Bees see red

Recent papers reveal a burst of interest in how visual processing in various animals is adapted to the natural world of shape, colour and motion. The relationship between the inner and the outer worlds is close because vision is constantly crucial to survival. Experimental spadework proves that, in quite different visual systems, every conceivable feature of the environment is marvellously matched by the physical characteristics of the processing mechanisms that normally respond to these features. Darwin was correct, and there are plenty of interesting relevant details for ecologists along the way.

Bees see red

But apparent exceptions occur. Do bees see red flowers? This is a question that partly depends on what we mean by 'bees', by 'see', by 'red', and by 'flowers'. Anyone can find flowers, such as red varieties of flowering plum (*Prunus*) or apple (*Malus*) on which bees forage. Long ago, von Frisch[1] inferred that worker honeybees (*Apis mellifera*) do not see red because they cannot be trained to distinguish red targets from all shades of grey or black (which is still the best practical test), although they discriminate blue, green or yellow targets very well in the same type of choices when looking for a reward of sugar. von Frisch used large areas of colour to which the bees could fly and his criterion for success was the landing of the bee on the target. These were discrimination experiments, in that the bees had to recognize the targets on their return.

Two colours are discriminated by a visual system only if they differ in the region of the spectrum where there is overlap between the spectral sensitivities of the three receptor types with a peak in the UV, blue or green (Fig. 1a). At least two parallel input lines can then act together differentially. Later work[2] showed that bees can discriminate pure monochromatic colours in large areas very well between about 360 nm and 530 nm with a wavelength resolution of 11 ± 5 nm (Fig. 1b). Following this, some ecologists and writers of texts[3] have concluded that red flowers are not adapted to being pollinated by bees. Some butterflies, beetles and wasps[4], however, have special receptors with a peak in the red part of the spectrum, but to date there is no behavioural evidence relating to the function of any insect photoreceptor for red.

In a new paper, Chittka and Waser[4] argue differently. These authors now show that some flowers that look red to us in fact reflect sufficient blue light to be useful in the colour vision of the bee. They also show that many red flowers reflect sufficient total light at the red end of the spectrum to excite those bees' receptors that have a peak sensitivity in the green/yellow near 540 nm and sensitivity stretching into the red. This is why the term 'red' must be defined. In most species of bees, receptors with peak sensitivity to wavelengths longer than 540 nm have not been found. If they have specific red receptors, honeybees do not use them in these tests. Some native bees may have specialized receptors for red, which is why the term 'bees' has to be carefully defined.

The exact behavioural cut-off for seeing an isolated flower is therefore a question of the minimum detectable signal, and how much of the reflected light at the yellow end of the spectrum can be integrated under the spectral sensitivity curve of the receptors with a green peak. A subsidiary question is to what extent do the receptors adapt to locally low levels of effective photons. All indications we have from the physiology suggest that bee vision rapidly adapts to the local intensity. At this meeting point of physiology, ecology and behaviour, we are still ignorant of the state of adaption of the eye.

Seeing in detection tests is not the same thing as distinguishing in discrimination tests. The latter requires memory, which is why the term 'seeing' must be carefully defined. Chittka *et al.*[4] calculate that the bees *detect* some red flowers, and they trained them to do so (as in Fig. 2), showing that there are sufficient effective photons. The bees still cannot

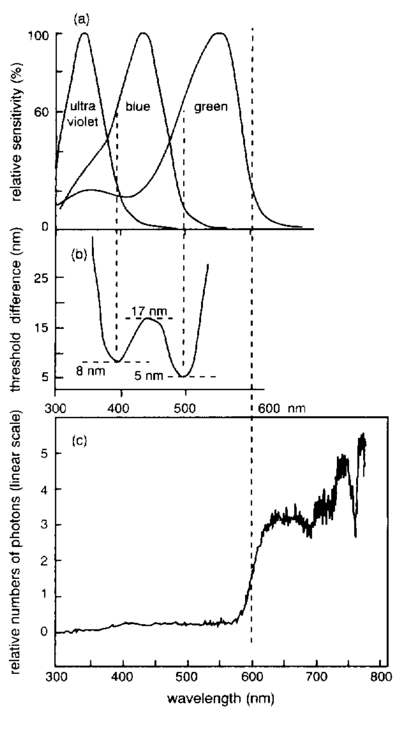

Fig. 1. (a) The spectral sensitivity curves of the three receptor types of the honeybee. (b) The required difference for discrimination between two monochromatic wavelengths, as a function of wavelength. Discrimination is best where the steep parts of the sensitivity curves overlap. (c) The reflected light at each wavelength (in relative numbers of photons) that is reflected in sunlight from the artificial poppy (*Papaver*) flower in the colour photo.

