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Do bees like Van Gogh's *Sunflowers*?

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Abstract

Flower colours have evolved over 100 million years to address the colour vision of their bee pollinators. In a much more rapid process, cultural (and horticultural) evolution has produced images of flowers that stimulate aesthetic responses in human observers. The colour vision and analysis of visual patterns differ in several respects between humans and bees. Here, a behavioural ecologist and an installation artist present bumblebees with reproductions of paintings highly appreciated in Western society, such as Van Gogh's *Sunflowers*. We use this unconventional approach in the hope to raise awareness for between-species differences in visual perception, and to provoke thinking about the implications of biology in human aesthetics and the relationship between object representation and its biological connotations.

Keywords: Bumblebee; Colour preference; Colour vision; Primate; SciArt

"And other eyes than ours
Were made to look on flowers…"
Christina Rossetti 1830–1894 (From the poem: *To what purpose this waste*)

"That not for man is made
all colour, light and shade…"
Edmund Gosse 1849–1928 (From the poem: *The farm*)

1. Introduction

The "Colour and Design" symposium of the Linnean Society, that gave rise to this special volume was numerically dominated by two distinct sets of participants—engineers/physicists and artists. Yet, colour is neither purely physics nor a domain of the arts: it is, to a large extent, biology. The coloured world we see is not the real or the physical world—instead, the colours we perceive are filtered through the specific sense organs that we have acquired in evolutionary history [1,2]. Colour vision systems differ widely between different animal species, and the reason is that different aspects of the coloured world are biologically relevant for different species. Our goal was to raise appreciation of this fact in an audience not specifically trained in the biology of vision.

The insight that flowers (and their colours) have not been created solely to please us humans dates back to the 18th century. The history of that discovery is a healthy lesson for those who think that science in the earlier days was less riddled by competition and strife. The idea that flowers are in fact sex organs, designed to attract the services of pollinators, is commonly attributed to Sprengel 1793 [3], who entitled his book "The uncovered mystery of nature…". When Goethe heard of Sprengel's progress with that book, he competed to publish his own botanical work [4]. Goethe [5] won the race, publishing his book in 1790. His work had a strongly different focus, and what Goethe offers on flower colouration (e.g., that floral colours are caused by

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the contaminating influence of male seed in the petals) shows he would have done better to leave the field to Sprengel. However, Sprengel himself was little more innocent: more than 30 years before him, Kölreuters [6] noted that "… anyone who had made these observations, would have much earlier discovered them [the causes of pollination in the activities of insects], and would have … *removed the curtain from this mystery of nature*"—which shows that Sprengel did not only borrow a key idea from Kölreuters, but that in fact the very title of Sprengel's volume stems in part from Kölreuters' original wording.

Flower colours are clearly important signals to bees, since flowers provide bees with nectar and pollen. But how do insect pollinators see colours? In 1874, Lord Rayleigh [7] pointed out that 'The assumed attractiveness of bright colours to insects would appear to involve the supposition that the colour vision of insects is approximately the same as our own. Surely this is a good deal to take for granted'. Lord Rayleigh was right: in 1924, Kühn [8] discovered that bees see ultraviolet light (Fig. 1), and in subsequent decades a wealth of information has been collected on how bees process colour information. Bees (including the familiar bumblebees and honeybees) have three colour receptor types, with maximum sensitivities near 340 nm (UV receptors), 440 nm (blue receptors) and 530 nm (green receptors); see [9], and references therein. Brightness, a parameter so fundamental to our own visual experience, has a relatively minor role in bee colour discrimination [10]. But bees use a single colour receptor, the green receptor, for detection of flowers from a longer distance [11]. How the information from the colour receptors is processed in the bee brain is still controversial, but it is certain that at least two colour opponent processes are involved, which compare responses from different colour receptor types [12,13]. Bee colour vision is optimal to code for floral colours [14].

Old world primates, including humans, have three colour receptor types whose spectral sensitivities peak at around 430 nm (blue receptors), 530 nm (green receptors) and 565 nm (so called red receptors, even though their peak sensitivity corresponds to yellow) [15]. The light sensitive pigment of human photoreceptors have some sensitivity to UV light, but such radiation never reaches the retina because it is absorbed by the lens [16]. C. Monet (1840–1926), an avid painter of flowers, had the lens removed from his right eye in 1923 due to cataract, and would therefore have been able to see UV patterns of flowers.

