

Colour constancy in insects

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Abstract Colour constancy is the perceptual phenomenon that the colour of an object appears largely unchanged, even if the spectral composition of the illuminating light changes. Colour constancy has been found in all insect species so far tested. Especially the pollinating insects offer a remarkable opportunity to study the ecological significance of colour constancy since they spend much of their adult lives identifying and choosing between colour targets (flowers) under continuously changing ambient lighting conditions. In bees, whose colour vision is best studied among the insects, the compensation provided by colour constancy is only partial and its efficiency depends on the area of colour space. There is no evidence for complete ‘discounting’ of the illuminant in bees, and the spectral composition of the light can itself be used as adaptive information. In patchy illumination, bees adjust their spatial foraging to minimise transitions between variously illuminated zones. Modelling allows the quantification of the

adaptive benefits of various colour constancy mechanisms in the economy of nature. We also discuss the neural mechanisms and cognitive operations that might underpin colour constancy in insects.

Keywords Colour vision · Computational colour constancy · Flower colour · Perception · von Kries adaptation

Introduction

Colours are used by many animals, including humans, to identify salient objects under considerable variation in natural illumination (Maloney 1984; Werner et al. 1988; Neumeyer 1991; Balkenius and Kelber 2004). If the spectral composition of the illumination changes, then so does the light reflected from objects (von Campenhausen 1986; Arnold and Chittka 2012). For example, the impression of blueness could, in theory, be generated by a blue object under white light, or a white object under blue light. This makes object identification by colour challenging under variable illumination conditions (Fig. 1), unless the viewing system possesses colour constancy, the ability of the visual system to compensate for illumination changes (von Helmholtz 1896; Land 1977; Skorupski and Chittka 2011). Viewing only a single surface, identifying the reflectance of the surface might be an impossible task—essentially like trying to solve $x \times y = z$, where z is the perceived colour whilst x (the object reflectance) and y (the illumination) are unknown (Lotto and Chittka 2005). Since object reflectance and illumination are unknown variables, infinite variations of y (illumination) and object reflectance x could have produced a perception of a colour z (Fig. 2). An ideal colour constancy mechanism would have to recover x , the

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Fig. 1 A fruit bowl under three different sources of illumination: artificial light (*left*), hazy daylight (*middle*), and clear blue sky (*right*). If the illumination of a visual scene changes, then so does the light reflected back from natural objects, resulting in different colour appearance. Unless the visual system can compensate for such changes so that colours of objects appear constant under changing illumination, valuable biological information can be lost. The banana, for example, appears *green* and unripe in the *right* image, over-ripe

in the *left* image, and just right for consumption in the *central* image. Thus even if shape vision allows the pinpointing the identity of the fruit, subtle changes in colour (in the absence of colour constancy) can corrupt information about palatability of natural objects. The same is likely to be the case for bees foraging from flowers, where subtle differences in colour often accompany changes in nectar availability (Weiss 1991). Reproduced, with permission, from Psychology Press and George Mather (Mather 2006)

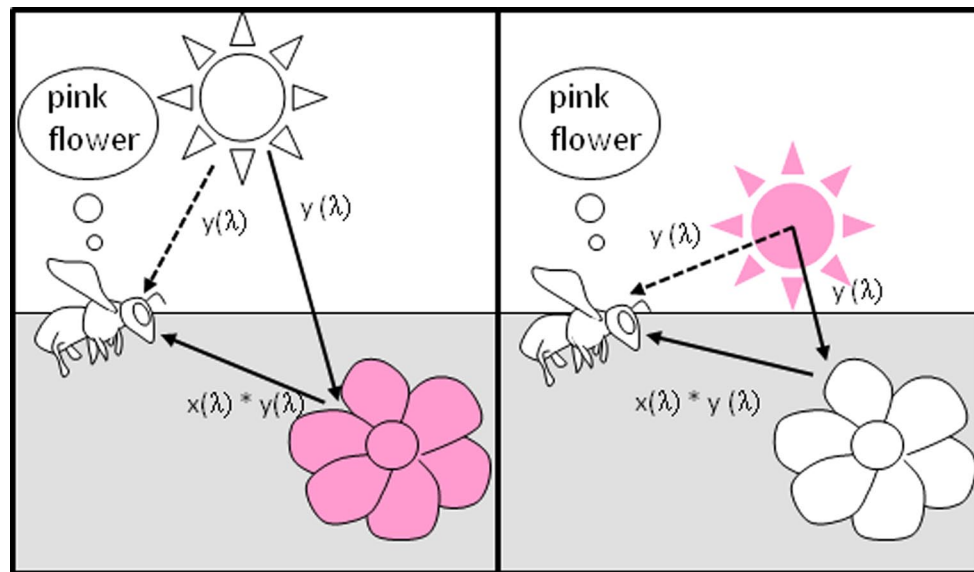


Fig. 2 Ambiguity in identifying target colour independently of spectral content of illumination. The light that reaches the eye from any object is a function of that object's reflectance $x(\lambda)$ and the illuminant $y(\lambda)$. Thus an impression of 'pink', for example, could in principle be generated by a pink flower under white light or a white flower under pink illumination (such as occurs at sunset—see *right panel*)—

—unless the visual system separately evaluates spectral content from dorsal eye regions (looking at the illuminant) and ventral eye regions (looking at flowers against their backdrop) and uses the former for an assessment of the latter. There is behavioural and neurophysiological evidence that this might indeed be the case (Ehmer and Gronenberg 2002; Lotto and Chittka 2005; Dyer 2006)

object colour reflectance independent of the illumination y (Maloney and Wandall 1986). This is not a trivial problem. How do biological systems achieve colour constancy, and which mechanisms work best for realistic and natural ranges of illumination changes?

