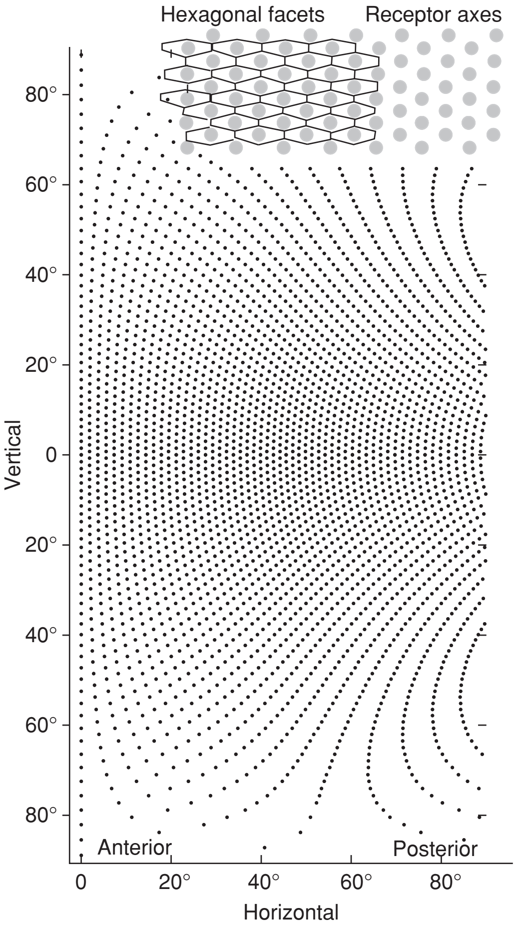

FIGURE 10.5 A map of the left eye of the worker honeybee viewed from behind. Each visual axis is shown in angular coordinates on equal horizontal and vertical scales. The densest region is near the equator, about 45 degrees from the front, which is on the left. The rows of hexagonal facets are horizontal but vertically compressed, as shown at the top, so that the rows of nearest receptor axes are vertical or oblique. Data from Seidl (1982), regularized and digitized by Giger (1996). The digital data are available free for personal use from Horridge (2009b; p. 107, Figure 5.11).

The Feature Detectors

To collect something more interesting than an array of separate responses, the receptors feed into arrays of feature detectors, each of which detects the coincident responses of a small group of about 7 ommatidia (Figure 10.6A–E). The feature detectors are the basic units of peripheral vision. Their properties define the whole mechanism. Those for orientation detect contrast and respond to edges of a particular orientation. There are at least three types with axes at 120 degrees to each other (Figure 10.6C–E). They are small, about 3 degrees long and wide, color-blind, green-sensitive, and symmetrical about an axis, so that they do not distinguish between black–white and white–black edges. The minimum size of the edge orientation detectors (3 degrees) was measured from the shortest lengths of edge in which orientation could be detected (Horridge, 2003d). The maximum size (3 degrees) was measured from the longest gaps that could be bridged in a line of dots or squares (Horridge, 2003c). The tuning to orientation is poor because they are short.

Besides the orientation detectors, an array of modulation detectors (Figure 10.6B) receive excitation from both blue and green receptors and have better resolution than the orientation detectors. They were postulated long ago (Jander, 1964), but their correct size was inferred from the best resolution of a regular grating (Horridge, 2003e). There are also at least three arrays of tonic color channels, peaking in the ultraviolet, blue, and green, that measure areas and intensities of color. There is, therefore, a limited variety of feature detectors inside the eye, responding to very local parameters outside the eye; namely, modulation, color, area, intensity, and local edge orientation (Figure 10.4D). Also, but not considered here, local motion detectors respond to successive modulation of two or more adjacent receptors and detect the direction of motion of contrasts across each region of the eye. They are green-sensitive and therefore color-blind.

The Cues

The cues are the basic units of visual recognition: About ten kinds have so far been defined. Just as the receptors count photons, each cue is the total of the coincident responses from its own array of feature detectors summed over a short period, so that a running average of each is continuously reported within the bee. Because the cue is a sum, only one cue of each type is learned in each local region of the eye. It is learned in the range of positions in which it was displayed during the training (Horridge, 1999, 2003a).

Being a sum of feature detector responses, each cue has an input quality, an input quantity, and a retinotopic position, which is a summarized code analogous to that in a neuron. In this transformation, the positions of the feature detector responses are lost in the summation into cues. The absence of a cue is itself a cue (Horridge, 2007).

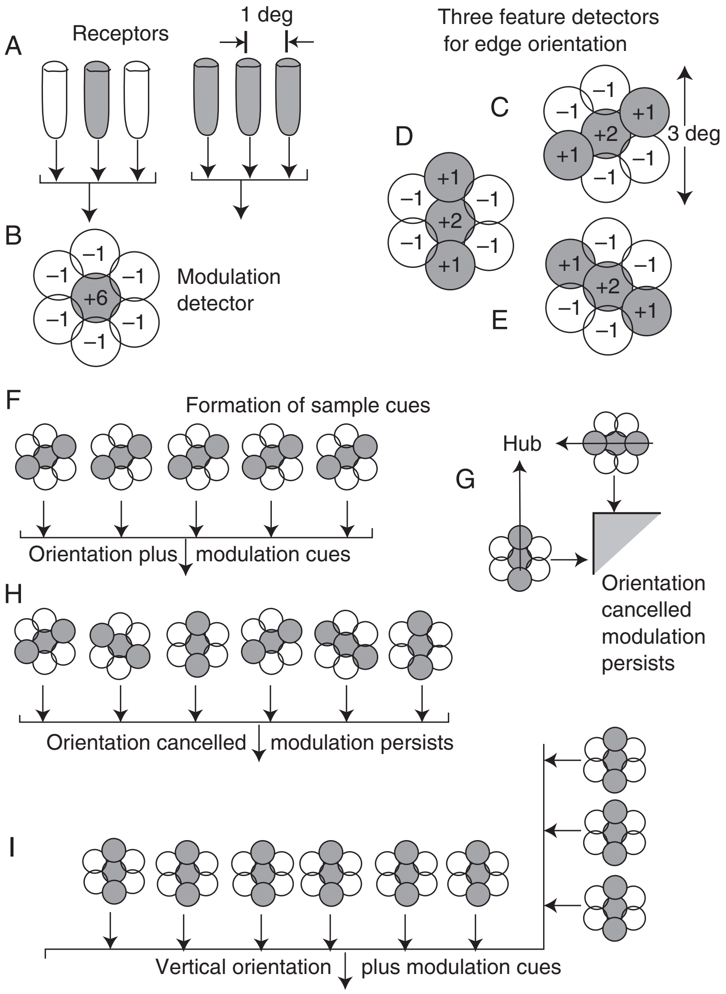

FIGURE 10.6 Receptors and feature detectors: the peripheral units of vision. **A**: Receptors sum upon feature detectors that are 3 degrees across. **B**: A spatial modulation detector. **C–E**: The three hypothetical orientation detectors that are compatible with data from the honey bee. These feature detectors are similar to Canny detectors, as used in machine vision. The response to a flash would sum to zero in all of them. From Horridge, G. A. (2005) redrawn and re-arranged with corrections. **F–I**: Arrangements of summation of feature detectors that detect various combinations of edges to form cues, irrespective of the pattern or exchange of black for white. Shaded areas are excited by light; white areas are inhibited.

This summation makes bee vision quite different from human vision or film. Orientation detectors with different axes are summed to make an average orientation, which may be zero, but even so, the total edge modulation persists (Figure 10.6G,H). Modulation is a measure of total edge length, irrespective of area or shape, and areas are separately summed irrespective of the length or distribution of edges. Therefore, the layout of the local pattern is lost at this point in the processing (Figure 10.6A–I), but the position of the center of each cue is preserved and used as a cue. Local regions measure about 10–25 degrees across, so there could be at least a dozen separate regions on each side of the head, with different cues in each.

In each local region of the eye, the most preferred cues during the learning process are (1) modulation (i.e., length of edge per unit area), and (2) isolated black spots. Large black spots are stronger cues than small spots. (3) The position of a black area or other cue is remembered to within 8 degrees in the vertical direction. (4) There is similar preference for radial spokes and (5) the average orientation of edges. The bees remember a difference between radial and (6) tangential edges, and (7) the positions of their centers of symmetry, but not the actual patterns. (8) Symmetry in a pattern of bars is preferred as a cue over the component edge orientations that generate the symmetry. The bees also remember (9) whether the reward hole is surrounded by a light, dark, or colored area. They recognize (10) the color of a patch and its position, but have difficulties identifying two or more patches that differ in color within a local region of an eye. The order of preference was found by training them with a choice of parameters, then testing them to see which cue they learned first (Horridge, 2007).

The Parallel Channels in Each Local Region

Large numbers of local orientation detector responses are summed in large fields in each local region of each eye to make cues (Figure 10.6F,I) with an improved signal-to-noise ratio. Other combinations of the same local orientation detector responses feed into quite different large-field detectors of circular and radial edges, irrespective of pattern (Figure 10.7B).

With some help from the anatomical plan of the optic lobe (Figure 10.4C) and its electrophysiology, we can now make a map of the channels in each local region (Figure 10.8). This is a formal plan of the system, omitting all those tedious neurons. The various channels for the different types of cue pass through the optic lobe in parallel (Figure 10.4D). The summation of the responses of each type of feature detector gives a quantitative measure of the corresponding cue but destroys the local pattern. Channels from green and blue receptors feed into large lamina cells that detect temporal modulation (on the left in Figure 10.8). Color channels detect position and are tonic (that is, they give a maintained response to a constant photon flux) or they are phasic and respond to contrasts. Their total in a local region is a measure of colored area, irrespective of pattern.