It is thought that the mammalian ancestors of primates had only blue and green receptors, and that the red receptor is an adaptation to frugivory [17,18]. Flowers do not play a major role in the diet of humans and other primates; the biological significance of human attraction to flowers is discussed later. It is clear from the above, however, that there will be both differences in perception and in meaning for human and bee observers

Fig. 1. A flower of *Iris pseudacorus* photographed in the visible (left) and in the ultraviolet (centre panel). The centre of the flower is strongly UV absorbing and appears as black, whereas the periphery reflects UV light. Right panel: a bumblebee worker probes the boundary between the two areas with her antennae. Photos by Prof. K. Lunau, with permission.

of floral colours—and that perceptual differences have evolved alongside the biological significance of the objects in question.

The authors of the current article, a biologist and an installation artist, were drawn to each other's work by the fact that bees and people obviously are both drawn to flowers, and that one of the most obvious ways that humans express this in western culture is by creating and appreciating paintings of flowers. By presenting such paintings to bees, we hope to address people with an interest in colour (but not necessarily a training in the biology of colour vision). We hope to stimulate thinking about the fundamental philosophical issue of whether perception reflects reality, about the nature of the image as object [19], and about the biological meaning of colour for different receivers. We emphasise that this review of bee and human colour vision is meant to point out only the most important differences. The interested reader is encouraged to obtain a more in-depth picture from the literature cited above.

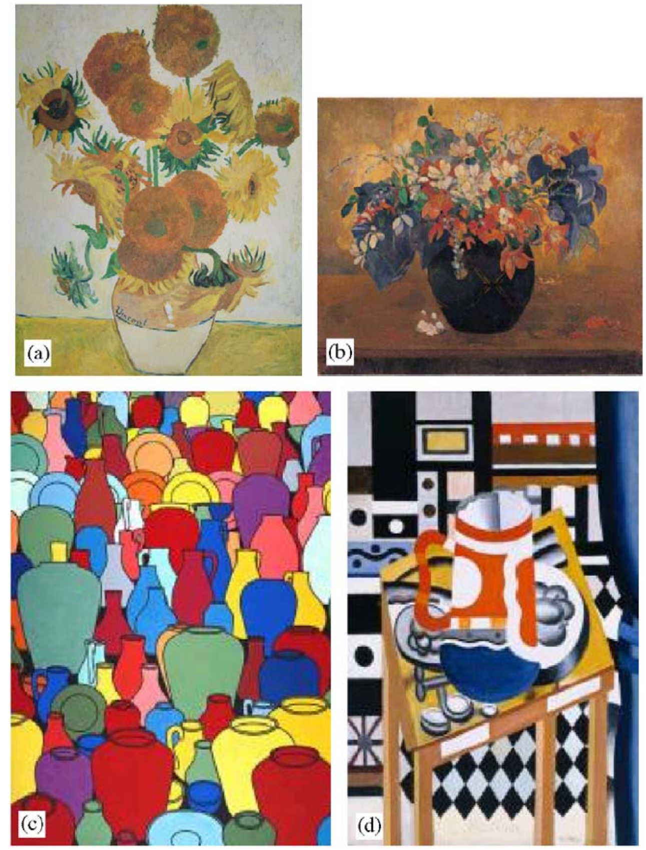

Fig. 2. Paintings used: (a) Vincent Van Gogh (1853–1890) *Sunflowers* (1888). The original is in the National Gallery, London. The copy was painted by J. Walker (acrylic on canvas-board 45.5 × 35.5 cm). (b) Poster of Paul Gauguin (1848–1903). *A Vase of Flowers* 1896; oil on canvas 64 × 74 cm (copyright: The National Gallery, London). (c) Poster of Patrick Caulfield (b. 1936) *Pottery* 1969; oil on canvas 213.4 × 152.4 cm. Presented by Mrs. H. K. Morton through the Contemporary Art Society; Tate Gallery, London; (copyright: Patrick Caulfield 2004. All rights reserved, DACS, London). (d) Fernand Léger (1881–1955). *Still Life with Beer Mug* 1921–1922, oil on canvas 92.1 × 60 cm; purchased with assistance from the Friends of the Tate gallery 1976; Tate Gallery, London; Copyright: ADAGP, Paris and DACS, London 2004. Posters of (a) and (b) are available in The National Gallery shop, posters of (c) and (d) are available in Tate Modern's shop.