Pollinating insects provide a powerful model system for studying the mechanisms and adaptive significance of colour vision because they exist in a mutual relationship with flowering plants that signal reward by colour (Menzel and

Backhaus 1991; Gumbert et al. 1999). Generalist flower visitors such as many species of bees and butterflies use their colour vision to detect flowers, to memorise the colours and patterns of rewarding flowers and discriminate against less rewarding flowers (Chittka and Menzel 1992). This interaction governs the life of the flower-visiting insect, and accuracy of colour choice is crucial for foraging success and therefore biological fitness (Faruq et al. 2013). Karl von Frisch (1914) clearly realised the biological

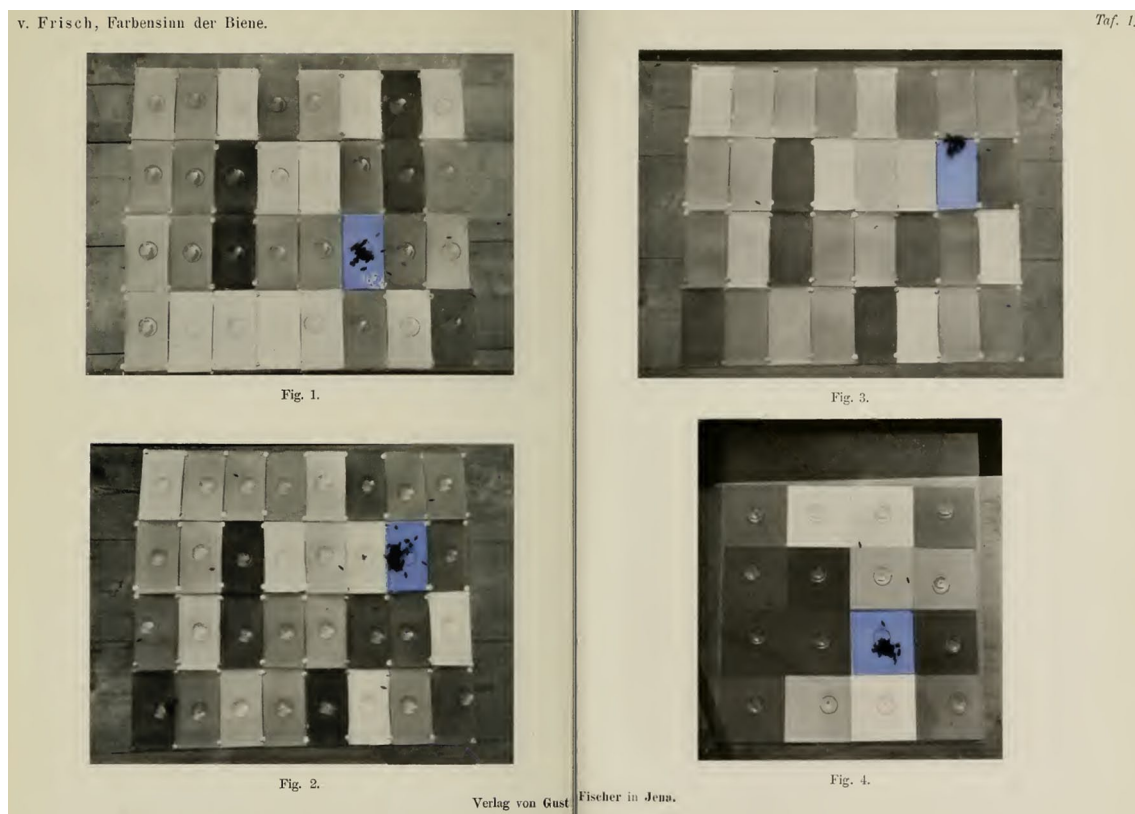


Fig. 3 Setup of Karl von Frisch's pioneering experiments to demonstrate that bees could identify colour targets independently of reflectance intensity (von Frisch 1914). Bees had been rewarded with sucrose solution from a small glass dish on 'blue' and subsequently had to pick the *blue square* from a range of shades of grey, and independently of target location. To ensure that chemosensory cues from dyes used for the *blue* and *grey* targets could not be used, the entire

arrangement was covered with glass (*bottom right*). A cluster of bees can be seen on the correct target in all panels. Note that, unusually for the time, the figure is actually in colour, using a special printing technique (von Frisch 1914). Modified versions of this design have been employed for various demonstrations of colour constancy in bees. Source: von Frisch (1914), with permission from Elsevier

relationship between flower colour and insect colour vision a century ago. Indeed the recognition of the importance of colour constancy in the identification of flower colour is sometimes attributed to von Frisch (Menzel and Backhaus 1991), although the authors of this article could not trace the source of this argument to the cited paper (von Frisch 1914). Nonetheless, we will see that many of the tests that have been employed to explore colour constancy in insects were in fact modifications of Karl von Frisch's design to explore colour vision in honeybees. In his 1914 publication, bees were given a sugar solution reward in a small glass bowl on a blue rectangular or square card (Fig. 3). Bees successfully located this target from within an array of equally sized rectangles or squares in various shades of grey, demonstrating the bees were able to locate the target based on spectral cues alone and independently of intensity and spatial position. This classic design has been modified in various ways to demonstrate that target colours can also be identified independently of the spectral quality of the illumination.