Fig. 2. Honeybees can be trained to take sugar solution at an artificial red flower. Here the target is a Remembrance Day poppy with black centre, on a green background. Although the target is moved about, the bees avoid an alternative real red flower. *Photo by Jeffrey Wilson.*

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discriminate between different shades of red except by intensity or the content of shorter wavelengths. But bees are poor at discriminating intensity in tests, perhaps because their visual mechanisms adapt to ambient light.

Flowers are not isolated spots

The matter is not so straightforward, however. Vision depends largely on detection of contrasts at edges. Each photoreceptor detects a small part of the image. As the local view belonging to each receptor scans across the natural world, the intensity in the receptor, and therefore also its response, is changed by each contrasting edge that is crossed. This process is called receptor modulation. The flat colours of the petals and the modulation caused by contrast at the edges are both useful inputs. Therefore the term 'flower' must be defined carefully in terms of intensity and contrast. Flower shape and symmetry are separate issues and the shape of the flower is not seen by bees as we see it.

Flowers commonly present themselves on a background of green, yellow or brown, all of which strongly excite the receptors that have a green peak. At least half of the honeybee's receptors are of the green-peak type, so red flowers are presented as dark on a bright background. Some flowers, such as bright yellow ones, will be light on a dark background to the green-peak receptors and dark on a lighter background to the blue-peak receptors. Blue flowers look bright on a darker background to the blue-peak receptors. The relative advantages of dark versus light flowers are not apparent to humans. Bees can learn to discriminate low contrast at an edge although they use only the receptor type with a green-peak.

Besides the importance of contrast, Chittka and Waser[4] point out that flowers generate relative motion against the background texture. Flowers are often on stalks and generate parallax with aid of background leaf textures. This cue is interchangeable with colour and edge orientation[5].

Vision of some features is colour-blind

A further question is raised by the apparent (or angular) size of the flower subtended at the bee's eye. Recently, Giurfa and others[6], following indications by Lehrer and Bischof[7], have found that chromatic contrast can be discriminated only when the target subtends at least 15° at the bee's eye. Chromatic contrast refers to the difference in excitation of two receptor types, as distinct from the intensity received by any one receptor type. Experiment shows that colours must be in large patches to be discriminated, as if the colour system has to smooth out a lot of noise. On the other hand, small objects, and fine gratings near the limit of spatial resolution[8], are detected against background by a mechanism that involves only the green-peak receptors and is therefore colour-blind. So, every small object is indistinguishable from a background of some appropriate grey level. Although colour is the preferred cue for discrimination, it is discriminated only as the bee comes close. This gives a selective advantage to large homogeneous flowers or composite flowers. In the absence of colour, bees discriminate black artificial patterns on a white background, so red flowers are not necessarily a disadvantage.

Even more curious and exciting, in a recent paper Giger and Srinivasan[9] have shown experimentally that the discrimination of orientation of edges by honeybees is colour-blind and effected by the green-peak receptors alone. As edges make up some of the features of shapes, this new finding implies that whatever bees discriminate in a shape, they are colour-blind in the discrimination of the edges. This demonstration implies that colours of flowers are separate cues from edges and shapes.

What is the use of flower colours if they cannot be discriminated from a distance and the orientation of their edges cannot be seen in colour? These recent papers show that a flower is not seen as a coloured form as we see it; it is detected as a set of separate cues, notably the average colour in each 15° patch, the average edge orientation in each similar sized patch, and some other cues such as size and symmetry. Bees separate an image into elements, some of which they find useful as cues to attract their attention, but in a discrimination they cannot re-assemble the image. Such a method of organizing memory avoids the huge load of information that is required to hold a picture with each feature in colour in its place. On the other hand, we, with our enormous visual system, think that re-assembly of the image is essential. The tiny brain of the bee shows that this is not so.

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