2. Material and methods

We used well-established conventional protocols to measure innate responses of bees to visual stimuli. A bumblebee (*Bombus terrestris*) nest box was connected to a flight arena. Bees were allowed to forage sucrose solution from clear Plexiglas squares. They had never seen natural flowers prior to or during the experiments. We then placed reproductions of paintings onto the floor of the flight arena. Experiments were performed in a laboratory with controlled constant illumination, which simulated natural daylight [20]. Each painting was presented to bees from three different bumblebee colonies. Each colony was presented with all four paintings (see below), but only once with each painting. Paintings were presented for periods of 4 min. Bees' responses to objects in the paintings were filmed using a digital video camera. We distinguished between approach flights (where bees visibly slowed down their flight to approach an area of the painting to a distance of lower than 5 mm) and landings (where bees touched down to probe an area) [21].

We chose two paintings that contained flowers, and two that did not (Fig. 2). These were: Vincent Van Gogh "Sunflowers" (© The National Gallery, London), Paul Gauguin "A Vase of Flowers" (© The National Gallery, London), Patrick Caulfield's "Pottery" (Tate Gallery, London; © Patrick Caulfield 2004. All rights reserved, DACS) and Fernand Léger's "Still Life with Beer Mug" (Tate Gallery, London; © ADAGP, Paris and DACS, London 2004).

JW painted a reproduction of Van Gogh's *Sunflowers* (Fig. 2a), using acrylic on canvas-board, laid on using a hog's hair bristle and sable. Copying was done by squaring up a photo-reproduction (transferring the squares to the canvas-board and copying the outline of the image square by square). This copy was used for photos displayed in Figs. 2a and 3a; the poster was used for behavioural tests. The spectral reflectance of posters, including the ultraviolet was measured using standard techniques [10]. In all posters, only some of the yellow and white shades reflected moderate amounts of UV light.

3. Results

Van Gogh's *Sunflowers* attracted most approach flights and actual landings over the observation period, followed by Caulfield's *Pottery*, Léger's *Still Life with*