Our review focuses on bees, but studies on other insect species are mentioned where appropriate. Honeybees and bumblebees, the most thoroughly explored insect models of colour vision and colour constancy, are typical in terms of their photoreceptor equipment across the diversity found in bee pollinators. Like humans, most species of bees are trichromatic (Menzel and Backhaus 1991; Chittka 1996). A crucial difference between human and bee colour vision is that the latter possess a UV receptor with a peak sensitivity (λ_{\max}) near 340 nm, in addition to blue (λ_{\max} ~435 nm) and green (λ_{\max} ~540 nm) receptors (Menzel and Backhaus 1991; Peitsch et al. 1992). Most species of bees have no red receptors (Briscoe and Chittka 2001).

While early musings about colour constancy viewed the capacity as an essential component of colour vision (von Holst 1957; Neumeyer 1991), we review the evidence that colour constancy in insects is neither perfect nor necessary for colour vision to function (Dyer and Chittka 2004; Skorupski and Chittka 2011). Nonetheless, colour constancy provides useful improvements for identifying

natural colours under conditions of changing illumination, and we quantify these improvements both from a modelling as well as an empirical perspective (Werner et al. 1988; Dyer and Chittka 2004; Faruq et al. 2013). We measure the extent to which a visual model with colour constancy outperforms a colour vision model with no colour constancy in foraging success, and we evaluate the biological usefulness of various computational colour constancy algorithms for foraging under conditions of changing illumination (Faruq et al. 2013). We discuss the possible receptor/neural mechanisms underpinning the colour constancy in insects.

We explore the extent to which bees ‘discount’ the illuminant while calibrating their colour vision (von Helmholtz 1896; von Holst 1957), and conclude that bees make adaptive use both of the spectral composition of illuminating light (Lotto and Chittka 2005; Dyer 2006), as well as integrating information from across visual scenes (Werner et al. 1988). However, the quality of colour constancy varies in different areas of colour space (Neumeyer 1980; Werner et al. 1988; Dyer and Chittka 2004). We evaluate bees’ strategies in dealing with the colour identification difficulties that come with imperfections of colour constancy, for example by minimising transition between differently illuminated patches in a visual scene (Arnold and Chittka 2012). We include an exploration of the implications of (imperfect) colour constancy for the optimisation of the colour signals that have evolved to address (and be recognised by) the colour vision of bees, i.e. the flowers of angiosperm plants (Dyer and Chittka 2004).

Behavioural demonstrations of colour constancy in insects

The first experimental explorations of colour constancy in an insect, the honeybee *Apis mellifera*, were performed by Mazokhin-Porshnyakov (1966). Like in von Frisch’s (1914) experiments, bees had to pick the colour target from within a checkerboard display of alternatives. In Mazokhin-Porshnyakov’s test, the target was yellow and had to be picked from within a range of different shades of green (Fig. 4). The bees correctly located the yellow target, no matter if the illumination was direct sunlight or blue sky only (Mazokhin-Porshnyakov 1966). However, while this demonstrates correct target identification in conditions of changing illumination, it is not a test of constant *perception* of colour. Even if the yellow target might have changed appearance under blue light relative to direct sunlight conditions, so long as it remained more similar to the training colours, the bees could have solved the problem by simple generalisation from the training colour to the most similar colour presented after the illumination change. This of course applies equally to many other tests of animal colour constancy.