The Labels on Landmarks

Each of the channels from a local region of the eye carries one or more cues, and the missing cues are also remembered, so no information about cue distribution is lost. The set of cues that coincide in a local region of the eye is the label on a landmark, whether or not a single physical landmark is out there. The summations imply that each eye region remembers one landmark label. The labels are the basic units of visual recognition of landmarks.

The Panorama of Local Regions

As everywhere, in all sensory mechanisms, the feature detectors are each labelled with the body position of their receptors; in this case, a retinotopic projection of the local regions of the eye. Each local region (Figure 10.8) is repeated around the eye, generating an array up to 300 degrees wide that simultaneously detects a number of landmark labels in different directions that together recognize a familiar place (Figure 10.9). The local regions divide the 300-degree panorama into parts, so that landmarks can be localized. The unit of place recognition is the whole array around the eye. The bee also measures the range of any large contrast in each direction as the eye moves. The final step in place recognition is the coincidence between the landmark labels and the memories of them from a previous visit. Most panoramas are rich in natural features, so there is usually abundant redundancy of cues.

It was by chance that the angle subtended by our experimental targets (Figure 10.1) was similar in size to the local regions of the eye, so our patterns were usually identified by two local regions, one at the front of each eye. What we thought was perception of a pattern on an experimental target turned out to be the detection of the label on the pattern that acted as a landmark. In the training apparatus, the bees do not set out to learn to detect a pattern or shape; they simply learn the coincidences of directional cues that identify the place of the reward, as they do in a natural scene. Patterns are for people: bees are limited to coincidences of cues.

To recognize where it is in the natural situation, the bee has available only what it has learned. When nearing their destination, bees adjust their orientation and position to maximize the coincidences of cues, which improves the fit between the image on the retina and the memory of it, as described by researchers on landmarks (Fry & Wehner, 2002). This implies separate memories in each local region of the eye. Large local fields allow for the motion of the bee in flight. For this system to be successful, there must be a compromise between too many small local eye regions or too few large ones.

The feature detectors are innate, and cues and labels are detected continually, but they depend on

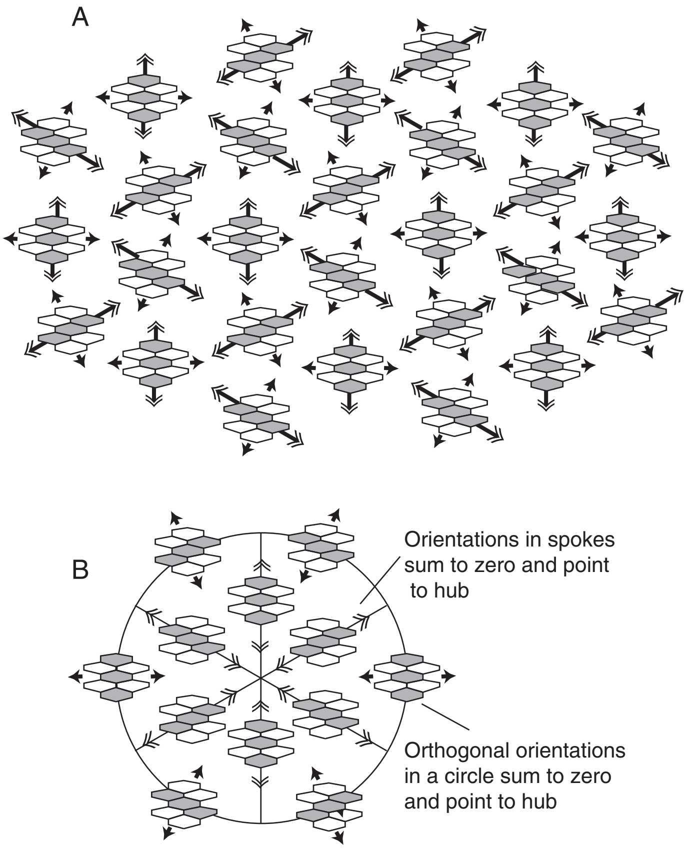

FIGURE 10.7 The integration of orientation detectors to detect radial and tangential cues and the positions of their hubs. **A**: The array of edge detectors with three different orientations. **B**: The orientation vectors (*feathered arrows*) point toward the hubs of radial patterns. At right angles to them, the simple arrows point toward the hubs of circles. When a pattern is displayed, the cue detectors sum the responses of each kind of vector separately. Therefore, the type of pattern and the position of the hub are detected but the actual pattern is lost. From Horridge, G. A. (2006) redrawn and re-arranged with corrections.

what is available in the image. The feature detectors, cues, and landmark labels are the letters, words, and sentences that define a place for a bee. In this analogy, the array of local eye regions writes a sentence that detects the place of the reward (Figure 10.9). Route finding requires a sequence of these memorized descriptions along the path to the reward, governed by what the bees preferred to detect in the parameters along the track.

The Size and Number of Local Regions

The size of the local regions is 15–30 degrees, as suggested by the resolution of landmark positions, but still sub judice. There is evidence from measurements of resolution that the size is different for each cue, and is probably influenced by the responses themselves. The bees detect a vertical shift in the position of a familiar cue on the target, up to about 16 degrees; but with larger shifts, the response to the shift falls away as the test cue moves off the local region. Other indications of regional size come from the resolution of the angle between landmarks and studies with patterns that subtend controlled angles (Figure 10.10). For example, a 45-degree rotation of a square cross subtending less than 50 degrees is not discriminated, but rotation of a large cross subtending more than 100 degrees is discriminated by the change in position of the black area at the ends of the arms (Figure 10.10C). With very large targets subtending 130 degrees (Wehner, 1967, 1969), or when the bee lands on the rewarded pattern (Gould, 1986; Lehrer & Campan, 2006; von Frisch, 1914), parts of the image fall into

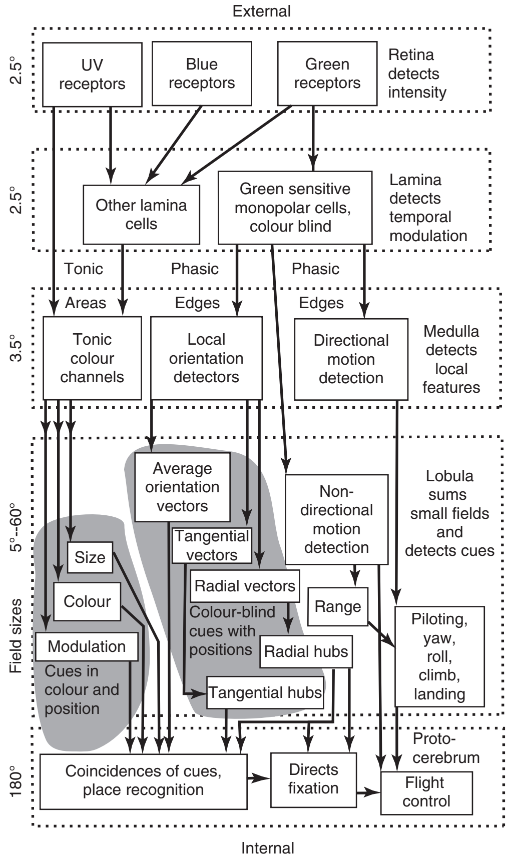

FIGURE 10.8 The arrangement of separate pathways in parallel in each local region of the eye, as inferred from a wide variety of data. This local system detects the state of one cue of each type, which together forming a landmark label. These local regions are arranged around the head, as illustrated in Figure 10.9. Revised from Horridge, G. A. (2000) redrawn and re-arranged with corrections.

several local regions of the eye, so that several positions of black or color are remembered separately (Figures 10.10D and 10.18), and the image provides several landmark labels like a panorama. Of course, this does not imply that the whole configural layout of a large pattern is remembered.

Directional motion detection, important in locomotion, is also summed in various combinations of directions in separate channels in large regions of the eye. Some components of the optic flow are handled by the bee as if they are cues, and remembered; for example, the angular velocity controls flight height and landing, and the integrated angular velocity at the side of the eye is a measure of the distance traveled.

HISTORY OF THE ANALYSIS

For a century, bees have been trained to recognize a pattern or distinguish between two patterns. An explanation compatible with the data was found intuitively, but until about 1996 it was never confirmed by the exhaustive testing of trained bees. The result was a confusing series of conclusions that were sometimes conflicting, often fanciful, but always delivered with conviction.

Electrophysiological Constraints

The analysis of the visual system was guided by the known properties of the retinal photoreceptors (e.g., Naka, 1961), the lamina ganglion cells (e.g., Laughlin, 1994), the numerous small neurons of the medulla (e.g., Osorio, 1991), and the large fields and puzzling multimodal functions of the lobula neurons (e.g., Horridge, Scholes, Shaw, & Tunstall, 1965; Maddess & Yang, 1997; Paulk, Phillips-Portillo, Dacks, Fellous, & Gronenberg, 2008) in other insects. The lamina cells preprocess the signal for the local detection of modulation. The responses of the numerous small neurons of the medulla suggest a location for the feature detectors, cues, and memory storage. A group of them could correspond to a cue. The lobula neurons below, like the cues, signal a quality, a quantity, and a position on the eye. The individual large-field and multimodal neurons in the lobula are excited in different combinations by different parameters, but most make no sense in terms of function unless they work in groups and generate landmark labels by coincidences. The idea that integration at all levels works by detecting expected coincidences of neuronal responses is one of the classical mechanisms of all nervous systems. The idea that coincidences are remembered if a reward is found is one of the classical explanations of learning.

