# SUMMARY OF THE MODEL OF BEES' VISUAL PROCESSING

For a bee, the **parameters** in the external panorama display two types of features—**areas** and **edges**—which are processed separately and not reassembled. Apart from motion detectors, the peripheral units of vision are feature detectors of two types: **intensity detectors** that respond to areas and **modulation** and **orientation detectors** that respond to passing edges. The feature detector responses are summed by type and position in each local region of the eye to form several types of **cues**, each with the position of its average. This summation destroys the local pattern. The cues are within the bee and must therefore be characterised by testing trained bees. Cues can be remembered. The coincidence of different cues in a local region is the **label on a landmark** in that retinotopic direction. Bees learn landmark labels **to identify a place** and find the reward. To a bee, a pattern is just another landmark.

The receptors and feature detectors

In each ommatidium of the compound eye, bees have three colour types of ordinary photoreceptors, with their spectral sensitivity peaking in the ultraviolet, blue and green. A change in the intensity of light in the receptors, such as that caused by a passing edge, causes a **modulation** of the electrical response propagated to the arrays of neurons below (Figure 1). The receptors feed into lamina neurons that amplify the modulation and cut out the persistent signal from constant illumination. These in turn feed into **feature detectors** of four kinds.

The feature detectors for modulation have balanced excitatory and inhibitory inputs that are arranged so that they detect contrast at edges but are insensitive to changes in brightness (Figure 2b). They are of two kinds: the pure modulation detectors that signal heterochromatic modulation but not the direction of edges, and the detectors of edge orientation that are green sensitive and colourblind. Both kinds detect simultaneous modulation of a small group of seven receptors (Figure 2). The sizes of these feature detectors have been measured as 3 ommatidia wide. There are also green-sensitive colourblind detectors of sequential modulation in adjacent receptors, which detect the direction of motion of a contrast across the eye.

Figure 1 Overview of the stages of visual processing of edges (on the left) and areas (on the right), from receptors to recognition of place. a) Receptor array. b) Lamina cell array. c) Formation of cues by summation. d) Formation of landmark labels by coincidences. e) Recognition of place.
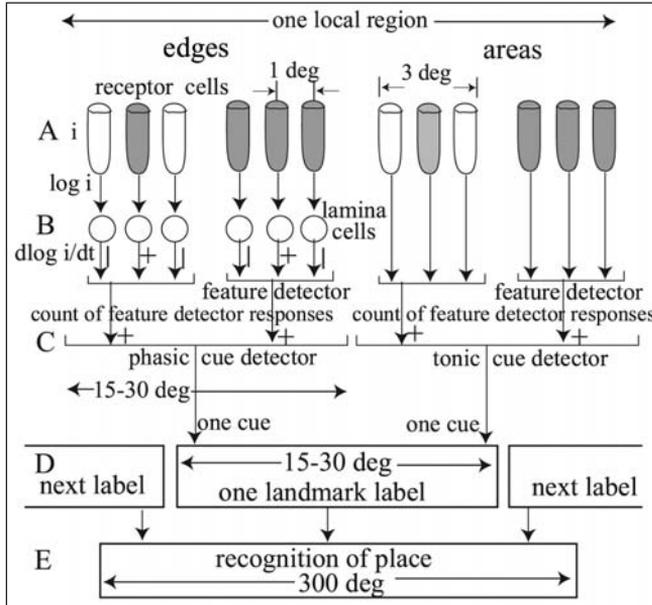
The feature detectors for edge orientation are symmetrical about their axis of orientation (Figures 2c–e), as shown by the inability of the bee to distinguish which side of an edge is dark and which is light. To be able to separate all edge orientations, there must be at least three kinds with 120° between the orientations of their axes, probably in line with the coordinates of the retina. They are green sensitive and colourblind.

The feature detectors for size, colour and brightness of areas of the image are probably the receptors themselves, because these features require a steady signal, not a modulated one (on the right in Figure 1). Between them, the feature detectors together respond to the parameters that the bees detect in the external panorama. The parameters are outside the bee; the responses of the feature detectors are inside.