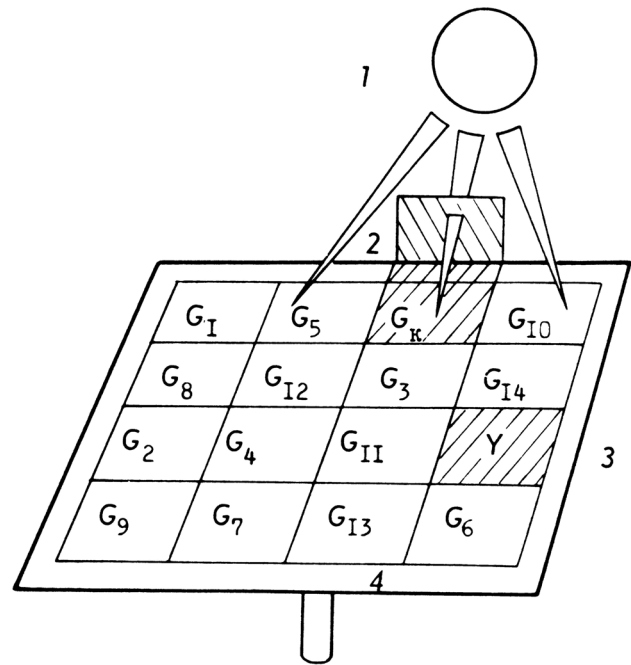


Fig. 4 Setup in which bees were tasked with disentangling object reflectance from illumination colour. This experimental paradigm, used by Mazokhin-Porshnyakov (1969) for exploring colour constancy is visibly inspired by Karl von Frisch’s (1914) pioneering test to explore colour learning in bees (Fig. 3). The setup was illuminated by direct sunlight (1). Light passed through a yellow filter (2) to illuminate a square of grey paper. Fifteen other squares were presented on a table (3) that could be rotated to prevent bees from spatial learning. One of these was the rewarding yellow target (Y) and the other 14 were various shades of grey. Even though light reflected from the grey square illuminated through a yellow filter had the same spectral composition as the yellow paper under direct sunlight, bees preferred the latter. Source: Fig. 126 from (Mazokhin-Porshnyakov 1969). Reproduced with permission from Springer Verlag

In another interesting experiment by the same author, bees were trained to select a yellow target from among various shades of grey, and were subsequently given a choice between this yellow target under direct sunlight, or a grey target illuminated through a yellow filter (Mazokhin-Porshnyakov 1969). Even though the spectrum of the light that reached the eye from these two surfaces indicated ‘yellowness’ in both cases, bees correctly located the yellow (not grey) target, showing that bees were able to disentangle surface reflection from illumination as sources of object appearance (Mazokhin-Porshnyakov 1969).

Neumeyer (1981) investigated colour constancy more specifically in the context of chromatic adaptation; to that end, she trained honeybees to recognise one of nine differently coloured papers (blue and yellow), whose illumination (projector light) could be altered in controlled ways. The results showed that most experimental illumination changes were well compensated by the bees, although a few changes were only partially compensated, as indicated

by a significant change in choice behaviour to the range of colours made available. Similar colour constancy demonstrations are also available for two species of hawkmoths, i.e. the nocturnal *Deilephila elpenor* and the diurnal *Macroglossum stellatarum* (Balkenius and Kelber 2004).

Werner et al. (1988) and Werner (1990) investigated colour constancy performance of the honeybee in detail, aiming specifically at the efficiency of colour constancy and the nature of the underlying processes. An experimental arrangement was used that merged Karl von Frisch's checkerboard experiment and the 'Mondrian' design developed by Edwin Land, a pioneer of the exploration of colour constancy in human vision. Land's 'Mondrians', named after similar paintings of Dutch painter Piet Mondrian (1872–1944), were complex, multicoloured patterns of rectangular papers, illuminated by three independently controlled projector lamps (green, red and blue). By changing the relative intensities from the three lamps and measuring the light reflected from each of the coloured papers, Land demonstrated that human colour perception does not primarily depend on the local light flux that reaches the eye from each patch but rather on an integration of spectral information across the scene, providing for colour constancy possibly by using contrast ratios (Land and McCann 1971; Land 1977).

Werner's 'Bee-Mondrian' consisted of 13 coloured glass filters, which were arranged in a 5×5 square checkerboard pattern, with black squares filling the spaces between the coloured filters (Fig. 5a). The display was illuminated from behind by a mixture short-, middle-, and long-wavelength light (UV, blue, green), approximately matching the spectral sensitivity of the honeybee's photoreceptors. In contrast to previous experiments, this allowed controlled variation of the illumination of all spectral domains of the bees' visual system, including the UV. The black background in these experiments meant that bees could not simply solve a colour constancy task by measuring the local contrast of target and alternative colours against the background: the reflectance of black does not change when the illumination is altered.

The visual stimuli were fully controlled by conducting the experiments in a room exclusively illuminated by light from the Mondrian display. As in Land's experiments, the task of the subjects was to recognise the target (i.e. training) plate after a change in illumination had occurred (Land 1977). These illumination changes were specifically chosen so that, after changing the illumination, one of the alternative plates (henceforth referred to as the 'matching plate') matched exactly the physical light flux of the training plate under standard illumination; in colorimetric terms (assuming a non-changing state of adaptation and no colour constancy) this would mean that the colour locus of the matching plate would shift exactly to the learned

colour locus, whereas the colour locus of the training plate would shift away from the learned colour locus (Fig. 5b). Therefore, without colour constancy, the bees should now choose the matching plate instead of the training plate; in the case of perfect constancy, the training plate would be preferred with the same frequency as under standard condition; imperfect colour constancy would be indicated by a decrease of choices for the training plate and at the same time an increase of choices for the matching plate. Colour constancy was tested for colours in various regions of the bee colour space. For most combinations of colours and illumination changes, it was found that bees recognised the training plate with high accuracy after an illumination change. This behaviour is consistent with colour constancy, although not all illumination changes were compensated equally well. A Mondrian design has also been used to demonstrate colour constancy in the swallowtail butterfly *Papilio xuthus*, in this case using reflecting colour stimuli rather than filters illuminated from behind (Kinoshita and Arikawa 2000).