Early Discoveries of the Parameters

Although there were earlier demonstrations of pattern learning, crucial advances were made by Hertz (1929–1931). When trained simultaneously on a variety of patterns on a flat white table, the bees detected some common features (at the time called parameters), and later they recognized these in unfamiliar patterns. In agreement with her ideas derived from the Gestalt theory of the time, Hertz called this "generalization." She also trained bees on a single pattern and found that they were attracted to unfamiliar patterns that displayed the same parameters. This was also called "generalization." This usage of

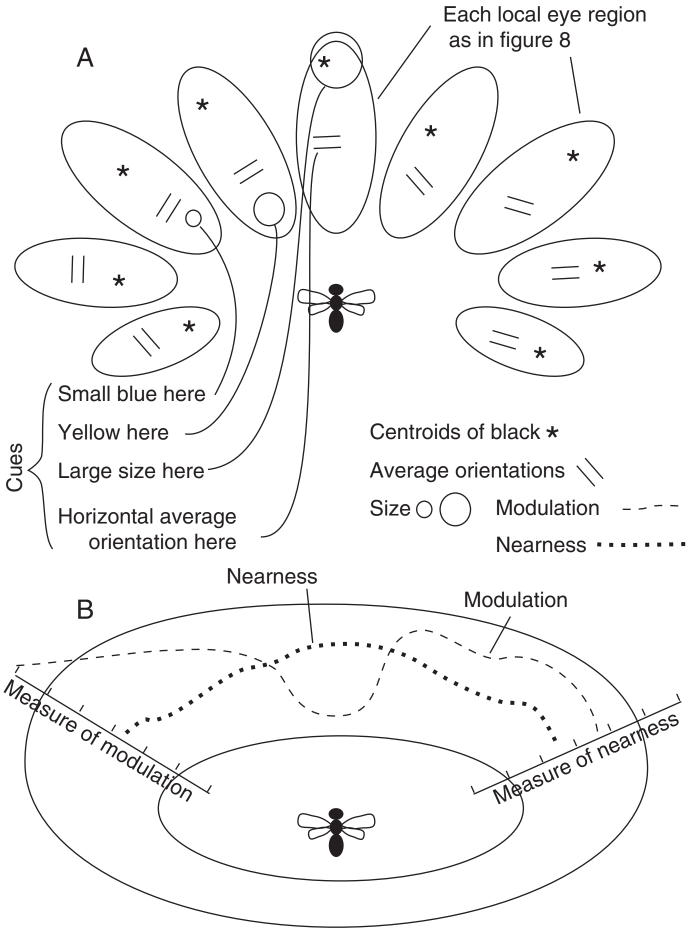

FIGURE 10.9 The coincidence of expected landmark labels in the natural panorama. **A**: The array of local regions, each of which detects one landmark label with the bundle of local detector channels shown in Figure 10.8. Trained bees recognize the expected cues in their expected directions and then detect the correct coincidence of landmark labels around the head to recognize a place **B**: In each direction, the moving bee continually measures the modulation (stimulation by edges) in each local region and the range of nearby contrasts from the relative motion. From Horridge, G. A. (2005) redrawn and re-arranged with corrections.

the word "generalization" was retained for bees, with no implications about comparisons with other animals. Hertz's parameters were size or area of black or color, the total length of edge in the pattern, gray level, and radial or circular symmetry. Edge orientation was not a parameter because the patterns were flat, and the bees had no memory of the directions of their flight paths. Later, the parameters of area and edge length were quantified (Anderson, 1977; Cruse, 1972), but no one considered the angular subtense in which the totals were measured.

When one pattern was presented versus another, the bees at first learned only the most preferred parameter, with edge length best and brightness or gray levels worst. In recent experiments, they learned to overcome an innate avoidance of rings, and when the preferred cue was displayed on the negative target, they learned to avoid it (as in Figures 10.2, 10.10, 10.17, 10.18, and 10.20).

For most of the century, generalization in bee vision was thought to be an indication that they recognized elements of similarity between patterns, something like the corresponding human ability. This is obviously not true for bees, because they also generalize to quite different patterns (Figures 10.2B–E, 10.3B–F, 10.10C, 10.12, 10.13, and 10.15). Generalization was also related to a main tenet of Gestalt theory, that the layout of the

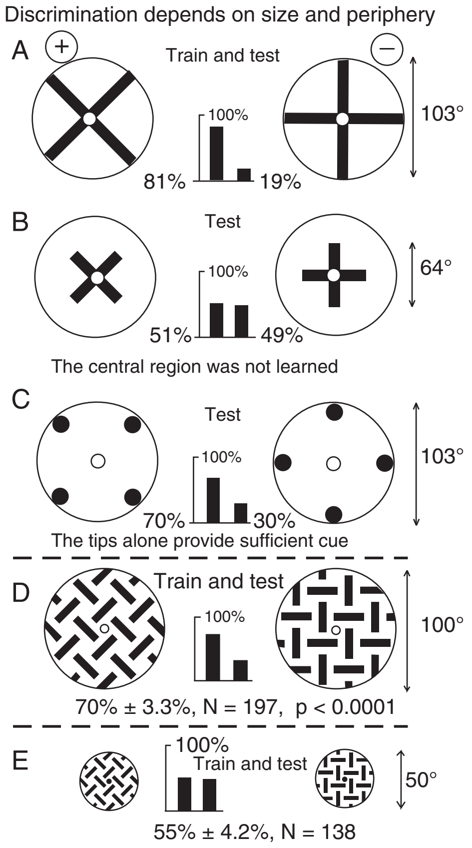

FIGURE 10.10 The significance of the angular size of the pattern. In very large targets that overlap more than one local region of the eye, the configuration of a pattern can be coarsely discriminated by the different locations of areas of black. **A**: Large training patterns. **B**: Failure to recognize the central parts of the patterns. **C**: Spots at the periphery are sufficient. **D**: Even some quite complex patterns can be discriminated if large enough. **E**: The same patterns subtending 50 degrees were not discriminated. From Horridge, G. A. (1996) redrawn and re-arranged with corrections.

image on the retina is assembled in the brain. We now know this to be a myth for the local eye regions of the bee. The division of the image of the panorama into landmark labels is a coarse representation that is clearly distributed across the eye, but recognition of place requires only the expected coincidences, not the reassembly of the parts of the image.

In the early work, from 1914 to 1968, the criterion was the landing on the rewarded pattern. From 1968 to 1973, in work by Wehner, the patterns were also huge, subtending 130 degrees at the bee's eye. In later studies (Dyer, Neumeyer, & Chittka, 2005; Gould, 1986; Lehrer & Campan, 2006, for example), again the bees landed on the patterns. So, for almost a century, the large image spread across several local regions of the eye in the learning period made it impossible to analyse the visual system because the cues in the different regions could not be separated for their identification. Moreover, in the tests, analysis was also impossible because several parameters were changed at the same time, even in a single eye region. The resulting data were not wrong, but they were certainly confusing and led to unjustified conclusions borrowed from the cognitive sciences. Furthermore, with large patterns, the bees learn several labels, so they will not accept test patterns that differ much from the training pattern. Therefore, the variety of tests is restricted because the bees simply go away, a problem usually not mentioned. The accidental adoption of the Y-choice apparatus (Figure 10.1) about 1988 isolated a sufficiently small region of the eye for isolation and analysis, from the parameters to the landmark label (Figures 10.4D and 10.8).

Confusions in the recent literature also arose when results from patterns of different sizes were compared. There were also errors of thought: for example, it was commonly found that bees discriminated between two or more patterns, from which it was inferred that the bees actually saw the patterns. When the parameters and cues were unknown, it was sometimes inferred that the bees remembered the whole pattern, even when the trained bees were not tested. Many recent conclusions, based on small numbers and variety of tests, continued to cause great confusion even until recently, because the researchers were unaware of the parameters in the patterns (Giurfa, Hammer, Stach, Stollhoff, Müller-Deisig, & Mizyrycki, 1999; Stach, Benard, & Giurfa, 2004; Zhang & Srinivasan, 2004).

A major difficulty for the newcomer to this subject is the large proportion of publications entitled "Cognitive perception," "Discrimination of pattern," "Shape perception," "The binding of visual patterns," "The concepts of "sameness," etc., when in fact the data did not logically demonstrate anything of the sort. For a century, the topic has been influenced by earlier titles in favour of an anthropomorphic interpretation of the results, before the necessary tests were done or the real units of bee vision were found. The experimenters adopted the terminology used for mammals and intuitively found their bee results consistent with it. Almost always, their data were good but their conclusions were usually wrong and certainly premature.

Later Discoveries of the Cues

From 1990 to 2006, in Canberra, beginning with orientation, we ran a long series of training and testing experiments with the same apparatus to establish the rest of the cues and to define the contents of the channels in a local region of the eye (Figure 10.8). Successive reviews tracked the progress (Horridge, 1994, 2000a, 2005a, 2006c, 2009; Srinivasan, 1994).

We immediately encountered the difficulty that the isolation and identification of each cue required the development of a suitable test set in each experiment because the bees were trained differently each time, as shown in the illustrations. When the positions and widths of vertical versus horizontal bars were shuffled during training (van Hateren et al., 1990), it was thought that the orientation cue was isolated, but the preferred parameter was the modulation difference. The orientation cue was isolated by training with oblique bars versus the same bars at 90 degrees. Parallel edges in a local region were summed, irrespective of position (Figures 10.2 and 10.6E). When the cues of orientation and position were removed by rotating both patterns during the training, the tangential and radial edges remained as effective parameters (Horridge & Zhang, 1995).

