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Pattern vision of the honeybee (*Apis mellifera*).
What is an oriented edge?

Abstract

Pairs of black patterns on a white background, one rewarded the other not, were presented vertically each in one arm of a Y-maze. During training the locations of the black areas were changed every 5 min to prevent the bees using them as cues, but cues from edges were kept consistent. Bees detect orientation even in a gradient that subtends 36° from black to white (normal to the edge). Orientation cues in short lengths of edge are detected and summed on each side of the fixation point, irrespective of the lay-out of the pattern. Edges at right angles reduce the total orientation cue. The polarity of edges in a sawtooth grating is weakly discriminated, but not the orientation of a fault line where two gratings meet. Edge quality can be discriminated, but is not recognised in unfamiliar orientations. When spot location is excluded as a cue, the orientation of a row of spots or squares which individually provide no net orientation cue is not discriminated. In conclusion, when locations of black areas are shuffled, the bees remember the sum of local orientation cues but not the global pattern, and there is no re-assembly of a pattern based on differently oriented edges. A neuronal model consistent with these results is presented.

Key words  Honeybee · Vision · Edge orientation · Filters

Introduction

In the past, it has often been assumed that the bees find cues in all parts of the patterns that they learn to discriminate. However, because the visual system of the bee is so different from our own and because the brain of the bee is relatively small, it is hard to imagine that bees reconstruct the image of the whole pattern from the individual receptor responses. In each discrimination experiment, the data shows only that they use at least one sufficient cue. When working with a group of bees, rather than a single bee, care is required to show that an individual bee can remember more than one cue, because some bees in the group may learn one cue and others another cue.

The main difficulty in the design of experiments, however, is that bees have several pathways in parallel in the processing of images on the retina. When the pattern is fixed relative to the fixation point of the bee, they can use the locations of contrasting areas of black or colour, especially if the areas are large. When location cues are ruled out by regular shuffling, the bee distinguish between certain arrangements of edges irrespective of location, and they discriminate as if colour blind. In the present paper the cue is the orientation of an edge. Because these processing pathways in parallel have been separated only recently, when studying the literature one must always distinguish between the actual observations and the conclusions of the experimenter. Some examples will illustrate.

Orientation in honeybee vision

Sixty years have elapsed since the discovery that bees can discriminate the orientation of a black bar presented vertically on a white background. The criterion of success was the landing of the bee on the correct pattern (Wiechert 1938). Bees trained on fixed patterns are able to discriminate a familiar orientation cue in unfamiliar patterns or with black and white interchanged (Wehner 1971). It is an important point that in this old work, when the bars were thin and had sharp black edges, the orientations and not the locations of fixed areas dominated the discriminations. Much later, it was shown that bees learn the orientation of bars that are presented in
repeatedly shuffled positions on the targets (van Hateren et al. 1990), and that they discriminate the average orientation but not the separate locations of several bars in one pattern (Horridge 1996a, 1997).

We have a good deal of information about the bee’s discrimination of orientation. When the orientation of an edge is learned, the rewarded and the unrewarded cues must be presented on the same side of the targets (Horridge 1998) and an orientation cue learned by one eye is not conveyed to the other eye (Giger and Srinivasan 1997). When two orthogonal bars of equal size are on the same side of the target, their orientations cancel (Horridge 1997). When they are on opposite sides, the bees fixate on the centre and discriminate the orientations on the two sides of the target separately (Horridge 1996a). The orientation can be discriminated in some illusory edges (van Hateren et al. 1990; Horridge et al. 1992). Edges that stand above a background texture are detected by parallax, and the bees land at right angles to an edge (Srinivasan et al. 1990). As the bees approach, they resolve a large scale orientation from a distance and they use more local cues when close (Zhang et al. 1992).

Detection of an edge (Lehrer et al. 1990), orientation discrimination (Giger and Srinivasan 1996) and discrimination of radial or tangential cues (Horridge 1999b) are all colour blind. Radial or tangential edges are discriminated by a separate mechanism from that which discriminates orientation (Horridge and Zhang 1995; Horridge 1999a).

There has never been any demonstration that bees can discriminate the separate orientations of two different bars or edges on the same side of the target. In fact, it had been shown that edges at right angles reduce the orientation cue (Wehner 1971). This result agrees with the proposal of orientation filters with large fields so that only one average orientation is discriminated (Srinivasan et al. 1994) by each eye separately (Horridge 1997, 1998). This severe limitation in the discrimination of the orientations of several edges implies that patterns that are dependent on orientations of edges are not re-assembled.

Two systems of visual processing

There are two systems of visual processing in the honey bee. The first remembers the location of at least one area of black or colour when the bee fixates and the pattern is stationary relative to the point of choice during the learning process. The input is the photon flux (intensity) at the receptor types irrespective of contrast at boundaries. The relative locations of two differently coloured areas, one above the other, are readily discriminated in colour (Horridge 1999b), but it is not known how many separate locations of fixed black areas one bee can discriminate in one pattern.

The input to the second system is the modulation of intensity (contrast) in the green receptors. Cues from edges are summed by coarsely tuned colour blind detectors of orientation, bilateral symmetry, and radial and tangential edges. The two systems are separable: the areas can be excluded by shuffling their locations on the target during the learning process, while the edges can be excluded by using patterns with no contrast to the green receptors. Once the two main processing systems in bee vision have been distinguished, a re-examination of old experiments with fixed patterns reveals that both systems were at work although confounded together (Horridge 1996b, 1999a, c, d).

Generalization of the average orientation cue

The ability to generalize an orientation cue was first demonstrated by testing trained bees in a forced choice with unfamiliar patterns or exchange of black for white (Wehner 1971). At that time, the recognition of the familiar cue in unfamiliar patterns was called ‘generalization’. In those experiments, and repeatedly in recent work, the orientation of the sharp black edges was a stronger cue than the locations of black areas, although the patterns were fixed. The interpretation of most experiments before 1990 is difficult because the experimenter cannot identify the cues that the individual bees have learned from patterns that are fixed relative to the point of choice during the learning process.

Later it was shown that the bees learn the orientation cue when the locations of edges and areas are regularly shuffled during the training (van Hateren et al. 1990). This result contributed to the postulate of dedicated large-field filters for orientation (Srinivasan et al. 1994). The ability to respond to one cue found in different patterns during training or tests is a characteristic of the action of filters, which extract the feature that fits their input requirement.

Instead of randomisation between many patterns, it is sufficient to alternate the locations of areas of black every 5 min while keeping the cue consistent. The bees learn to ignore the cues that the experimenter repeatedly changes, and they learn to rely on a generalised cue if there is one consistently available. This is the technique adopted here.

Discrimination of a square cross

The first example of the delicate relation between experimental results and their interpretation is the bees’ discrimination of a square cross, that will later be re-examined in the experiments (see Figs 9, 10). When the criterion is the landing on the correct pattern, a square cross is discriminated from a round or rectangular shape, although both are moved relative to the reward hole on a vertical target (Friedlaender 1931). The bees could find and fixate a cross in a way that they could not with some other shapes.

When bees make a decision at a defined range and fixate on the reward hole in front of vertically presented