Colour constancy in patchy illumination

Using an experimental arrangement similar to the Bee-Mondrian described above, and again drawing inspiration from Karl von Frisch's checkerboard design, Lotto and Wicklein (2005) examined colour constancy in bumble bees (*Bombus terrestris*). Their multicoloured matrix was divided into four panels ('patches') each of which was governed by a different illumination. Bees were trained to recognise a target colour plate, which was present in each of the panels and therefore seen by the bees in four different illuminations. It was found that bees discriminated the target plates successfully, and irrespective of the prevailing illumination; they continued to do so even if they had not previously experienced one of the illuminations. The authors concluded that bees use the relationship between the target and its background to uncover the colour of the target, irrespective of the illuminant (Lotto and Wicklein 2005).

Under natural conditions, such patchy illumination presents foraging animals with a challenge, as the targets being sought may appear to vary in colour depending on the illumination, compromising target identification. In one experiment, it was explored how the bumblebee *Bombus terrestris* copes with colour discrimination under patchy illumination (Arnold and Chittka 2012). Light patches varied between unobscured daylight and leaf shade, such as a bee might encounter in and around woodland. Bees were better at discriminating a pair of similar colours under simulated unobscured daylight illumination than when foraging under leaf-shade illumination. Under patchy illumination,

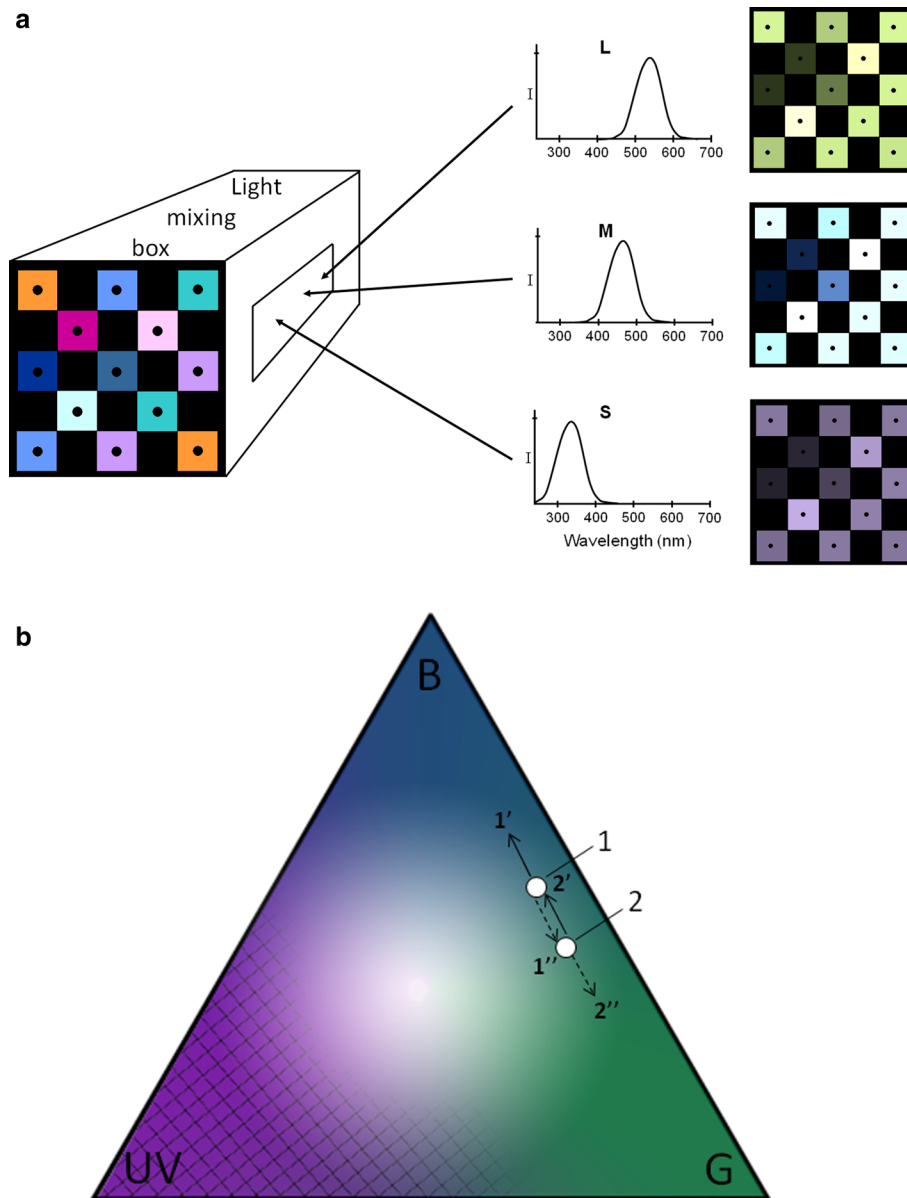


Fig. 5 A test of colour constancy in honeybees (Werner et al. 1988). **a** The 'Mondrian' display consisted of a checkerboard of 13 transparent glass filters (colours on left show their approximate appearance to a human observer under white light); illumination was provided from behind by a mixture of three light sources (with intensity peaks in the UV, blue and green), whose spectral radiance (middle column) corresponds roughly to spectral sensitivity functions of the three types of photoreceptors of the honeybee with spectral sensitivity peaks for UV (λ_{\max} at 344 nm, blue (λ_{\max} = 436 nm) and green (λ_{\max} = 544 nm) receptors (Peitsch et al. 1992). The column on the right shows the approximate appearance for human observers when the display is only illuminated by a single one of the three light sources. Bees approached the Mondrian display from the front. **b** An example of a pair of colour loci and their shifts in the colour triangle under the assumption of no colour constancy. The colour triangle is a stimulus space in which colour loci are determined by relative photoreceptor quantum catches. If one assumes, for modelling purposes, that the