At about the same time, Srinivasan et al. (1994) found that the orientation parameters are cancelled in the cue when two equal bars at right angles form a square cross (Figure 10.10B) or any pattern (Figure 10.11G, H, and J) on the same side of the target (Horridge, 1997b). As a result of this cancellation of orientation, there was no orientation cue in a square cross (Figure 10.11F), a square (Figure 10.11G), a line of spots or squares, square steps that were separately resolved, or a random texture. The cancellation of orientation was complete with orthogonal bars that intersected, and orientation returned as the bars were separated to about 20 degrees. Orientation and color cues on the left and right sides of the target were independent, but radial and tangential cues were detected irrespective of side, with all cues in parallel (Horridge, 1997b).

For years, ignorance of the several cues in parallel, the mutual cancellation of differently oriented edges, the separate orientations and colors on the two sides, and especially the separate totals of responses to edges and areas irrespective of shape, led to confusion. For example, the two pairs in Figures 10.11E and 10.11J look similar, but bees easily discriminate Figure 10.11E by the difference in average orientation on the left and right sides. Some researchers took no account of radial or tangential cues at all (Stach, Benard, & Giurfa, 2004).

Although I was familiar with the separation of edges and areas in crab vision (Horridge, 1966), I was slow to see that, in the bee, the summation of receptor responses formed cues of area; summation of edge detector responses formed cues of modulation, irrespective of local pattern; and that the averaging of local orientation and of the positions of black areas formed two more cues, also with expected positions, and all cues were in parallel but separate.

For a time, it was thought that bees detected the orientation of an illusory edge (van Hateren, Srinivasan, & Wait, 1990), but this result could not be repeated (Horridge, 2003A). It was also proposed that the orientation of a patterned bar raised 6 cm over a patterned background was revealed with the aid of parallax (Zhang, Srinivasan, & Collett, 1995), but this result also could not be repeated, because a background that was resolved destroyed the orientation cues (Horridge, 2003A). Furthermore, in work in Canberra from 1990 to 1996, each bee was allowed more than one visit per test and could learn which side to go at the second visit, improving the marginal scores and invalidating some results in that period.

A Limited Variety of Cues

Much of the research effort from 1926 to 2006 was a search for parameters. There were surprisingly few of them. Until 1990, there were only the modulation or length of edge, the size or area of black, and the recognition of circles and radial patterns. Although discovered a century ago in the bee (Turner, 1911) and later in the wasp (Jander, Fabritius, & Fabritius, 1970), the discrimination of edge orientation was not accepted until 1990. Later, it was found that, irrespective of the pattern, bees discriminated the positions of the common centers of combined black areas (Figure 10.12).

A whole new concept was introduced with the discovery that bees discriminate the positions of hubs of circles (Figure 10.13) and spokes (Figure 10.14) by a mechanism with a distributed administration like that for orientation (Figure 10.6E), which ignored pattern layout (Figure 10.7B).

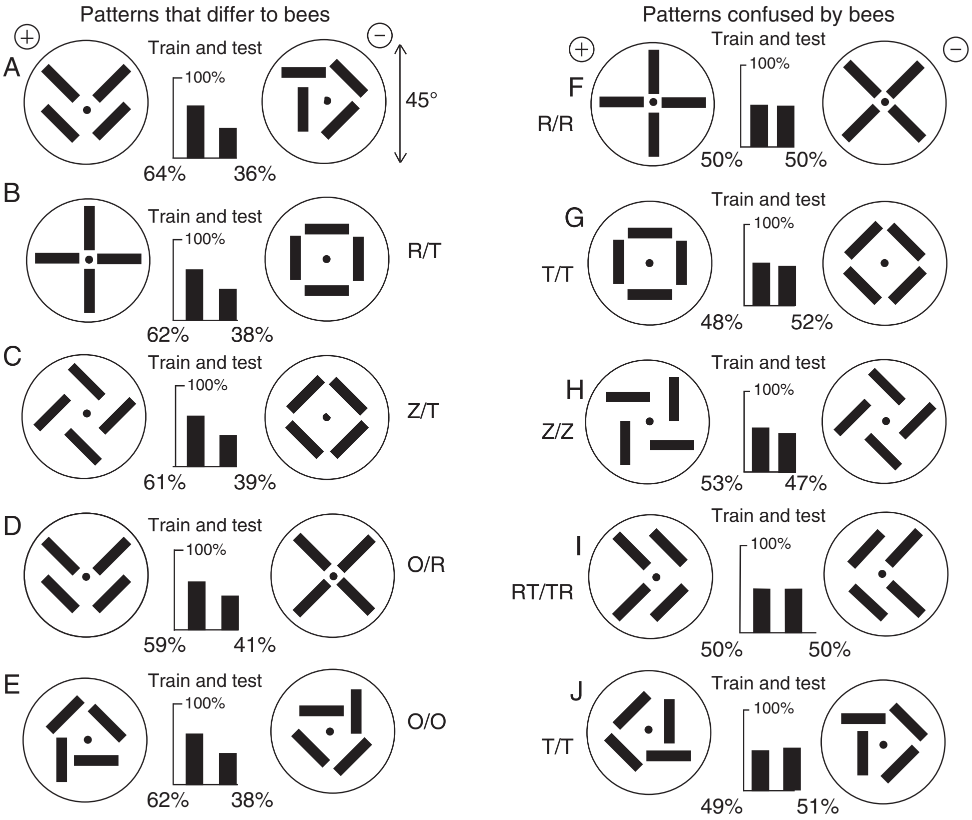

FIGURE 10.11 The patterns that were used initially to distinguish between parameters of orientation, radial and tangential edges on the two sides of the target, and symmetry. The cues of modulation, area, and position of the center were similar on the two targets and were not learned. **A–E:** Pairs of patterns not confused in training. **A**: Rad/tan and symmetry difference **B**: A rad/tan difference **C**: No cue versus tangent cue **D**: Orientation and radial cues **E**: An average orientation difference on right and left sides of the targets. **F–J**: When cues were similar on the two patterns, neither the individual bars nor the whole patterns were discriminated. The cues on the two sides are indicated by the letter O, orientation; R, radial; T, tangential; and Z, zero. From Horridge, G. A. (1996) redrawn and re-arranged with corrections.

Bees also discriminate the presence or absence of black around the reward hole (Figure 10.15).

Once the cues had been listed, it became possible to train bees to discriminate between two patterns with several known parameters, and then test them to find the order of preference for the available cues (Figure 10.16). Bees trained to come to a single pattern displaying several parameters were also tested to see which they preferred to use (Figure 10.17).

Cues Proved to Be Localized

Some confusion preceded the eventual demonstration that the cues were remembered in the local eye regions where they occurred during the learning process. For a time, there was a proposal that the whole training pattern was remembered (later called the *eidetic image*), and that it was compared with each test pattern (Wehner, 1969). This idea was eventually corrected in a series of papers in the past decade showing that the bees do not recognize the training pattern (as in Figures 10.2, 10.3, 10.11, 10.12, 10.14D, 10.15, 10.18, and 10.20). They remember the cues in the range of places where they are displayed during the training (Horridge, 1998, 2003A). This agrees with the general finding that each sensory channel is line-labeled with its position on the animal.

For comparison, there is no evidence that crabs discriminate shapes or patterns, but they have a retinotopic memory of the positions of outstanding contrasts in their surroundings, and when displaced, even during a brief dark period, they adjust their eyestalks to bring the eyes back to the former view (Horridge, 1966). Probably many arthropods that

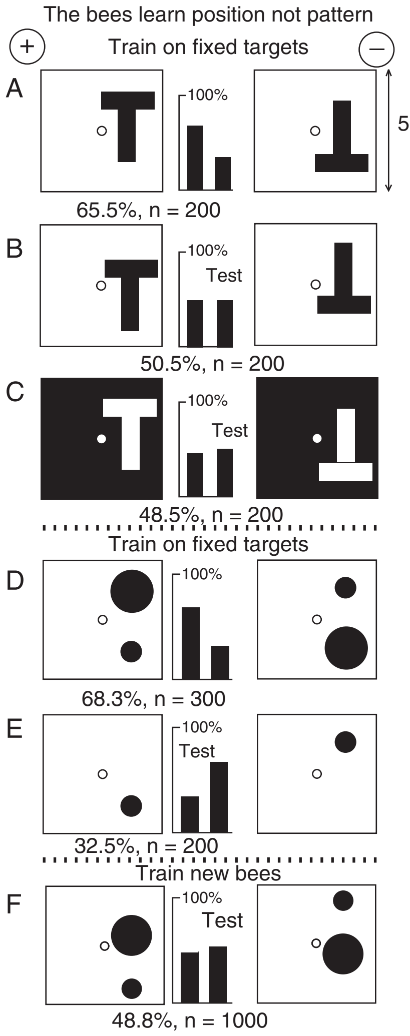

FIGURE 10.12 The center of black within the local region is remembered, irrespective of the pattern. **A**: Training patterns. **B**: Failure with the centers moved to the same horizontal level. **C**: Failure when black was exchanged for white, because the bees had learned the positions of black, not the edge orientations or shapes. **D**: Training with two separate spots on each target. **E**: Test with the small spots only; the bees prefer the black at the top. **F**: In a test with the common centers of gravity at the same level, the bees show no preference.(From Horridge, G. A. (2003) redrawn and re-arranged with corrections.

