

The relevance of honeybee vision to the design of seeing systems.

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

1. INTRODUCTION

The first chapter in the application of insect vision to seeing systems, piloting and control, has almost been completed. For many years it was thought that the vision of the fly, as illustrated in the optomotor response of pinned down animals, represented insect vision. Fixed insects respond to the passing of edges by the spatio-temporal correlation between adjacent visual axes and therefore to the temporal frequency of passing edges, irrespective of pattern or the angular velocity across the eye. But a visual system that behaves like this is unsuitable for guiding in free flight, preventing crashes or steering towards a target, never mind pattern perception. Around 15 years ago, we realized that freely flying bees can measure the range and size of a nearby target [1]. They can do this because they can measure the angular velocity of contrasts that move across the eye as a result of their own motion, and they can measure their own velocity relative to their surroundings as they fly. Bees can also integrate the angular velocity over time to give the distance travelled [2]. This is active vision. As a result, we have been able to copy these principles into freely flying vehicles that can manoeuvre themselves in the air at high speed.

The second chapter, navigation, is about the interaction between dead reckoning, the use of landmarks and the polarization pattern of the sky. At present my understanding of this topic in insects is in a state of flux and it is a subject that I leave to others today.

2. PATTERN DISCRIMINATION, HISTORICAL

The third chapter, seeing pattern, is my main theme now. What insects, in general, and bees, in particular, actually see has been a puzzle for as long as they have been studied. As in the case of piloting and control, applications to robot vision have been delayed by a legacy of almost a century of erroneous conclusions from a limited number of good experiments. However, the topic has at last become a little clearer and useful to engineers in modern terms.

Almost a century ago, von Frisch made two major discoveries [3]. He trained bees to discriminate between two or more shapes displayed on a vertical surface by rewarding one pattern but not the other with sugar syrup. The feeder containing the sugar was in a little box; the patterns were displayed on the front of the box, and a reward hole was at the centre of each pattern. The boxes were shuffled about to make the bees look at each one, and learn something about the pattern to obtain the reward, rather than learn where to go relative

to landmarks. Von Frisch found that the bee would not learn to discriminate between a square, a round disc or a triangle of similar size and colour although he trained them for 5 days. It was not realized that the black reward hole has salience for the bees or that the only cue presented by these closed shapes was the position of the centre relative to the reward hole, which was the same for all. On the other hand the bees quickly learned to discriminate between a variety of flower-like patterns with concentric circles or radially arranged sectors in blue and yellow, also with a central reward hole. This difference between results was largely ignored for 80 years because not understood.

Von Frisch had several pupils, some of whom tried other ways of studying pattern discrimination in bees. In 1928 Baumgärtner, also with presentation on a vertical surface, found that quite a large patch of colour is required if freely flying bees are to discriminate between two colours, and that a small region immediately below the reward hole is the place where bees most easily detect a cue. The bee gets a particularly good look at this place as she prepares to land on the lip of the reward hole [3].

In 1933 another pupil, Mathilde Hertz found that bees discriminate between two or more black and white patterns of similar size displayed on a horizontal surface if they differ in disruption or length of edge. This is a parameter (i.e., a number), related to the spatial frequency, and independent of pattern, that might act as a summary for a small memory. In fact, because the patterns were horizontal on a white table, disruption, radially symmetrical shapes, and colour, were the only cues that the bees could use.

Independently in 1931, Friedlaender, with presentation on a vertical surface, found that radial patterns also have salience for bees and that the bees can use their centre as a reference point [3]. She also found that the bees learn to discriminate the position of a patch of black, but fail if it is moved relative to the reference point, which could be the reward hole or the centre of a radial pattern. It is an ancient observation that bees fail to see their own hive if it is moved a short distance, although still in full view. The bees behave as if they cannot correlate the image with the memory of it if the pattern is moved. These facts led to the view that the image of a fixed pattern is learned as a fixed projection upon the eye and the projection is carried into the optic lobe, as the so-called "eidetic image" (4).

As an explanation or a mechanism in vision, an eidetic image is nothing but a replacement of the original image. To "see" or act upon an image, the

stimulus carried in each receptor axis must be related to that arriving in the adjacent receptors, so that some meaning other than a bare copy can be extracted from the receptor array. Moreover, the bee is not stationary relative to the pattern; vision of insects is all active vision. Most of the input to the receptors is irrelevant anyway and, as will be seen, is excluded by filters (5).