photoreceptor adaptation states do not change when the illumination changes, the colour loci of particular filters (see **a**) can be turned into one another by changing the illumination in specific ways. Colour loci of two filters, 1 and 2 are shown in the blue–green area of the colour triangle, under white light (white dots). Following an illumination change towards blue, the colour loci of both filters (1 and 2) shift towards blue in such a way that the new locus of colour 2 (i.e. 2') becomes identical with 1 (whereas 1 moves further up and becomes 1'). Conversely, under more green light, both colour loci shift towards green so that the former 1 becomes 1'' (which is identical with 2) and 2 becomes 2''. Thus bees trained to filter 1 under white light should choose filter 2 under bluish light, and bees trained to filter 2 under white light should choose filter 1 under greenish light, if they had no colour constancy. However, bees were able to recognise the training filter well under most illumination changes, demonstrating colour constancy (Werner et al. 1988; Werner 1990)

colour discrimination performance was substantially poorer than in homogenous light. Accordingly, bees with prior experience of simulated daylight but not leaf-shade illumination initially preferred to forage in simulated daylight, whereas bees with prior experience of both illuminants did not exhibit this preference. Bees also switched between illuminants less than expected by chance. This means that bees prefer illumination conditions with which they are familiar, and in which rewarding flower colours are easily distinguishable from unrewarding ones. It thus appears that bees use adaptive spatial foraging strategies to cope with the imperfections of colour constancy in conditions of patchy illumination (Arnold and Chittka 2012).

Von Kries receptor adaptation and colour constancy

A simple way of calibrating the visual system in responses to the changes in the spectral content in the illumination is photoreceptor adaptation. Most biological receptors increase their sensitivity in cases where overall levels of stimulation are low, and decrease sensitivity when stimulation is high. Von Kries (1905) suggested that the sensitivity of a photoreceptor is scaled in line with the overall intensity of the light in the receptor's spectral domain. This self-shunting of receptors ensures that receptors can meaningfully code information over intensity ranges of several logarithmic units (Laughlin 1989).

To the extent that different spectral receptors can adjust their sensitivity independently of each other, such receptor adaptation can also be considered one of several possible mechanisms in achieving colour constancy. As a result of photoreceptor adaptation, and the fact that ambient light conditions are usually depauperate in the UV, the UV receptor in bees has been empirically shown to be up to 16 times more sensitive than a green receptor under some conditions (von Helversen 1972). Such adaptation can be modelled by a multiplicative scaling of receptor sensitivity, by applying the coefficient rule of von Kries (1905), as suggested by Ives (1912); see also Brill (1995) for human colour constancy. One way to model receptor adaptation using a von Kries-type response of the photoreceptors, is to assume that a half-maximal response is generated when receptors view the adaptation background (Laughlin 1989; Chittka et al. 1992).

Von Kries photoreceptor adaptation provides a simple means to compensate for spectral changes in illumination, using inbuilt receptor properties (Laughlin 1989). It has no computational demands for integration of information from across the visual field, integration of spectral cues from overhead light with light reflected from visual scenes, or learnt information on how colours are likely to shift in familiar types of lighting conditions. Yet it has appreciable

benefits for colour constancy. In modelling studies where bee colour vision without colour constancy was simulated by keeping the adaptation states constant under changes of illumination, it was found that the level of perceptual colour shift was substantially larger when the receptors did not adapt to changes of light than when they did using von Kries receptor adaptation (Dyer 1998; Faruq et al. 2013). As noted by Worthey and Brill (1986), the success of von Kries adaptation critically depends on the overlap between the spectral sensitivity functions of the receptors (see also Osorio et al. 1997; Dyer 1999). Predictions can be made about deviations from perfect colour constancy in various parts of colour space (Dyer 1999; Dyer and Chittka 2004) and these correlate, to some extent, with experimental data for illumination constancy (Neumeyer 1981) as well as relational constancy in bees (Dyer and Chittka 2004); see also Balkenius and Kelber (2004) for hawkmoths.

Since photoreceptors do not convey any information about their adaptation states to the brain, the animal has no direct access to the quality of illumination that might have produced an adjustment of the receptors' adaptation states. One view about von Kries-based colour constancy is therefore that the visual system might effectively 'discount' the illuminant by adapting to the average spectral quality of a scene (von Helmholtz 1896; von Holst 1957). In this view, information about the spectral composition of the illumination might be lost in its entirety. However, there is a valuable information in natural illumination, for example about weather conditions as well as time of day (Chittka et al. 2013), and a visual system would thus do well not to eliminate such information entirely.