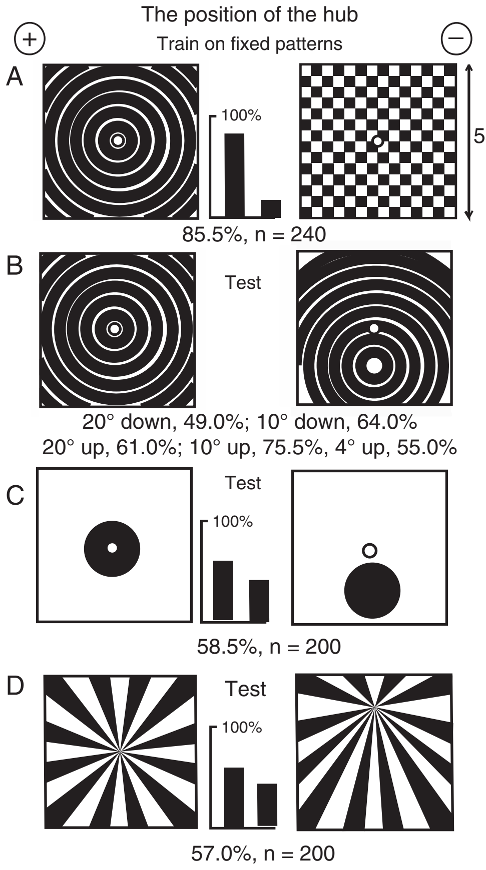

FIGURE 10.13 Bees learn the position of the hub irrespective of the pattern. **A**: Training patterns. **B**: Percentages of correct responses for shifts of the hub down or up. There is an optimum response near a shift of 10 degrees. **C, D**: The trained bees recognized the position of the hub in unfamiliar patterns. From Horridge, G. A. (2006) redrawn and re-arranged with corrections.

recognize a place have a corresponding mechanism, with continual updating as they move.

No Reassembly of the Image

For almost a century there was total confusion as to whether bees have an additional mechanism that reassembles and detects the layout of the pattern. “In view of the suspicion . . . that the bees might be reacting only to parts of the pattern and not to the whole, or the Gestalt, it was interesting to find out whether the arrangement of a number of similar parts made any difference to their attractiveness.” This quote (Carthy, 1958, p. 144) was probably derived from a pioneering paper by Lashley (1938), who found that rats learned only a minimal part of the training pattern. Full marks for the warning. Bad luck in that, when the image parts are rearranged, the bees may scarcely notice.

Until quite recently, an additional mechanism that remembered the layout or the global aspects of a pattern was in fact accepted. For example, “That insects are able to compare a stored neural image . . .

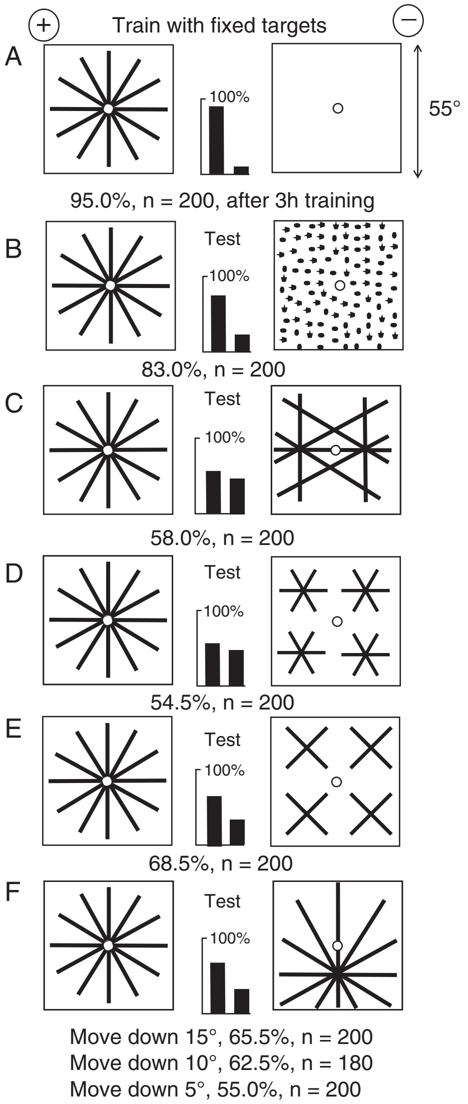

FIGURE 10.14 With a radial pattern, the bees remember the position of the hub and the modulation level. **A**: Training pattern versus a white target. **B**: Test showing they had not relied on the white target or the position of black. **C, D**: No preference for the rewarded training target versus similar ones with different layouts of the bars. **E**: The square crosses are detected as a different radial state. **F**: Percentages of correct responses in tests with different positions of the hub. From Horridge, G. A. (2007) redrawn and re-arranged with corrections.

with a current neural image . . . has directly been shown in honeybees" and, with reference to a proposed eidetic image of a sector pattern (as in Figure 10.18A), "The only factor that can account for the bees' ability to discriminate . . . is the exact retinal position of the black and white sectors" (Wehner 1981, p. 476). Actually, for 25 years, no factors were tested, and when the tests were done, the positions of two horizontal sectors were a sufficient cue (Figure 10.18D). When bees discriminated between a large bar or cross subtending 130 degrees, and the same was rotated, the threshold rotation was 4 degrees, so that the cue could not be the orientations of the bars, but was the difference in positions of black areas (Wehner, 1967, 1969).

The idea of an eidetic memory arose from experiments with very large targets that overlapped several eye regions. Later, tests on similar targets showed that locations of cues in well-separated parts of the pattern were detected by adjacent local eye regions that retained separate memories of locations of black or other cues (Figure 10.10).

The evidence against pattern recognition was repeatedly obtained when trained bees could not tell the difference between the training patterns versus quite different patterns that displayed the same cues that they had learned in training (Figures 10.2, 10.3, 10.14C,D, 10.15B,I, 10.17C, 10.18B, 10.20B,D).

Symmetry

The investigation of symmetry was revived by Møller (1995), who found that foraging bees avoided flowers with spoiled symmetry. When bees had been trained to come to a neutral checkerboard pattern, the frequencies of their choices between a large variety of other patterns showed a preference or an avoidance that was clearly related to the symmetry displayed, irrespective of the actual pattern (Lehrer, Horridge, Zhang, & Gadagkar, 1995). Bees learned to discriminate between two similar patterns if one displayed a vertical axis of bilateral symmetry. When trained on a variety of patterns, with only the vertical axis of symmetry in common, they discriminated the vertical axis in unfamiliar patterns (Horridge, 1996A).

A clue to the mechanism comes from the discrimination of edge orientation and color, in which the two eyes function separately (Giger & Srinivasan, 1997). Also, symmetry is learned more slowly when not centered on the reward hole (Figure 10.17F), again suggesting that the bee orients to the reward hole, so that the two sides of the target fall on the two eyes. When six to eight cues on the two sides are similar and centered at the same heights, there is a strong probability of bilateral symmetry.

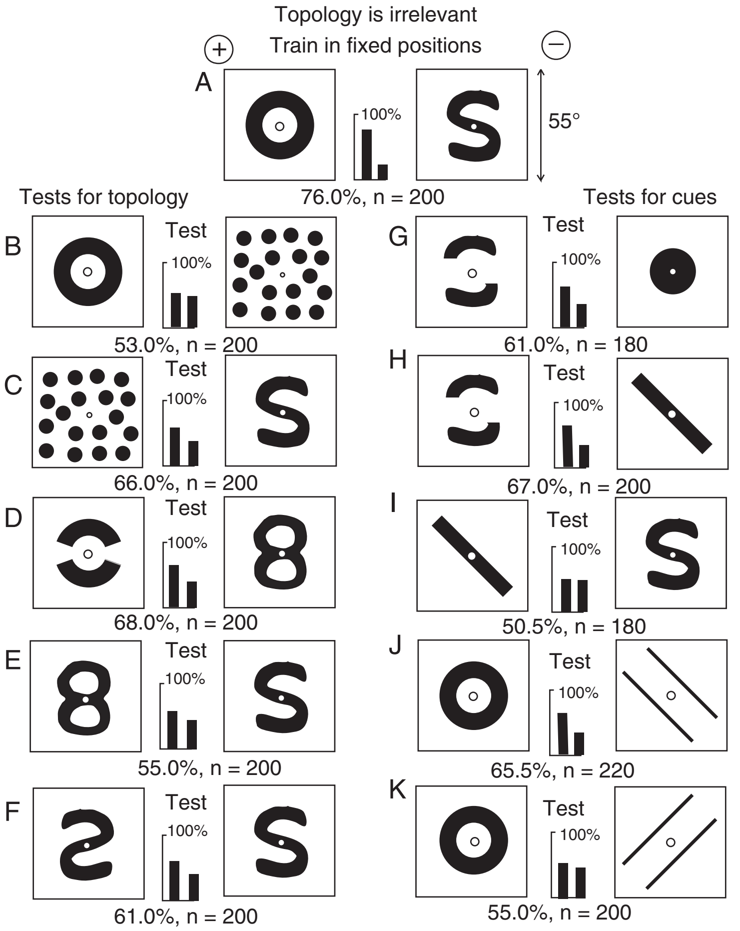

FIGURE 10.15 An example in which two cues were learned on the unrewarded target. **A**: Training patterns. **B**–**F**: Tests that show that the topology is not relevant. **B**: The trained bees did not recognize the ring. **C**: They avoided the S. **D**: Discrimination depends partially on the black near the center, not on the topology. **E**–**F**: Discrimination depends partially on the orientation cue on the S. **G**–**K**: Tests that reveal the cues. **G, H**: The cue is the black near one center but not the other. **I**: No preference with the orientation cue and black around both centers. **J, K**: The orientation cue is isolated. The training patterns were similar to those used by Chen et al., (2003) to infer that bees discriminated the abstract topology.

Whether bees discriminate mirror images or rotated patterns depends on the size of the pattern and on the cues displayed. For example, radial or tangential cues, or the height of the center of a black area, are not changed in a mirror image, and average orientation is unaltered by 180 degrees rotation (Figure 10.11E,J).

