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Pictures at an exhibition: Bees view Van Gogh's *Sunflowers*

"For the Rays to speak properly are not coloured. In them there is nothing else than a certain Power and Disposition to stir up a Sensation of this or that Colour. For as Sound in a Bell or musical String, or other sounding Body, is nothing but a trembling Motion, and in the Air nothing but that Motion propagated from the Object, and in the Sensorium 'tis a Sense of that Motion under the Form of Sound; so Colours in the Object are nothing but a Disposition to reflect this or that sort of Rays more copiously than the rest; in the Rays they are nothing but their Dispositions to propagate this or that Motion into the Sensorium, and in the Sensorium they are Sensations of those Motions under the Forms of Colours." Newton, *Opticks*, 1704

Lars Chittka and Julian Walker took bumblebees to an exhibition of paintings by Vincent Van Gogh, Paul Gauguin, Patrick Caulfield, and Fernand Léger. These were naïve laboratory-reared bees that had never seen real flowers before and had always sucked sugar solutions from artificial feeders. Reproductions of these paintings were placed on the floor of a test flight arena, and the responses of bees from three different colonies were recorded. Each colony was tested once with each painting, and the number of approach flights made by bees to parts of the painting, as well as the number of landings on to specific parts of the paintings, was recorded. The whole process was videofilmed. Two of the paintings contained flowers: Van Gogh's *Sunflowers* and Gauguin's *A Vase of Flowers*, while the other two did not: Caulfield's *Pottery*, and Léger's *Still Life with Beer Mug*. The bees were most attracted to the Van Gogh painting, which received the highest number of approaches and landings while Gauguin's flowers received the least attention. In the two floral paintings, the flowers were the targets of most of the approach flights. This was extremely interesting considering that these bees had never seen natural flowers before. Thirteen of the fifteen bee landings on to the Van Gogh painting were on the yellow flowers. In the Caulfield painting, bees were most attracted by the large yellow vase at the bottom of the painting, while in the Léger reproduction, light blue squares and a checkerboard pattern received the most attention. Although the Gauguin painting received the least attention, most of the approaches by the bees in this painting were to flowers.

These experiments were part of a project on Sci-Art being conducted by Chittka (a behavioural ecologist) and Walker (an installation artist) of Queen Mary College, University of London, whose aim is to explore the interface between aesthetics and science. The results were reported in the *Colour and Design* symposium conducted by the Linnean Society of London and the Institute of Mechanical Engineers, in which physicists, engineers, artists and biologists participated. Chittka and Walker (2006) echo Newton: ..."colour is neither purely physics nor a domain of the arts: it is, to a large extent, biology". Colour is firmly within the realm of psychophysics. Bumblebees are trichromats with receptors that peak in the ultraviolet (350 nm), blue (440 nm) and green (540 nm) regions of the electromagnetic spectrum. Van Gogh's yellow sunflowers were "bee green" evoking the strongest responses from the bee's green receptors, and Van Gogh's signature (blue calligraphy on a yellow background) evoked many approaches by the bees because it provided the strongest colour contrast: "bee blue" against "bee green". On the Gauguin painting, a majority of approaches were to the blue flowers (stimulating the blue receptors: "bee blue"). Bees also appear to have an innate preference for blue, and when flower-naïve bees, that have never seen flowers before, are given a choice of various hues, they will prefer bee blue and ultraviolet-blue over other hues when all else is kept constant (Giurfa *et al* 1995). Yet, there are fewer blue flowers and more blue-green flowers in nature (Chittka *et al* 1994). This may be because bees are better at discriminating blue-green flowers than blue flowers under conditions of variable light illumination; i.e. they are able to better maintain colour constancy in nature with blue-green flowers than with blue flowers (Dyer and Chittka 2004). By colour constancy is meant the ability to perceive the same colour under