In one study, the question of whether bees 'discount' the illumination in colour choice experiments was essentially turned on its head by training bees to use the illumination colour as a contextual cue in a colour choice experiment (Lotto and Chittka 2005). In this test, rather than choosing *the same* colour target despite changes in illumination (the classical colour constancy paradigm), bumblebees (*Bombus terrestris*) were here asked to choose *different* (indeed opposite) colours depending on the lighting conditions. Had bees fully 'cancelled out' the spectral quality of the light, they should not have been able to solve this task. However, bees were able to use both the intensity as well as the chromaticity of the illuminating light as a cue to choosing the correct colour (Lotto and Chittka 2005). One possibility to explain these results might be that adaptation to the illuminating overhead light is incomplete, and thus some information about its spectral quality might be used directly as a contextual cue to choosing the correct target colour (Dyer 2006). However, in experiments in which the overhead illumination was the same, but target and background colour were made consistent or inconsistent with shifts that could have been produced by change in illumination

colour, bees were highly sensitive to the contrast between target and background, showing they did not simply use the spectral distribution of the illuminant to solve ambiguous colour discrimination tasks (Lotto and Chittka 2005).

Neumeyer (1981) also analysed honeybees' choice behaviour as a function of test duration and found that the colour constancy response after an illumination change was immediate and the percentage of correct choice remained unchanged throughout the 2-min tests. This is important because it contrasts with the slow time course of chromatic adaptation which was recorded in a comparable test setting (Neumeyer 1981). Neumeyer concluded that colour constancy in bees cannot be mediated by adaptation alone and instead is mediated by an interplay of adaptation and spatial contrast mechanisms.

Calculating colour loci in bee colour space, given a particular change in illumination and an assumption of von Kries photoreceptor adaptation, is straightforward, since it involves simply the calculation of an integral between an illumination spectrum, the spectral sensitivity of the (adapted) photoreceptor, and stimulus reflectance (Rushton 1972; Chittka et al. 1992). Even given the (optimistic) assumption that photoreceptors adapt so fully to the light reflected from the average background that the background appears grey, the colour constancy produced by such adaptation is far from perfect (Neumeyer 1981; Dyer 1999), and the predicted degree of colour constancy is poorer where there are larger differences in the illuminants (Dyer 1999; Faruq et al. 2013). For some stimuli, colour shifts have been reported to be especially large in shorter than in long-wavelength regions, which appears to be mirrored by some experimental evidence for relatively poor colour constancy in the UV (Dyer and Chittka 2004). However, the predicted shift depends strongly on the particular type of the object reflectance and the illumination; for typical flower colours, Faruq et al. (2013) found particularly large shifts in the blue–green, but not the UV region of bee colour space (Fig. 6). Thus, the relative rarity of pure UV coloured flowers cannot be easily explained by poor colour constancy in that spectral domain, as had been suggested earlier by Dyer and Chittka (2004). Thus, while von Kries receptor adaptation provides a useful peripheral calibration of the visual system in the face of illumination changes, it provides neither perfect colour constancy nor can it explain the empirical results on insect colour constancy fully. Indeed, it has been argued that colour constancy should not be perfect to allow the viewer to identify changes of the illumination in the environment (Skorupski and Chittka 2011; Chittka et al. 2013).

Depending on the success of the compensation provided by photoreceptor adaptation, illumination changes may result in relative shifts of colour loci, affecting their relative positions in colour space. Such *relational colour*

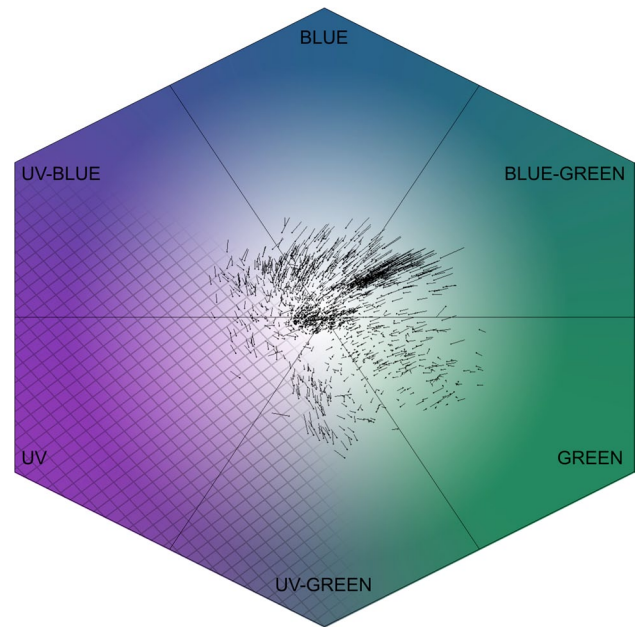


Fig. 6 Colour loci of 1,572 flower colours in a hexagonal bee colour space, and colour shift under an illumination change, assuming von Kries receptor adaptation. In this colour space, angular position (as measured from the *centre*, the uncoloured point) corresponds to bee-subjective hue (so that colour loci in the *top* corner indicate bee *blue*, *top right* corner—bee *blue–green*, *bottom right* corner—bee *green*, and so forth). The distance between two colour loci corresponds to their discriminability. Large colour shifts might corrupt the identification of flower species by colour. The distance from the *centre* to any of the corners is 1, and *circles* indicate distances from the *centre* at steps of 0.1. *Straight lines* represent colour shift from daylight normfunction D65 [dot end; (Wyszecki and Stiles 1982)] to forest shade lighting [tip end; (Endler 1993)] for each flower plotted, assuming von Kries receptor adaptation and no further correction. The *line* from the dot to tip represents the perceptual colour shift of flowers under D65 daylight to forest shade lighting. Note that shifts in different areas of colour space occur predominantly in different directions. Shifts appear especially pronounced in the blue–green and UV–green areas of colour space, and less so in the green and UV–blue regions (Faruq et al. 2013)