One Cue of Each Kind in Each Local Area of the Eye

To demonstrate that each local eye region has one channel for each kind of cue, bees were trained with a pair of patterns alternating with a different pair at corresponding positions on the two targets (Figure 10.19). When one pair displayed quite a different cue to the other pair, the bees learned both discriminations simultaneously, as if nothing was unusual. When one pair displayed the same type of cue as the other, but in a different state, they learned nothing, although all four patterns were different. The training was repeated with many other pairs of pairs. Different colors are different states of one type of cue. The results show that there is only one final common path for each type of feature detector in each local area (Figure 10.8). The experiment was possible because the local eye regions were similar in angular size to the experimental targets in the Y-choice apparatus (Figure 10.1). Of course, at a

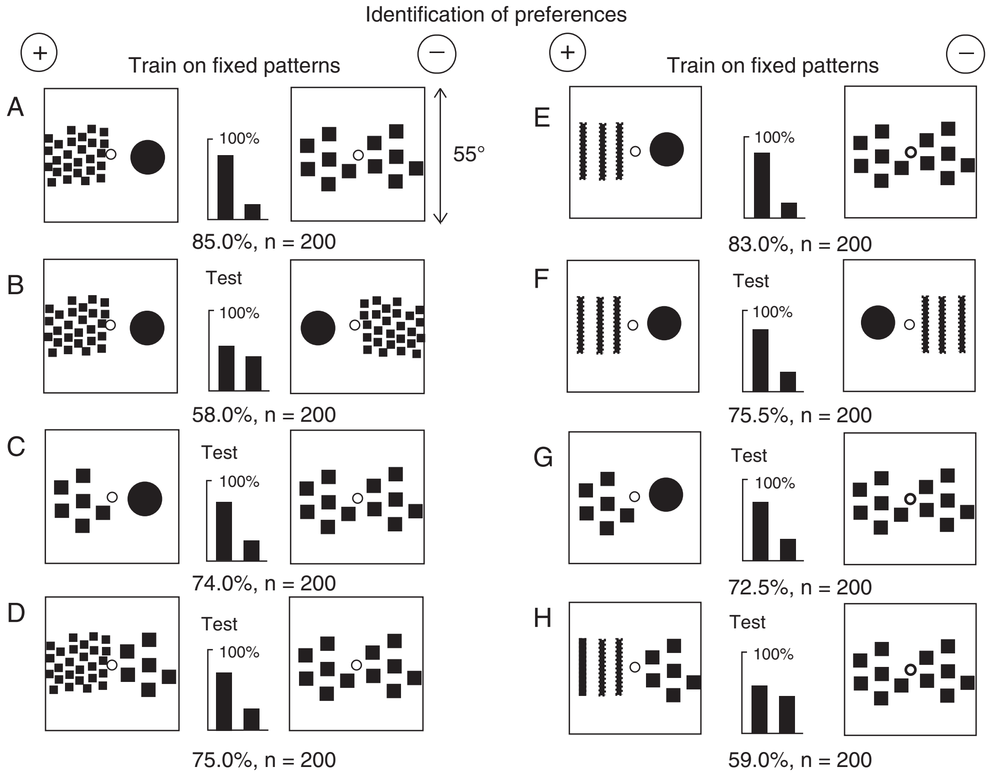

FIGURE 10.16 Two experiments on preferences for cues during training. **A–D**: Similar preference for strong modulation and a black spot. **A**: Training versus a neutral pattern. **B**: The trained bees scarcely distinguish between the training pattern and its mirror image, so they do not remember the spot's position. **C, D**: Strong responses to the spot and the modulation presented separately versus a neutral pattern. **E–H**: New training patterns reveal a preference for a black spot over oriented bars. **E**: Training patterns. **F–H**: The mirror image test reveals that the new position of the orientation was noticed. **G, H**: Strong response to the spot versus a neutral pattern, but poor response to the orientation cue. Similar experiments revealed the order of preferences for other cues. From Horridge, G. A. (2007) redrawn and re-arranged with corrections.

different time or place on the route, the bees can learn the same cue with a different response.

The Centered Square Cross, Square, and Disc

Although quite different in shape, a centered square cross, square, or disc display similar parameters of modulation, symmetry, area, a centered position, and lack of averaged orientation. A centered ring or a hollow square lack the black area around the reward hole, which is a sufficient difference for discrimination from other patterns of similar size (Figure 10.20), but these patterns are not discriminated when off center. Similarly, a disc and a square cross of the same area differ in radial or tangential cues, which are most easily detected when centered. In the past, the obvious difference in the shapes of these patterns for humans, together with ignorance of the effective parameters for bees and the lack of tests describing what the bees had actually learned, led to the erroneous conclusion that shape is remembered in generic form (Zhang et al., 1995).

PROPERTIES OF THE MECHANISM

No Localized Feedback Loops

The system described in Figures 10.4D and 10.8 has no efferent feedback circuits that loop back to more peripheral layers of the optic ganglia, apart from the external loop activated by the bee's own motion. All the integration is a form of summation, as illustrated in Figure 10.6, which implies that within each local area the separate positions of the various inputs are not recoverable in the outputs, which prevents a

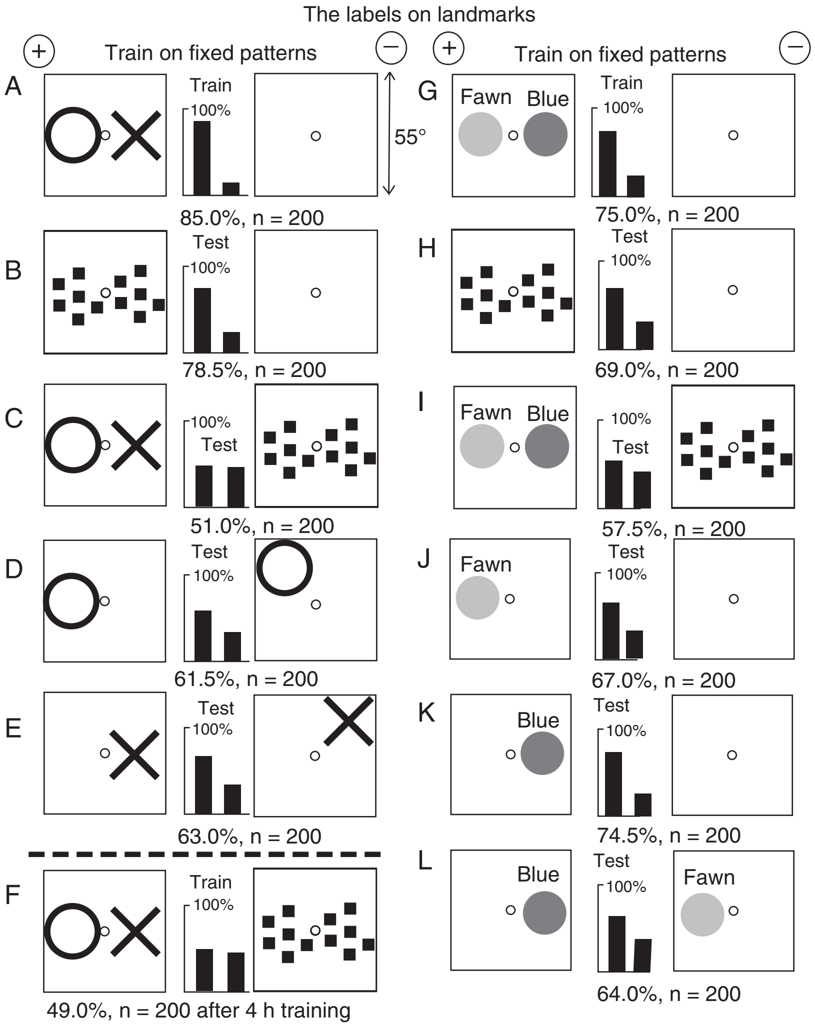

FIGURE 10.17 Two experiments to isolate the cues on a single landmark. **A**: Training with a ring and a square cross on the rewarded target versus a plain white target. **B**: A complete change of the pattern has little effect, showing that the bees avoid white or go toward black. **C**: With black on both sides, there is no preference for the training pattern. **D, E**: The bees recognize the expected position of black. **F**: New bees cannot be trained to discriminate the cross or circle when they are off-center because they detect no difference in cues (but see Figure 10.20). **G–L**: A new training experiment with a fawn and a blue spot on the rewarded target versus a white target. **H**: The trained bees preferred the unfamiliar pattern of black squares to the white target. **I**: The trained bees could scarcely discriminate the colored training target from the black squares. **J, K**: In its expected position versus the white target, the blue spot gave a larger score than did the fawn spot, as it would with no training at all. **L**: When given a straight choice, the trained bees preferred the blue spot as they would with no training at all. (**G–L** after Horridge, 2007, redrawn and re-arranged with corrections).

detailed spatial representation centrally. The decreasing number of neurons as we go down the optic lobes leads to the same conclusion. Recordings from the high-order optic neurons make no sense in terms of pattern perception, suggesting that the overlapping large fields function by coincidences in groups that are labelled with a time of day.