Figure 2 The convergence of receptors on the four types of feature detectors for edges, all of which are insensitive to intensity changes. a) The receptors. b) The radially symmetrical modulation detector; this detects edges, not just small spots. c–e) The detectors of edge orientation with bilateral symmetry are green sensitive and colourblind; they cannot distinguish between the two sides of an edge. The numbers show the relative excitation and inhibition by light.
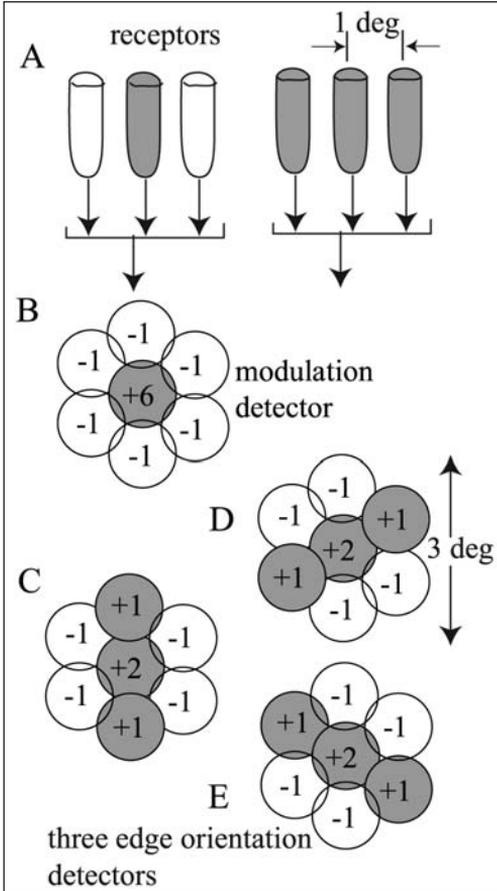

Source: After Horridge (2005a).

The cues relating to edges

The cues are formed by the summation of responses of each kind of feature detector within the local region on each side of the target or pattern, as though the bees look towards the centre and divide the view between their eyes. Just as the receptors count photons, each cue detector totals the coincident responses of its own array of feature detectors in a local region of the eye (Figure 3). There can be several different cues in a local region, but because they are totals, there is only one of each kind. Although simple and sparse, the cues in a local region are

usually sufficient to identify a small pattern ($<40°$) or a landmark. The absence of a cue is itself a cue. If they are rewarded, the cues are learned and remembered in the range of positions where they were displayed during the training.

Figure 3 At least three different orientations are separated by the edge orientation detectors (Figures 2c–e). The responses of these are summed in such a way that edges at right angles cancel, so the pattern is lost but the predominant orientation and its position remain.
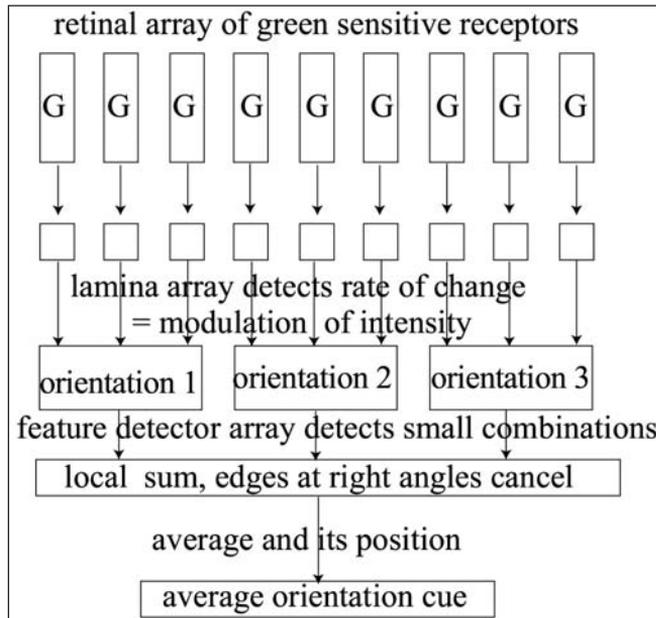
The summation of edge orientation detectors to form cues smoothes out the detail in the local region (Figure 3). The bees detect and learn the cues but they have no information about the distribution of the feature detectors that were summed. Consequently, there are many pairs of different patterns that the bees cannot distinguish. In tests, the trained bees detect familiar cues in unfamiliar patterns but the real patterns are of no interest.

To a bee, the orientation cue with its position is a kind of average orientation of edges in a local region. The responses of the edge orientation detectors are summed in such a way that edges at right angles cancel, so the pattern is lost but the predominant orientation and its position remain (Figure 4d). This is the first counter-intuitive property of bee vision. For example, in a square or a square cross the orientation cue is cancelled by the edges at right angles to each other that are resolved by the feature detectors for edge orientation. The greatest gap that can be spanned in a row of small squares is 3°. This is a measure of the maximum size of the edge orientation detectors. Similarly, orientation is destroyed when a bar is broken up into squares or cut into square steps.

