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Honeybee Vision: In Good Shape for Shape Recognition

Over the past seventy years, the question of how bees learn and recognise objects has generated more controversy than consensus. New research now suggests that bees distinguish between shapes largely on the basis of their outlines.

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The tireless lifestyle of a foraging honeybee predisposes it to learn and recognise nectar-bearing flowers quickly and accurately, so that it may return to visit them again and again. While there have been many studies documenting the ability of bees to learn and discriminate the colours, shapes and other geometrical properties of objects, we still know relatively little about how these shapes and colours are represented in the bee brain, and about how they are distinguished. A recent study by Lehrer and Campan [1] suggests that the shapes of objects are recognized in terms of the profiles of their outlines.

Imagine, for example, that bees can be trained to distinguish between a triangle and a circle of the same area. What is the basis on which they could make this discrimination? There are at least two possibilities. One is that each object is memorized and represented in the brain in a 'facet-by-facet' or 'pixel-by-pixel' fashion, rather like a digital image in a computer (see reviews [2–4]). Such a representation would, in effect, list the positions of all of the pixels that are contained within each shape, and specify the colour and intensity of each of these pixels. This would be an accurate representation of the object but, like a bitmapped image stored in a computer, it would be an expensive representation in terms of memory

requirements. If objects are indeed represented in this way, then one way in which the triangle could be distinguished from the circle would be determining which representation produces the better overlap with the image that is currently being viewed, on a pixel-by-pixel basis.

Another possibility is that each object is represented largely in terms of the geometry of its outline, together with a specification of its overall colour [5]. Such a representation would be more economical in terms of memory, as it would only require specification of the positions and orientations of the edges of each object, together with some information on the object's overall colour. With this representation, the triangle could be distinguished from the circle on the basis that the outline of the former shape possesses only three orientations, while the outline of the latter shape possesses all possible orientations.

To examine this question, Lehrer and Campan [1] trained bees to distinguish between a blue square and a yellow square, by associating the blue square with a reward of sugar water. The bees learned this discrimination well. The choice preferences of the trained bees were then tested by presenting them with various pairs of stimuli. It turned out that the bees preferred a blue triangle over a green triangle, and a blue triangle over a violet triangle. Clearly, then, the bees had learnt

the colour of the rewarded stimulus, namely, blue, and they were able to choose the object of the correct colour even if it had an unfamiliar shape. But had the bees also learnt the shape of the rewarded stimulus?

To investigate this, the trained bees were tested further by presenting the rewarded shape (square) together with a triangle, a diamond, or a circle. In any given test, the two stimuli in question had the same colour. This colour was blue in one group of tests, yellow in another group and black in a third group. In all of these tests, the trained bees consistently preferred the stimulus that had the correct shape (square). Thus, during the training (blue square versus yellow square), the bees had learnt not only the colour of the rewarded stimulus (blue), but also its shape (square) — although they were not being trained specifically to discriminate shapes. And in the tests they were able to choose the correct shape regardless of the colour of the object, thus suggesting (though not proving) that they were using just the outlines of the objects to analyse their shape.

Can bees, trained to distinguish between two differently shaped objects, continue to distinguish between these objects when they are of a novel colour or texture? This question was investigated in another series of experiments in which bees were trained to distinguish between a black diamond and a black circle, by rewarding them on the diamond (Figure 1). The bees learned this discrimination well. The trained bees were then subjected to a series of tests in which they were offered a choice between the diamond and the circle, presented in a range of different colours and textures. In several

groups of tests, the shapes were: (A) blue on a white background; (B) yellow on a white background; (C) black on a randomly textured background; (D) blue on a randomly textured background; (E) yellow on a randomly textured background; or (F) randomly textured, and positioned 5 cm in front of a similarly textured background (Figure 1).