3. INCORRECT STRATEGIES

In the 20th century, further investigation of the mechanism of honeybee vision was hindered by two errors that were a product of the scientific methods of the time, the first derived from experimental physics. Progressive changes of one variable were made, while the percentage of correct responses of the bees was measured at each change, and then a mathematical relation was found that fitted the results. There are serious problems with this method for the analysis of vision, apart from the fact that the changes to the stimulus are arbitrary and the mathematics is meaningless because many relationships may fit the data. There are many parallel lines carrying excitation into the optic lobes, and the division of excitation between them is unknown. The output is an unknown mixture of several different responses in different proportions at different times. The actual cues that excite each of these lines optimally must be found by experiment before a useful control of the stimulus is possible. The filters and parallel lines that detect these cues have been perfected in evolution to match the repertoire of the bee and the properties of the visual environment, so they are likely to be efficient and economical for use by a small brain. They are the cues and corresponding filters likely to be of use for artificial vision in a similar environment.

The second error was to suppose that the bees see the patterns. This was an anthropomorphic but understandable assumption because the bees appear to look at the patterns. It was supposed that the bees compared one pattern with another during the training and during the testing, much as humans might do. A theory was developed in which the image of one pattern was laid over the image of another pattern in the memory of the bee, adjusted and rotated if necessary to give an optimum fit between the two, and the areas of overlap and non-overlap of the two patterns measured. This would give a single number (called a parameter) that the bee could easily remember and use to compare with that from other patterns. The calculations made by the experimenter made a better fit to the results generated by the bees when another term was added representing the difference in the length of edge between the two patterns [6]. Several efforts were made to find the simplest way that the bee could calculate a single parameter that fitted the results of tests with different patterns [7]. This whole story fell apart when it was realised (a) that bees discriminate many patterns irrespective of size (b) that the bees cannot discriminate the pattern if it is rotated or moved, let alone manipulate

it towards minimum overlaps (c) that there is plenty of evidence that bees detect cues, not the patterns (d) that there is no evidence that demonstrates a comparison of the lay-out of spatial patterns. The conclusions from all this early work failed to provide a model that can be implemented in artificial seeing systems, but the data was usually good, and can be re-interpreted.

In the early 1960's onwards, the idea that visual processing depends upon filters was gaining acceptance, based upon recordings from crayfish optic tracts, retina of frog and mammalian visual cortex, together with early computer models and psychophysics. The separate responses of the receptors are combined in groups by higher order neurons that act as filters and pass on the excitation to deeper processing layers. From the 1970's onward, the idea that all neuronal processing involves many channels in parallel also became accepted. In mammals, each type of interneuron is reduplicated many times. In insects, however, many of the higher level neurons appear to be unique and have very large fields, often involving the whole eye, so it is impossible for them to represent an image that is laid out spatially.

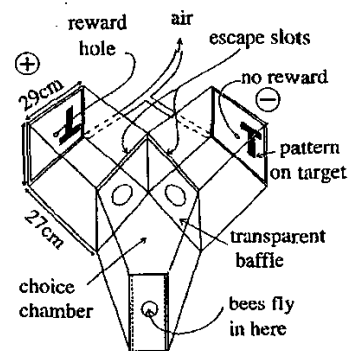


Fig. 1. The Y choice apparatus now used for training and testing bees. About 2 h is required for training, and trained bees are given 200 tests.

4. BEES USE CUES

In the late 1980's there was a shift in the experimental strategy with trained bees. Bees were trained to measure size or range [1] or the orientation of bars presented on a vertical surface [8] by keeping one possible cue constant while all other aspects of the stimulus were randomized. So it was proved that bees discriminate range, size and orientation irrespective of the actual pattern or the location of the cue within the experimental area of the target. A cue is the signal passed by a filter. Relatively simple filters explain these results. The idea of a modified spatial lay-out of the pattern projected into the optic lobe is not actually ruled out; it may still be there, but the cues are not re-assembled into a pattern.

The use of training patterns in which all possible cues except one are shuffled led to the discovery that bees discriminate radial and tangential edges relative to the reference point (the reward hole), and also they detect symmetry about an axis [3]. These findings were anticipated by the demonstration of spontaneous preferences for these cues by untrained bees. The more complicated filters can be considered as preformed templates that match certain expected combinations of edges. Processing by preformed filters is a yes/no process, and is therefore extremely fast.

The detectors of edges turned out to have three unexpected properties [5]. Bees discriminate the orientation of very fuzzy black and white edges that have an intensity gradient down to about 2% per degree, presumably to compensate for the poor spatial resolution of the eye. Secondly, the orientation cue is a peculiar sum of the orientations of edges, such that equal lengths of edges at right angles cancel their orientation cue. Third, very short edges down to about 4° long, make a contribution. These three properties of the orientation cue mean that the eye is exquisitely sensitive to the "average" orientation in a large area, which would allow the bee to detect a useful cue, but not individual edges, in a scene of mixed textures.

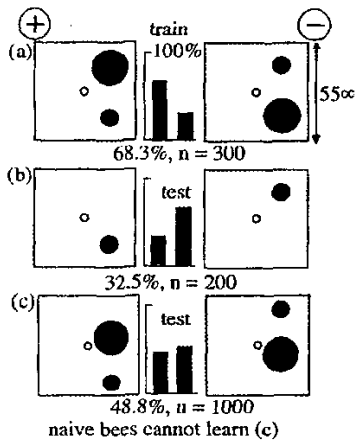


Fig. 2. Bees learn the position of the centroid, not the individual spots.