Figure 4 Examples to illustrate the summation of feature detectors for edge orientations in various ways to form cues; pattern is lost but cues emerge.
a) A line of detectors with oblique orientation. b) Detectors with vertical axes.
c) Mixed orientations cancel. d) The orientation cue is cancelled in the edges of a square but weak hubs are detected at the corners. e) and f) A tangential and a radial cue and their hubs. The orientation is cancelled but the modulation and position of the hub remain.
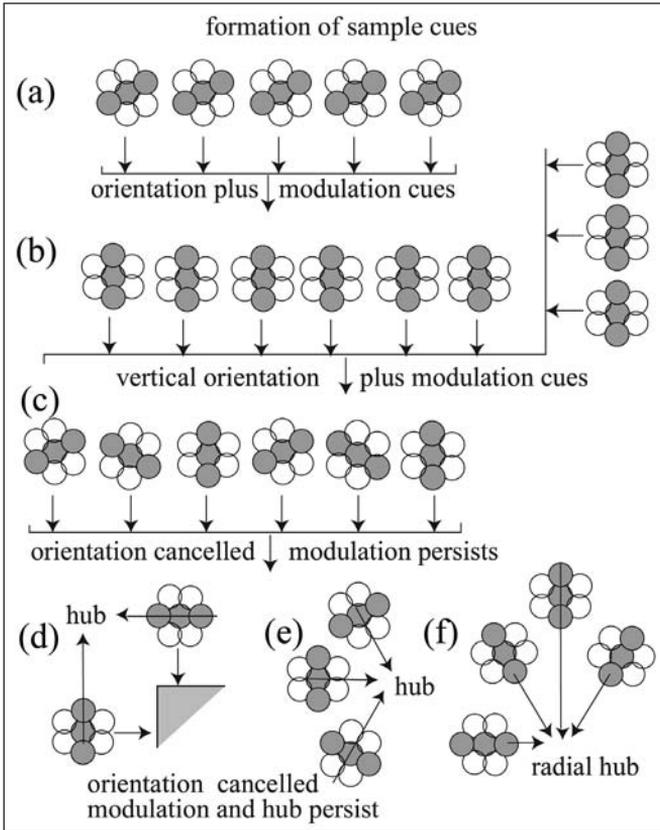
The edge detectors also collaborate to detect the hubs of radial or circular patterns (Figures 4e and 4f). The type of pattern—radial or tangential—and the position of the hub can be learned, but again, the real layout of the pattern is lost in the summation.

There are surprisingly few types of cues. There is an order of preference for learning the cues in the training situation, with total modulation in a local region the most preferred, then area, position of centre, a black spot, colour, radial edges, bilateral symmetry, average orientation and finally tangential or circular edges, which are avoided. Heterochromatic modulation (Figure 2b) and green-sensitive edge modulation (Figures 2c–e) are separate cues. Despite searches, no more cues have been found. This is a small but obviously adequate collection of cues for the varied life of a bee (Figure 5).

Figure 5 Representations of the cues in human terms, in order of preference. In the outside world, the parameters look like this to us. The bee detects only excitation that is processed as it passes from neuron to neuron. Each of these cues is represented in the bee as a quality, a quantity and a position on the eye. A neuron's activity can be defined in the same way.

feature	weak	strong
modulation		
area		
radial		
bilateral symmetry		
orientation		
tangential		

Cues related to areas

The responses of blue, green and presumably the unstudied UV receptors are totalled separately in the local areas on each side of the target. They are totalled as the number of excited receptors multiplied by the brightness. The position of the centre is a cue, but areas are not related to edges, so there is nothing about shape. This is the second counter-intuitive property of bee vision.

The positions of blue, green and yellow areas are discriminated separately, but not all the areas are learned separately, blue being the preferred and sometimes the only position learned, even when on the unrewarded target. The positions of the centres of two areas of black or colour can be remembered as cues, but where they are close together, the bees detect their common centre. This merging of the two areas diminishes as the spots move apart, from an angle subtending 5°, until at 15° they are quite separate.

Much of the natural panorama displays a variety of colours and orientations of edges with a strong modulation cue for bees, but within each local region the orientation can be cancelled out and nearby areas summed together, so only the modulation of green and blue receptors and the average colour of the local areas remain.