In each case, the trained bees showed a strong and significant preference for the correct shape (diamond). Clearly, the bees were able to recognize the correct shape irrespective of the colour or texture of the object or the background. This strongly suggests (but does not prove conclusively) that the bees were evaluating the shapes by using only the information that was available at the boundary between the object and the background. It was only the boundary that was invariant across all of the test stimuli. Case (F) is particularly interesting: Here the object is camouflaged against the background and is visible only because the image of the object moves against the image of the more distant background as the bee approaches the object. The object ‘pops out’ because of the abrupt change in image motion that occurs at the boundary between the object and the background.

This test reveals that bees can recognize previously learnt shapes even when the shapes are visible only through the motion contrast that is present at their boundaries — there is no contrast in intensity or colour between the object and the background. Here again, there is the strong likelihood that the analysis of shape was based exclusively on the information at the object’s boundary, because the object had the same appearance as the background (although its image moved at a different speed on the retina). It is noteworthy that, in all of the tests, the preference for the diamond was at least as strong as with the training stimuli, and in some cases, it was even stronger. This makes it unlikely that the specific internal colours or textures of the training stimuli

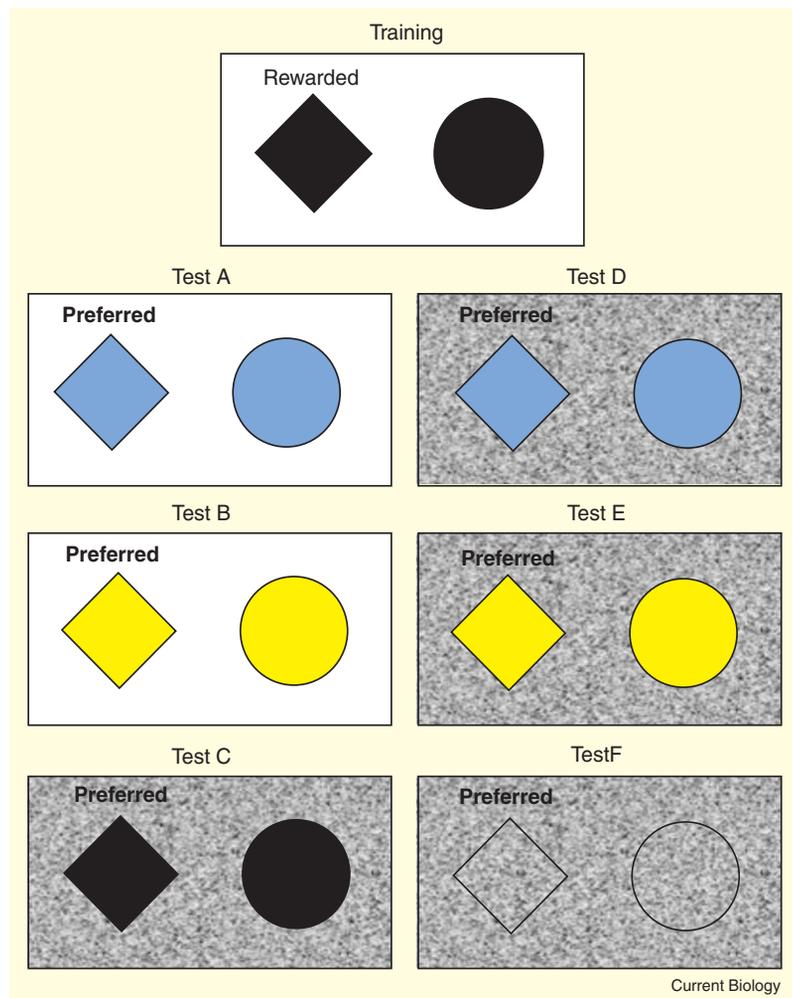


Figure 1. Bees, trained to distinguish between a black diamond and a black circle by reward on the diamond (top panel), are able to recognize the diamond even when the colour or the texture of the object or the background are varied, as shown in the other panels. This suggests that the shapes of objects are recognized largely on the basis of their outlines.

played a role in the analysis of the shapes of the test objects.

It would have been interesting to examine, in a further test, the trained bees’ preferences when they were offered outline versions of the diamond and the circle — say, black outlines on a white background. In such a test, the information about each object would be restricted exclusively to the boundaries (see [6], for example, where an analogous experiment is described).