The filters in parallel input channels are progressively inferred from numerous experiments with shuffled or alternated arrangements of the training patterns, and tests with one cue at a time [5]. Failure of the bees to learn to discriminate, or failure of trained bees in tests, means that no cue is detected. However, in the bees' normal behaviour the visual recognition of a goal relies upon contrasting features that are fixed in space, while the bees are mobile. Therefore, to discover

the strategy of the bee that gives the illusion of an eidetic image, we must work with choices between patterns that are fixed in space relative to the choice point.

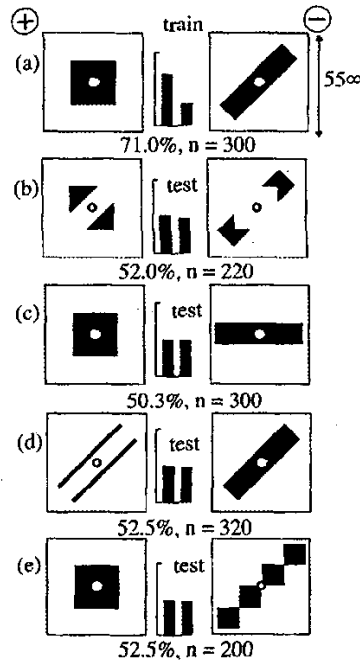


Fig. 3. Bees detect cues, not patterns. (a) Train on two shapes of same area. (b-e) Tests fail when there is no difference in the orientation cue, although other cues are available to human vision.

When trained in a Y-choice maze (Fig. 1) with the pairs of patterns fixed on the targets, bees rapidly learn to discriminate between some patterns, depending on whether any of the appropriate cues are available. They learn a difference between the vertical positions of the centres of two black shapes of similar size (Fig. 2) irrespective of the shapes. They can also learn a difference in size between two shapes centred at the same place, irrespective of shape. When the cues are moved relative to the reference point, discrimination fails. When the cue is the orientation of an edge that is fixed in space, discrimination usually fails if the edge is moved more than about 10°. The bee must then go back to the previous point of reference and make another attempt. Individual edges appear to have no salience for the bees' vision. When the shape is a large black spot, a radial pattern, or is coloured, moving it has less effect,

as if these shapes have salience so that the bee can look for them and detect the cue. There is no evidence for, and much against, the idea that the bees see the patterns (Fig. 3). The bees discriminate the cues at the places where they have learned to look for them in relation to a reference point, and there is no evidence that the cues are re-assembled in the brain. There is no pattern perception in insects, only looking for cues at the right place (Fig. 4).

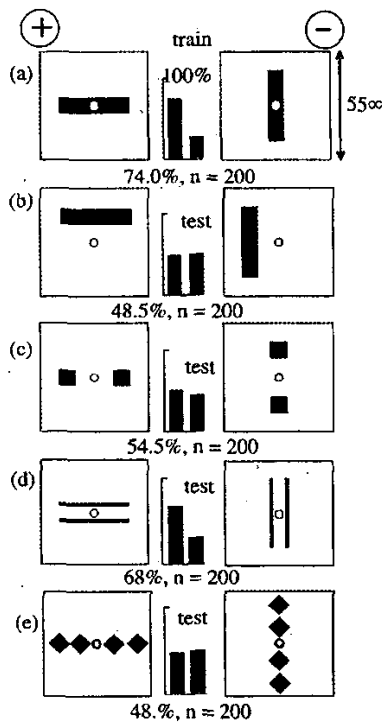


Fig. 4. After training on two bars placed centrally, discrimination fails when there is no orientation cue at the expected place.

When bees discriminate between a square and an oblique bar of the same area centred on the same place, both fixed relative to the point of choice, the only cue is the orientation of the bar, and discrimination is lost if this cue is removed (Fig. 3). The bees do not look for the bar if it is displaced, but the area of the bar can be removed without complete loss of the discrimination, as long as the edge cue remains in place. Neither the bar nor the cue has any salience for the bees. Results are similar with the other cues.

Discrimination of the location of coloured patches is a little more complicated. Individual bees can

simultaneously discriminate at least two different locations of different coloured patches (of sufficient size) but discrimination of any location requires contrast to the green receptors, so that at least three different kinds of parallel channels are involved in such a task.

5. CONCLUSION

Bees detect the cues, not the patterns, and they learn where to look for them. The bees discriminate the same set of cues whether they are fixed or shuffled relative to the choice point, but when cues are shuffled they learn to look for them only within the range of places where they were learned. The general conclusion is that the bees have a small variety of filters to detect cues and they learn to look in exactly the right direction from each choice point to pick up the next cue.

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