Landmark labels; place recognition

The group of cues that is detected at the same time in a local region of the eye forms the label of a landmark, irrespective of whether there is a single or several real landmarks in that part of the panorama. The label can be learned. All that matters is that the bees remember the coincidence of responses of cues in that local region of the eye. Landmark labels are therefore retinotopic—that is, at a place on the eye. The group of landmark labels at wide angles to each other that is detected at the same time by the whole eye makes the key to the recognition of a place (Figure 6).

Figure 6 The display in the panorama that is detected by the bee. Each oval subtending about 30° represents a local region in the bee eye. Within each region no more than one cue of each kind is detected. The combination of landmark labels, with their directions, enables the bee to recognise a place.
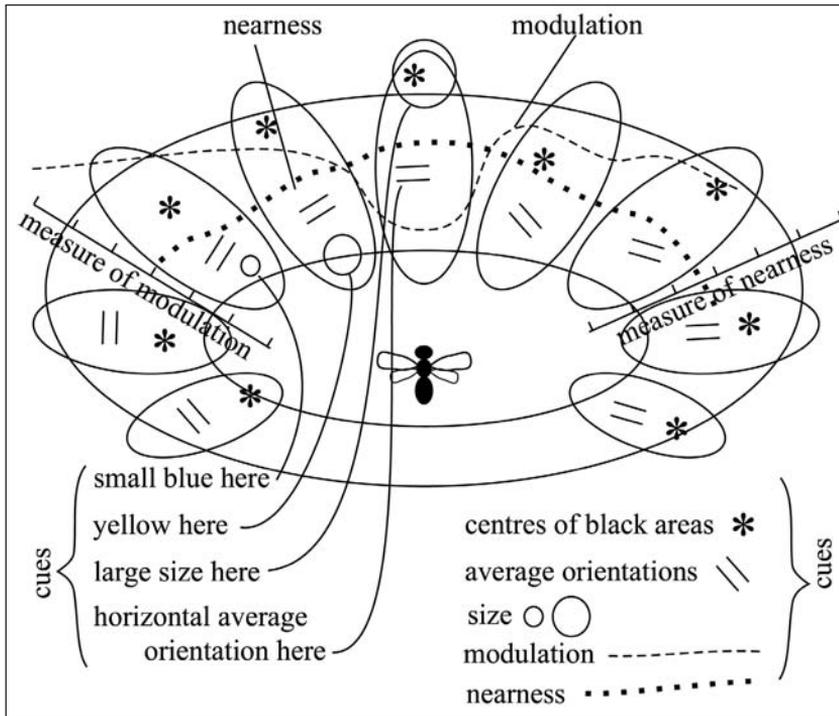
The resolution of orientation of an edge on a vertical surface is poor because the feature detectors are independent and so short. A difference of 45° is the limit for a single bar, 30° for a parallel grating. At each stage in processing, there is a compromise between the resolution, which is better in small summation fields, and the sensitivity or the ability to find the target, which is better in large fields.

The mechanism is designed for a very large visual field for the whole eye, and it works for a compound eye of any size. At each level in processing, the coincidence of inputs is the signal to pass the response to the next level. The whole process from receptors through to feature detectors and then to cues and landmark labels (Figure 1) is done region by region on the eye, and therefore in coordinates related to the position of the head and body axis (Figure 6). For this reason, bees scan the scene in the horizontal direction as they fly and orient their head and body to detect landmark labels and identify the place of the reward. In Skinner's terminology, learning the labels to recognise a place must be done by 'operant' conditioning, which is now part of 'active vision'. The control of the bee's active vision is largely unstudied.

Resolution in the processing hierarchy

Parts of the above model were inferred from measurements of resolution of features, cues and landmarks (Figure 1). Resolution depends on the angular sub-tense and shape of the field of the detector and on the separation between detectors, and is not the same for each cue. At the level of receptor responses, electrical recording gives $2.5°$. For the feature detectors, we have for modulation a resolution of $2°$, which is better than for a single receptor on account of the lateral inhibition (Figure 2b). For directional edge detection, bees have $3°$ (Figures 2c–e), and for detection of a small black spot, $2–3°$. At the level of coincidences of feature detector responses to form cues, we have: modulation in regions of $20°$ across; orientation in regions of $15–20°$ across; position of areas of black or colour, $12–16°$; for the position of the centre, $5°$. At the level of coincidences of cues to form a landmark label, we have areas up to $45°$ across for the summation and a resolution of $15–20°$ for the separation between neighbouring landmarks. The three stages of processing have resolutions of approximately $2–3°$, $5–20°$ and $>20°$. The fields of the cues are two to 10 times the diameter of the fields of the feature detector.