Processing Dependent on Coincidences

The bee visual system evolved to make full use of the feature detector arrays without reassembling the image. Thus, in each local region, feature detector responses of each kind are integrated to form cues, but the positions of their individual responses are

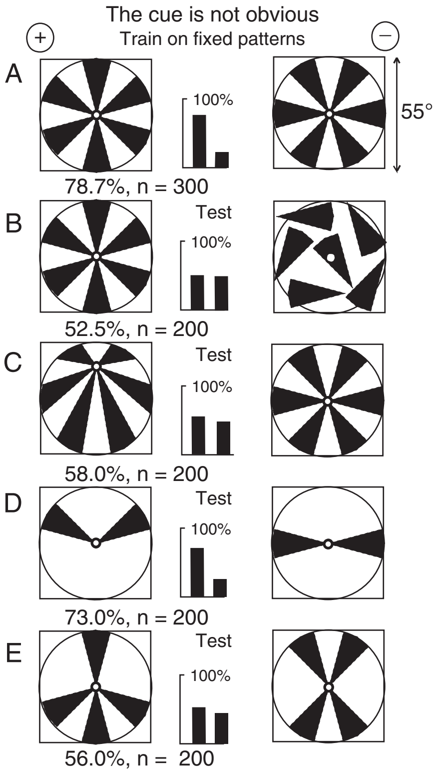

FIGURE 10.18 The curious discrimination of patterns of sectors. **A**: Training patterns, one rotated by half a period relative to the other. **B**: The trained bees failed to recognize the rewarded pattern versus the rearranged pattern. **C**: The bees had not learned the position of the hub because this cue was the same on both training targets. **D**: The trained bees avoided the pattern with horizontal sectors. **E**: They failed when the horizontal sectors were removed. The cue in the training was therefore the position of the horizontal sectors on the unrewarded target. (From Horridge, G. A. 2006) redrawn and re-arranged with corrections.

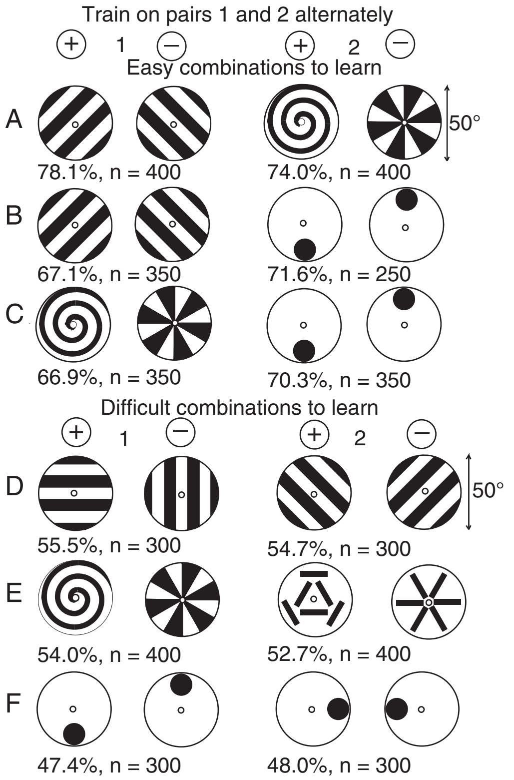

FIGURE 10.19 The demonstration of only one channel for each cue in the local region of the eye, when training with patterns subtending 50 degrees. The bees were trained on (1) the left-hand pair, alternating every 10 min with (2) the right-hand pair at the same place. **A**–**C**: Combinations displaying different cues were easy to learn. **D**–**E**: Combinations with different states of the same cue were impossible to learn, even after 5 hours of training. From Horridge, G. A. (1999) redrawn and re-arranged with corrections.

lost. This is the level of evolution reached by bees. To anyone interested in artificial vision, it is obvious that the next step, the assembly of the image, requires a huge investment in separating the significant groups of pixels from the meaningless ones, labeling them, and binding together the significant combinations of pixels into new temporary templates. An impasse is soon reached, with too many combinations and no instructions for selecting the meaningful ones. The bee, however, is stuck with preformed detectors and local groups of cues.

The cost of not assembling the image is that the bee visual system is limited to coincidences of predetermined cues. The advantages are a gain in speed and no further increase in weight. The bee system is a compromise between numbers and complexity of local eye regions that is sufficient to recognize a familiar place. More, smaller, local regions would confer better resolution of the panoramic layout but would still not add a stage of further processing.

Bees Prefer Modulation

Long ago, Hertz (1929–1931) showed that bees discriminated a parameter that she called *die figurale Intensität*, translated as "disruption" or "modulation." It is a measure of the flicker induced at the eye by the motion of the bee relative to the total contrast in a local region of the eye, and is the highest priority cue. The modulation detector was suggested by Jander (1964). Bees trained to come to a variety of patterns

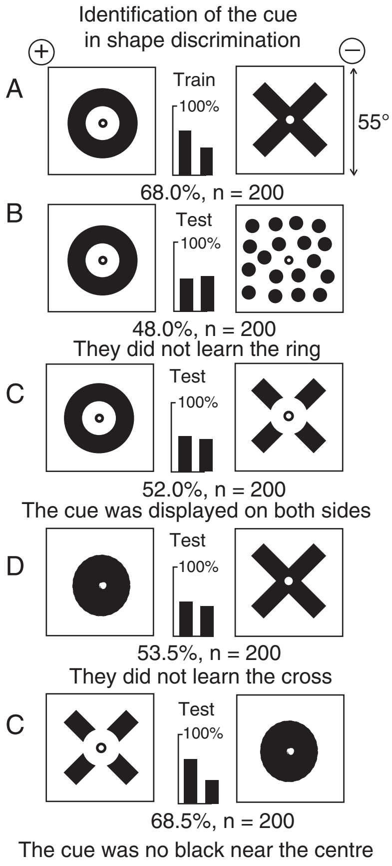

FIGURE 10.20 Discrimination between a ring and a square cross (see also Figure 17F). **A**: Training patterns. **B, C**: The trained bees fail to distinguish the ring from a pattern of spots or a hollow cross, so they did not recognize the ring. **D**: The cross is not distinguished from a solid black disc, so they did not recognize the cross. **E**: The cue is the black around the center, irrespective of the pattern. These training patterns were used by Zhang, Srinivasan, and Collett (1995) to infer discrimination of shape, but clearly there is no discrimination of these shapes. From Horridge, G. A. (2006) redrawn and re-arranged with corrections.

with similar disruption measured this common character and then preferred unfamiliar patterns that had a similar ratio of edge length to area. Bees trained to discriminate between a single pattern with a high ratio of edge to area versus one with a low ratio preferred the high ratio in totally different patterns. The simplest training patterns were a checkerboard, grating, spiral, or sector pattern, versus the same at a different scale. The trained bees responded to modulation differences of 30%, irrespective of a total change in the test pattern (Horridge, 1997A). Modulation cues are not color-blind and are therefore not the sums of responses of the orientation detectors or directional motion detectors.

Relations Between Cues

Basically, the cues in the different channels and eye regions are separate in their destinations but are linked at their inputs because the responses of the same arrays of receptors and feature detectors are summed in different ways to form the cues (Figures 10.6E, 10.7, and 10.8). With a training pattern on each target, the bees learned to ignore the parameters that were displayed on both targets.More accurately put, they learned them on one target and unlearned them on the other. They remembered only the most preferred of the available cues, with their positions to within 8–10 degrees in the vertical direction. Within the local region of the eye, patches of black were processed as a single patch, with a common center (Figure 10.12). Parameters that extended over two or more local regions, however, were learned as two separate cues (see Figures 10.9 and 10.10).

There was an order of preference in the learning of cues. Results were often anti-intuitive. A patch of modulation or an isolated spot were preferred over parallel bars and radial spokes that were more salient to human vision. When a weak and a strong cue were presented together, the weak one was scarcely noticed (Figure 10.16H). When the preferred cue was displayed on the unrewarded target, bees learned to avoid it.

Radial or circular patterns (Figure 10.7) and orientation (Figure 10.6E) are detected by a distributed array that works with any pattern but does not preserve the pattern itself. Radial and tangential cues remain effective when rotated about the center, and are not separated on the two sides of the target. Three or six equally spaced spokes are readily discriminated but not four, five, or seven (Horridge, 2000b). Within each local area, the orientation vectors of the feature detector responses are integrated together to indicate the position of a hub of radial edges (Figures 10.7B, 10.14F). Vectors at right angles to these indicate the position of a hub of tangential edges (Figures 10.7B, 10.13). The type of hub and its position in the local region to within 8 degrees is remembered, but the actual pattern is lost (Horridge, 2006a).

A salient out-of-place cue, or lack of an expected cue, counts as a cue, and is avoided. Counting the absence as well as the presence of unexpected cues makes full use of the recognition mechanism.

When Recognition Fails, Learning Restarts

Bees learn only the cues for the task in hand, and relearn if the task changes. They readily learn to come to a colored patch, but forget and relearn if the color or other cues are changed. Similarly, they relearn the situation if an unfamiliar cue is added. This implies that they learn very little at any one place, but learning is continuous while they search for food. Changing the pattern while retaining the preferred cue, or adding an additional familiar cue, had little effect.

Is There More to Bee Vision?

All known examples of discrimination and failures to discriminate can be explained by the known parameters, feature detectors, and cues. There is no evidence of a further mechanism, but, more importantly, there is abundant positive evidence that shapes and local layout are not recognized. In other directions, much remains to be explored. For example, there may be cues that depend on patterns of polarized or ultraviolet light, 60-degree angles, or particular sequences or combinations of other cues, such as a black spot in the center of a radial pattern, or the characteristic motion of another bee.

CONSEQUENCES OF A CENTURY OF EFFORT

The analysis of the bee shows what experiments must be done with a variety of other animals at a similar level of complexity, such a jumping spiders, crabs, octopus, and fish, and how to do it. As many of the illustrations here show, failures to discriminate in training or in tests are an essential part of the analysis. The appropriate test sets were discovered by trial and error, and a list of honeybee cues is now available, so that a test set can be designed for any discrimination, and the properties of the cues and their interactions can be described in further detail.