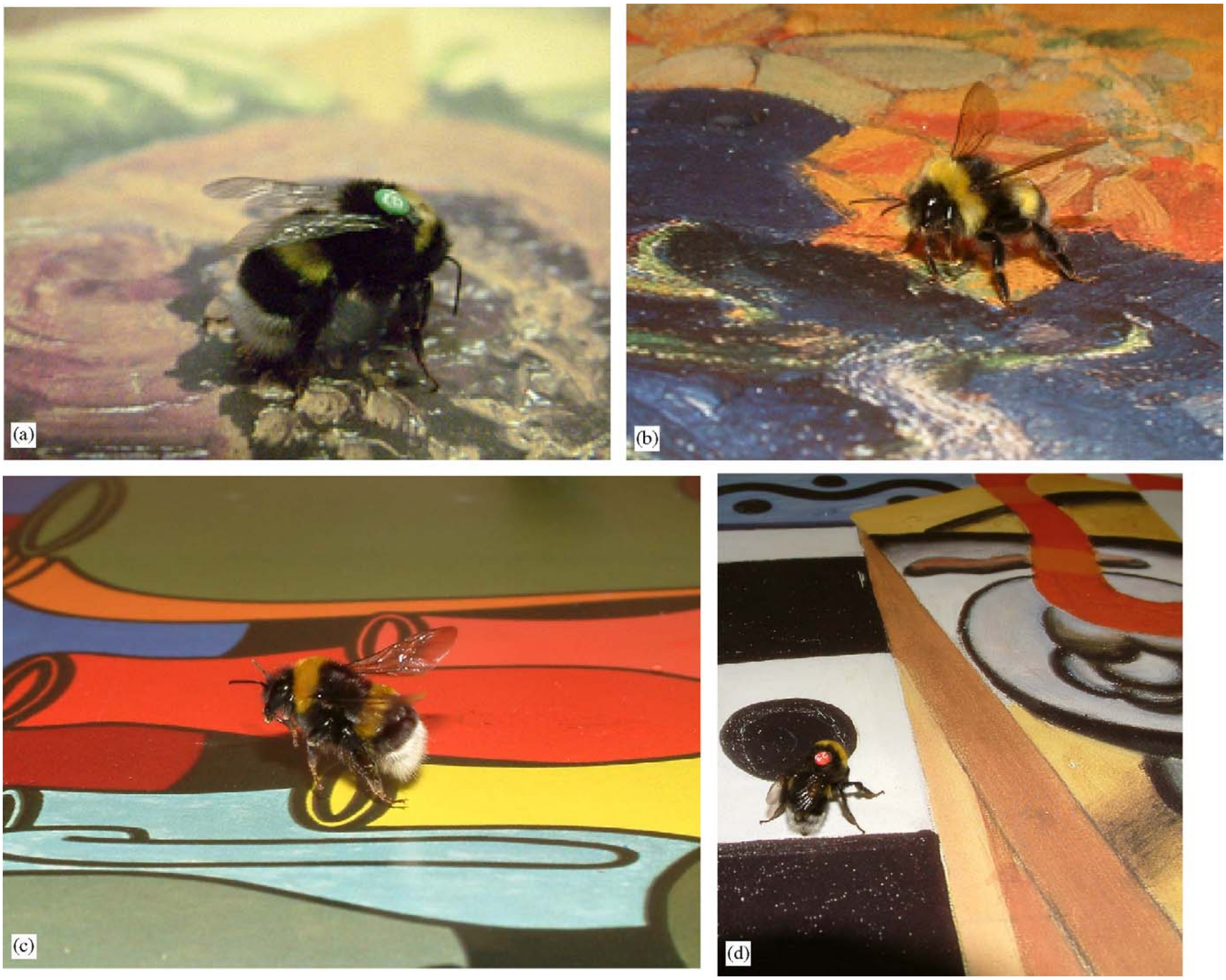

Fig. 3. Bees exploring paintings: (a) *Bombus terrestris* worker exploring Van Gogh's "Sunflowers". Some bees bear number plates on their backs to allow for individual recognition, (b) a *Bombus terrestris* male is landing on the edge of a blue flower of Gauguin's "A Vase of Flowers" (the most attractive portion of the painting for bees, (c) a worker bee hovering over Caulfield's "Pottery", and (d) another worker landing on a high contrast edge in Léger's "Still Life with Beer Mug".

Beer Mug, and finally Gauguin's *A Vase of Flowers*. In detail, bees showed the following responses:

Van Gogh's *Sunflowers*: Of 146 approach flights, 99 were to flowers. Bees mostly approached the high contrast margins of flowers, or the contrast between periphery and centre. All of Van Gogh's sunflowers are bee green, i.e. they stimulated the bees' green receptors most strongly. Interestingly, 17 approaches were to the blue-on-yellow *Vincent* signature. This comprises an especially high colour contrast (bee blue vs. bee green). 15 landings were recorded in total, of which 13 were on flowers.

Gauguin's *A Vase of Flowers*: Of 81 approaches, 25 were to blue (bee blue) flowers in the upper right part, while the remaining approaches were distributed over 24 other areas of the painting, with 7 approach flights to a cream coloured flower at the top of the painting coming second. Two landings occurred on the blue flowers in the upper right, 9 were distributed over other flowers of the painting.

Caulfield's *Pottery*: With 17 out of 138 approach flights, the large yellow (bee green) vase at the bottom right was the most popular item. The light blue dish at the bottom centre came a close second with 16 approach flights. Only 4 landings were observed.

Léger's *Still Life with Beer Mug*: The light blue square with three black dots and a serpentine black line, on the left side, slightly above the middle, was frequented most strongly (24 out of 117 total approaches). The checkerboard area at the bottom centre was second most popular, with 17 approaches. Only four approach flights terminated in landings.

In summary, when bees were confronted with paintings containing flowers, the majority of landings were indeed recorded on flowers (Fig. 4). Bees approached non-floral

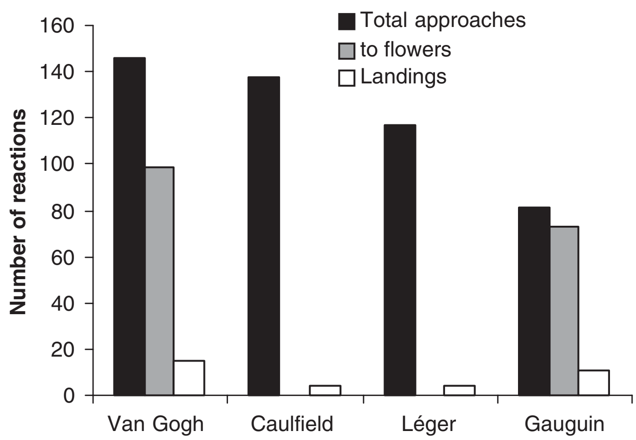

Fig. 4. Bees' reactions to the four paintings (arranged from left to right in decreasing order of popularity). Twelve minutes of observation time were evaluated for each painting.

objects in the paintings without flowers only insignificantly less frequently than they approached floral parts in the two floral paintings (χ^2 test, $= 0.702$, $df = 1$; $p = 0.402$). However, the fraction of approach flights that terminated in landing [20] was significantly higher in the paintings with flowers (11%) than it was in the paintings without flowers (4%; $= 6.048$; $df = 1$; $p = 0.014$). Thus, even though there are no strong UV patterns present, there is evidence that the flower paintings have captured the essence of floral features from the viewpoint of a bee, and that these features are recognised by bees that have never been exposed to flowers before.