Keywords. Colour vision; insect-plant interactions; sensory ecology

conditions of different spectral illumination. Why should colour constancy matter to a bee? If a bee has discovered a rewarding plant species whose flowers are of a particular colour (and shape etc.) it would pay the bee to be able to find these flowers reliably without making mistakes. Similarly, it would pay the flowering species to produce flowers that did not vary in hue so that bees could lean to reliably associate cues such as colour with a reward (nectar and/or pollen). This would facilitate constancy of the pollinator to the flowering species that would reduce the likelihood of heterospecific pollen being deposited by the pollinator on the flowers' stigmas. Within the pollination market, therefore, when flowers of many species are simultaneously calling for the pollinator's attention, it would make more sense for flowers to code their colours in the blue-green area of the spectrum rather than in other regions in order to enable their pollinating bees to achieve colour constancy, and thereby flower constancy. Colour constancy is also an important issue from a physical perspective because the colour (spectral quality) of sunlight varies at different levels after it is filtered through clouds, and is absorbed and reflected by vegetation (Endler 1993). Furthermore, bees are often the most important pollinators in most landscapes (Neff and Simpson 1993). Therefore, Van Gogh's *Sunflowers* were calling out to bees while Gauguin's flowers were not so appealing. The ultraviolet-blue-green trichromacy of bees is believed to have been present in the Devonian ancestor of pterygote insects (Briscoe and Chittka 2001), more than 400 myr before the rise of angiosperms. Thus, whether flower colours have adapted to insect colour vision or whether insect trichromacy was an exaptation for insect-plant interactions is a matter for much new exciting research in the field of sensory ecology (Chittka and Briscoe 2001). Red flowers, on the other hand, are less common in nature, and are predominantly bird-pollinated (Raven 1972; Rodríguez-Gironés and Santamaría 2004). Unlike bees, birds have a red receptor and can discriminate red against a background of green foliage much better than a bee can (Chittka and Waser 1997).

What is the relationship between humans and flower colours? Chittka and Walker (2006) make the interesting observation that, judging from the colours of flowers stocked by florists, the most common and most appealing colour produced by artificial selection in floriculture appears to be red, while bouquets of blue flowers are rarely offered. Why is this so? While most mammals are dichromats, primates, especially the catarrhine Old World monkeys, are trichomats, with a red receptor. Was blue-green-red trichomacy in primates under active selection? The frugivorous primate ancestors of humans apparently needed to be able to discriminate ripe fruit (usually purple or red) from unripe green fruit against a green leaf background, and this special requirement may be the origin of the particular sensitivities of human colour receptors (Osorio and Vorobyev 1996; Sumner and Mollon 2000; Kelber *et al* 2003). This may explain the preference in humans for red flowers relative to blue ones. And so, in nurseries and gardens, humans begot flowers and "*the flowers begot us, their greatest admirers. In time human desire entered into the natural history of the flower, and the flower did what it has always done: made itself still more beautiful in the eyes of this animal, folding into its very being even the most improbable of our notions and our tropes……For the flower it was the same old story, another grand coevolutionary bargain with a willing, slightly credulous animal – a good deal on the whole, though not nearly as good as the earlier bargain with the bees* (Michael Pollan: referring specifically to the co-evolution between tulips and humans that originated in the Ottoman Empire and was later played out in the flower markets of Holland where, in the 17th and 18th centuries, tulips with rare colours were worth the equivalent of rare jewels; Pollan 2002).

In the end, every story of adaptive evolution or co-evolution between eyes and flowers must be tempered by constraint and history (Goldsmith 1990; Armbruster 2002). Was insect colour vision exapted to flower colours? Can flowers explore all colours in the ultraviolet-visible spectrum or are there biochemical and evolutionary constraints that restrict floral colour space? Is there always strong selection pressure on flower colour and is this pressure exerted only by pollinators? Is floral colour affected by random genetic drift and pleiotropy? We know today that El Greco's elongated figures were a matter of style rather than a consequence of his presumed astigmatism, while Monet's later paintings were coloured by his failing vision and cataract. Perceptual constraints, as well as current and historical evolutionary forces, facilitate the exciting melding of science and art, so that questions such as what makes a Mondrian or Miró appealing (to humans and to bees) can be asked and perhaps answered. Is there accounting for taste, after all?

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*e*Publication: 13 November 2006