One important lesson is that, in the analysis of any mechanism, it is most important to discover as soon as possible the kind of system that one is dealing with, otherwise a great deal of effort is wasted. For example, because bees use several eye regions and switch from one cue to another, it would be useless to rely on quantitative measures of learning ability or performance scores in tests with targets that are undefined with respect to the parameters that the bees actually use. But that is exactly what has happened for the past century. Moreover, several training parameters were changed simultaneously in a single test, and erroneous conclusions were reached intuitively when a rigorous deduction could have been made from numerous varied tests. Other animals have as yet yielded little because these principles have not been understood. Also, it would be a great waste of time to analyse the spatiotemporal properties of the image of the environment before one knows which features are of interest to bees. First, find the feature detectors, then measure the panorama with them. We were fortunate in finding the apparatus in Figure 10.1 with a pattern size that isolated one or two eye regions, so that the feature detectors and cues could be isolated one by one.

It took a long time to realize that the bee visual memory is not like wax that can be moulded to any input, but is a set of independent preformed boxes that are ticked when their appropriate input arrives, so that it is entirely dedicated to the limited needs of the bee.

One outcome of this sustained effort on the bee is that we now have a comprehensible model of bee vision. It is still surprising how a few successive summations of receptor responses result in such a subtle performance without reassembly of the image. It marks an unavoidable glass ceiling in the evolution of vision, however, because the next level of complexity requires a new and more complex stage in which individual areas are separately identified and edges are assembled into shapes around the areas. That may require a warm-blooded vertebrate brain.

Bee Vision Is Rich, but the Cues Are Few and the Map Is Sparse

Bees that recognized simple landmarks made use of very few cues (Horridge, 2006b). Indeed, only three or four labels with their directions are required to recognize a familiar place because the combinations of cues are quite specific and have expected positions in two dimensions. Only a single cue is sufficient to form a label. The sparser the maps, the less memory is used for the route to and from the reward. Vision is always switched on, and the map is serialized as the bee follows a route. Because it is an inefficient use of energy to detect more than is required, the evolution of bee vision complexity stopped at a very modest level.

A century of confusion, controversy, and unjustified conclusions shows that the road was indeed rocky and the anti-intuitive results were difficult to interpret. In a sense, the small number of cues was fortunate because it made their identification easier. The cues appear to be innate and the same in every bee. The analysis would have been impossible using available methods if there had been a greater variety of feature detectors and cues, or if different individuals learned different cues, as in the rat (Lashley, 1938). Although much is known about their visual recognition of food, mates, predators, or ecological situations, we have no idea what parameters, features, cues, or labels other animals actually detect. It is relatively easy to show, as in the octopus (Young, 1961), that the image is not reassembled but the real task is to identify the feature detectors and cues. Also, honeybee vision is subtly adapted to the recognition of place, and other animals have different needs. We can get over the difficulty of how this mechanism evolved by suggesting a progressive change in the number and variety of feature detectors and cues.

Measurements of Resolution

The feature detectors select the input from the image, so the measured resolution is the value for the feature detectors involved in the test, not the inter-ommatidia angle (Horridge, 2005b). The lowest limit of the resolution is about 2.5 degrees for the modulation cue in black and white, as measured with vertical stripes of adjustable period versus a plain gray target. The limit with colored gratings with no blue contrast was slightly larger. With an oblique black–white grating at 45 degrees versus the same at 135 degrees, the limit was near 3.5 degrees because there was no modulation difference and the orientations had to be detected. The size of the minimum patch of a few dozen ommatidia to discriminate a color depends on the photon flux (Vorobyev, Brandt, Peitsch, Laughlin, & Menzel, 2001). A minimum modulation difference of 30% was remembered, irrespective of change of pattern (Horridge, 1997a). The resolution of the orientation cue is very poor, greater than 30 degrees in most cases, because the detectors are so short and independent (Figure 10.6D–E). The positions of the center of a black area, of a strong orientation cue, or of a radial or tangential hub were remembered to within about 8–10 degrees in the vertical direction (Figures 10.12, 10.13, and 10.14F).

Generalization, Errors of Recognition

A variety of work over the past century showed that when bees were trained with several patterns, or trained bees were tested with unfamiliar patterns, they remembered something that the patterns displayed in common. By analogy, with higher animals, this was called *generalization*. Even Hertz's earliest experiments showed that the bees remembered the sums of simple parameters, such as area and length of edge, and they could confuse quite a different pattern with one with a similar cue. Later researchers, however, failed to deduce the preferred cues from the great variety of accepted patterns that were totally different from the training patterns (Figures 10.3F, 10.10C, 10.13C, 10.13D, and 10.20E).

Generalization was the consequence of reducing the bees' useful image to the size of the target during the training, by the technique of shuffling the patterns on a table or by interchanging the rewarded and unrewarded training patterns, as in Figure 10.1. This procedure forced the bees to learn to ignore everything outside the pattern itself, except distant landmarks, and remember only the label of a single pattern at a time. The few cues learned in the local area of the eye were adequate for the single task in hand but insufficient for unmistakable discrimination from any other pattern. Effectively, the bees were trained with blinkers for one task with a limited number of cues. As a result, the essential nexus was broken between the local area with depleted recognition of one pattern as a single landmark, and the whole eye that could recognize a place unambiguously by using the wide panorama. Generalization in bees was therefore a consequence of ambiguity through restriction of cues, and was caused by the training regime (Horridge, 2009a). Belief, based on analogy with other animals, that generalization in the bee was a cognitive mechanism, led to confusion for years and failure to make the proper tests (Giurfa, Hammer, Stach, Stollhoff, Müller-Deisig, & Mizyrycki, 1999; Stach, Benard, & Giurfa, 2004; Zhang & Srinivasan, 2004).

Other Cognitive Visual Abilities of Bees

Besides generalization, it has been proposed that bees recognize some abstract properties of visual images, such as similarity, categories of patterns, human faces, edge orientation from parallax, global properties of patterns, detection of symmetry, shape, and topological differences, by means other than simple cues, as if they had some kind of cognitive ability similar to that of primates. The most significant error of thought was that bees actually saw and remembered the pattern or the scene. Next came the proposal of a cognitive ability that was compatible with successful training but not further defined or tested, and therefore left unexplained. In each case, these wild guesses have been replaced by demonstrations of the parameters and cues that the bees actually detect (e.g., Figures 10.2, 10.3, 10.10, 10.12, 10.15, 10.18, and 10.20). The mechanistic analysis of the visual processing of the bee is closer to the logic of reverse engineering than to comparative psychology, and far from ethology. A qualitative description of the complete mechanism in no way spoils the marvels of the performance, any more than an evening sunset is spoiled by the laws of physics.

The Neuronal Mechanism of Bee Learning Is Out of Reach

Although some of the neurons of the bee visual system are individually identifiable, it is impossible to observe the recognition mechanism in action by recording from them, for two or more reasons. The key action is the detection of coincidences of feature detectors, coincidences of cues, and then coincidences of labels that finally trigger recognition. Although the detection of coincidences is the basic mechanism of integration in all nervous systems, it would be a lucky strike indeed to identify the process in action here, because in insects we do not find convergent synaptic inputs upon a convenient neuronal soma. How would nerve impulses be recognized as a vital part of the visual process? And, when recording from one or two neurons, we are ignorant of what is happening in other neurons anywhere in the system.

Second, successful visual recognition is the result of a learning process. In a physiological preparation with electrodes in place, we are ignorant of where the learning takes place, or when it has occurred. Furthermore, the image is not stationary, and visual processing is at work continually in time.

Third, observation of the relevant coincidences is a will-o'-the-wisp indeed, because arrays of coincidences occur, not a single identifiable event. The way forward is the progressive perfecting of model visual systems based on the principles progressively deduced for the bee and other animals, using a variety of approaches, and then testing them using a computer implementation. These and similar thoughts about explanations of behavior were expressed in an earlier review (Horridge, 1968; p. 398 *passim*).

AFTER ALL THIS, WHAT DOES THE BEE SEE?

Far from being a pattern perception device, bee vision destroys the pattern in the image and replaces it by the layout of a few labels. This is the sparse code for a small brain, and we have familiar ones that open garage doors or control mobile telephones. Bee vision is a set of coincidences like the contributions of numerous molecules to the flavour of a soup or the smell of coffee. Moreover, vision is not a separated modality, as it is in humans, for there are neurons that respond to other modalities in the bee optic lobe, and the visual cues are linked to odors and the time of day.

Bees do have a mind's eye, one that can be demonstrated by training the bees to prefer a place or a pattern when one odor is present at a particular hour, but to prefer a different place or pattern when a different odor is present. The bee's mind may be small, and the choice limited, but there must be something in there that the odor acts upon.

Several kinds of lapses from human conscious vision may help us to imagine what bee vision is like. Recently, each evening, I have walked out of my house and down a path toward a lake. My mind is far away from the immediate scene, and I remember seeing nothing, but like a blind person I am aware of where I am by a variety of sense modalities. In humans, the progress of subliminal perception can be recorded by brain imaging or event-related potentials, so there is no doubt of its existence, even if no stimulus or outcome is reported.

Classically, subliminal perception was regarded as an automatic process that was not affected by consciousness. The term "unconscious inference" was introduced in 1867, by Helmholtz, who considered it to be continuously operating with the aid of previous experience but only emerging into consciousness when amplified by attention (Gregory, 1981, p. 362). Another example is subconscious priming, when a word is flashed so briefly on a screen that it is not seen but can still be correctly reported. Other examples are masked perception, inattention blindness, and diverted attention, all of which block conscious vision, although the stimulus may be correctly reported later.

Some brain lesions cause a condition called *blindsight*, in which a human subject has no conscious vision in a part or whole of an eye, but is able to report correctly a simple parameter such as a color, a black spot, or a large familiar object, and its position. Perhaps it means something to suggest that bee vision is all blindsight.

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