4. Discussion

Our results are in line with those of controlled laboratory measurements of visual pattern attractiveness for flower-naive bees. When bees are given a choice between a variety of hues (and other factors are kept equal), they will prefer bee blue and UV-blue over other colours [22,23], which is what we also found. The evolutionary explanation for this might lie in the fact that flowers with these colours offer high-nectar rewards in nature [20]. Hence, "favourite colours" (in bees) have biological significance; we assume that selection has favoured individuals, which prefer colours associated with nutritional desirability.

Another key factor in colour attractiveness is detectability: targets are especially well detectable if they make a strong colour contrast with the background. Moreover, in bees, detectability from longer distances is enhanced when strong green contrast is provided (i.e. the difference in green receptor signal between target and backdrop) [10,11]. All of the targets heavily frequented in the present investigations combine these features to a high degree. Flower patterns cleverly arrange attractive contrast features in a concentric (or bilaterally symmetric) fashion in order to direct the bees to the salient areas. Once naive bees probe the flowers and receive a reward, they will rapidly learn to recognise the floral features (colour, shape, scent, plane of symmetry, size) that allow them to find more flowers of the same species [24,25].

How do human observers react to presentations of bees visiting flowers in paintings? We presented video material and photos to a small number of artists and scientists. The first typical reaction was amusement: viewers commented on the absurdity and surrealism of seeing live bees in an out-of-place context (paintings), yet in another sense the bees do seem to belong (since the paintings contain flowers). In some cases there was an assumption that the fact that the bees were attracted to the centres of the flowers in Van Gogh's painting indicated that the artist had "unwittingly" captured some essence of the flower, which rendered the painted flower attractive to bees. Some artists, however, also felt that bees were mistaken, or were indeed "invading" the painting, whereas biologists felt that the intimate signal-receiver relationship between flower and bees had been strangely thwarted. Inherent in all these interpretations is the implication that flowers in paintings are not really meant for bees. They are created by humans for human observers. This raises an interesting question: why is it obvious that flowers rendered by painters should be different from those which have evolved to attract bees?

Indeed, for thousands of years, humans have reshaped flowers to their liking, either through horticulture or through pictorial representation [26]. Flowers play a major role in most cultures, and the flower trade is a global multibillion-dollar enterprise. For example, the Netherlands alone exported cut flowers for more than 2 billion dollars in 1992 [27]. Could there be an evolutionary explanation for human attraction to flowers, and the fact that humans obviously prefer different floral features from those which selection has acted on to address bees?

In our evolutionary history, paying close attention to flowers might have conferred strong selective advantages [28]. Even if flowers may play only a minor role as food for primates, they can be indicators of resource availability: they might correlate with the presence of water, and indicate future availability of fruits, nuts and honey [28], and they can be used to identify plants for medicinal purposes. Is human aesthetic appreciation of flowers in part based on a primordial interpretation of a landscape with flowers as one that could support human foraging? If flowers carry different information for humans than for bees, then human horticultural selection and pictorial representation is expected to emphasise the traits that indicate relevant resources for humans. One floral feature that has been clearly exaggerated by human selection is flower size, and the number of floral petals and sepals. It remains to be determined whether these floral traits are indicative of future fruit set or water availability. What about flower colour? It is clear that human colour selection on flowers would have excluded the ultraviolet, but even within the human visual range, qualitative inspection of any flower store indicates that flower colours have been strongly altered to match human preference. Blue flowers seem underrepresented, whereas red and orange colours are common, despite being rare in natural flowers in European temperate habitats [23]. Curiously, however, these are the typical colours of primate-eaten fruits [17]. Could human flower colour preference be a result of our primordial lifestyle as frugivorous mammals, a lifestyle which has shaped the way we see colours [17,18]?. Clearly, a SciArt project such as this one cannot provide scientific answers to these questions. For that, we will have to employ conventional scientific practise. But we hope that our collaboration will stimulate thinking about the evolutionary roots of the connotations and perception of natural objects, and their representation in the arts.

5. Conclusion

This paper describes a SciArt investigation of colour perception in bees, and how this differs from humans. The study was carried out as a collaboration between a biologist and artist using a biologically defined protocol. The results are reported and explained in scientific terms, while at the same time using language intelligible to an arts audience. Readers interested in human colour perception are referred to a paper in the same issue of this journal [29].

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