The new study by Lehrer and Campan [1] thus offers provocative evidence in support of the notion that the visual system of the bee does not store the images of learned objects in their entirety. Rather, it extracts features — namely, the profile of

the object’s boundary, and some information on the overall colour or texture of the object. The object is represented in a compact and caricatured form, as in a cartoon. An economical representation of this kind would allow more objects to be memorized. It may also expedite the process of recognition, as it would require fewer comparisons to be made between the object that is being viewed, and its representation in memory. These advantages are likely to come at a price, however, because information on the internal detail of the object is likely to be sparse. Thus, the system may not be able to distinguish between objects that have similar outlines, colours and textures, but which differ in

the details of their internal structure. Further experiments would be necessary to explore this question.

Lehrer and Campan [1] would have almost certainly pursued this fascinating line of investigation further, and obtained more compelling evidence in support of their hypothesis, were it not for Miriam's untimely death on August 26, 2005. Miriam's work over the past thirty years has led to several important advances in our understanding of pattern recognition, colour vision and movement perception in

honeybees, and revealed striking parallels between the ways in which visual information is processed by bees and higher vertebrates, including humans. She will be sorely missed by her colleagues, collaborators and friends all over the world.

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Plastid Division: The Squeezing Gets Tense

The discovery of prokaryote-related mechanosensing proteins in the envelope membranes of chloroplasts could indicate a way in which the division of individual chloroplasts within a large cellular population is controlled. Might chloroplasts feel the squeeze?

Kevin Pyke

What we see today in plant cells as plastids, typified by the chlorophyll-containing chloroplasts in green tissues, have had a long and complex evolutionary past. Plastids arose from free-living photosynthetic organisms which became entwined in an endosymbiotic relationship with early eukaryotic cells [1]. Many of the original genes that enabled function of the free-living endosymbiont were transferred to the nucleus during evolution, and many were hijacked for subtly different functions to enable the errant endosymbiont to be controlled by the cell's master nucleus. An interesting story currently being unravelled is that of how the plastid divides in the cytoplasm of the plant cell, and how that mechanism is controlled both at the level of the individual plastid and more globally for entire populations of plastids within a cell.

Research into the basic mechanism by which plastids divide has exploited mutants and

searched for homologues of genes which function in prokaryotic cell division. This work has uncovered a diverse collection of functional proteins which contribute to the plastid division mechanism [2], with a contractile plastid division ring in the middle of the plastid composed of FtsZ proteins [3], which pinches and pulls in the plastid envelope membrane until it separates and re-fuses, forming two distinct smaller daughter plastids [4]. But although protein-based models of a basic plastid dividing mechanism can now be proposed [5], several major questions remain. In particular, how does the cell regulate plastid division in relation to cell size, such that the mature cell has the required complement of plastids [6]? Whilst leaf mesophyll cells are generally packed with green chloroplasts, other plant cells contain much smaller and less densely packed populations of plastids [7]. Consequently the endpoint of plastid division and expansion in different cell types is very different.

As they reported recently in *Current Biology*, Haswell and Meyerowitz [8] have identified two mechanosensory proteins in the plastid envelope membrane [8], closely related to proteins of bacterial membranes which help protect those prokaryotic cells against osmotic shock [9]. This raises the possibility that monitoring of plastid envelope tension might be an important mechanism by which plastid division and morphology are controlled. Loss of function of these two proteins, MSL2-1 and MSL3-1, perturbs chloroplast division, resulting in enlarged chloroplasts. In the case of non-green plastids, the organelles take up a spherical morphology suggesting problems with osmotic balance. Both proteins also co-localize on the internal plastid envelope with MinE, a protein which directs positioning of the plastid division ring [10].

So how might mechanosensing facilitate global control of plastid division in the context of the whole cell? Chloroplast division and expansion in developing leaf mesophyll cells is highly co-ordinated such that the product of chloroplast number and their size is maintained in relation to the total surface area of the cell [6]. In such cells, chloroplasts are densely packed and their envelope membranes are distorted by adjacent chloroplasts to produce a 'honeycomb' appearance