constancy allows for reliable stimulus identification and discrimination under a variety of illuminations (Foster and Nascimento 1994; Nascimento and Foster 1997). Dyer and Chittka (2004) explored this phenomenon in bees and found that indeed, colour discrimination behaviour under changes in illumination is consistent with predictions of relational colour constancy.

Post-receptoral mechanisms underpinning colour constancy

There is considerable evidence that more central nervous processes (i.e. beyond adaptation in the retina) are also involved in colour constancy. For humans, these have been

explored in the retinex theory developed by Edwin Land (1977, 1986; Land and McCann 1971). Retinex here combines elements of the words *retina* and *cortex*, highlighting the importance of both peripheral as well as cortical mechanisms in primate colour constancy. Indeed in humans and other primates, colour constancy results from a series of processing steps which start in the retina and continue in the primary visual cortex and temporal visual pathways (for reviews see Gegenfurtner and Kiper 2003; Werner et al. 2005). In insects, too, there is evidence that more central nervous processing might also be involved in maintaining colour constancy in bees (Werner et al. 1988; Lotto and Wickelmaier 2005). Numerous variants of the retinex theory have been developed for humans (Hurlbert 1998; Ebner 2007); in this section, we discuss how post-retinal processes are also involved in colour constancy in bees.

A simple way to identify a target colour after an illumination shift is to use the local contrast the target makes with its backdrop (unless the background is black, which is, however, rare under natural conditions). Spatial contrast contributes to colour constancy because the resulting signals represent ratios, which tend to be invariant under changes of daylight illumination (Foster and Nascimento 1994). A strategy of encoding contrasts is therefore at the heart of many models for colour constancy. Various forms of retinex algorithms, for example, employ the computation of ratios within each chromatic channel and their subsequent integration across the entire visual field (Land and McCann 1971); for an application to honeybees, see Werner et al. (1988).

Contrast signals can be established at different stages of a visual system, via processes such as lateral inhibition (Neumeyer 1998). Neuronal interactions mediating lateral inhibition have indeed been identified in insects, for example in the first optic ganglion, the lamina (Ribi 1975; Laughlin 1981; de Souza et al. 1992). In particular, the contrast encoding characteristics of the fly's large monopolar cells have been connected to normalisation processes such as histogram equalisation (Laughlin 1981), a technique used in digital image processing for optimising image contrast (Gonzalez and Wintz 1977). Simultaneous colour contrast results in the well-known observation that the perceived colour of a target can depend on its immediate surround, so that, for example a grey target, when it is viewed against a yellow backdrop, may be perceived as bluish (the complementary colour of yellow) (Neumeyer 1998). Indeed, behavioural effects of simultaneous colour contrast are well established in bees (Kühn 1927; Neumeyer 1980; Lunau et al. 1996) and flies (Fischbach 1979). The relation between target and background was also found to be a significant factor for colour constancy in Lotto and Wickelmaier's experiments (2005). Neumeyer (1998) views simultaneous colour contrast as a by-product of the mechanisms

mediating colour constancy, but it is likely the other way round: mechanisms for lateral inhibition are ubiquitous in the nervous system (Chittka and Niven 2009; Skorupski and Chittka 2011), and indeed exist in single-celled organisms (Wolff et al. 1986). Thus it is likely that the behavioural need for colour constancy simply co-opted lateral inhibition mechanisms or general-purpose neural decorrelation mechanisms that predate the evolution of colour vision (Skorupski and Chittka 2011).

In addition, the phenomenon of successive (temporal) colour contrast is well established in numerous insects, e.g. bees (Neumeyer 1981), aphids (Moericke 1950; Döring and Chittka 2007) and flies (Fischbach 1979). Bees appear to employ a temporal strategy for encoding contrast, which is supported by the particular temporal response patterns of colour-coding neurons in the 2nd and 3rd optic ganglion, the medulla and lobula (Riehle 1981; Yang et al. 2004). While scanning across the multicolour array of a visual scene, these neurons could potentially encode temporal local contrast.

A significant role for more long-distance integration of spectral information across the visual scene has been implicated by Werner et al. (1988)'s Mondrian experiments on honeybees. Here, colour plates were separated by black patches (like in a checkerboard pattern), and this meant that local contrast could not have supported colour constancy, since the light flux from the black fields did not change when the illumination changed. Furthermore, it was found that colour constancy was adversely affected by a reduction in the number of colour plates, but worked more successfully if additional colour plates were presented in the periphery of the visual field, even if separated by 100° visual angle from the target plate (Werner 1990).

Various retinex algorithms employ the computation of ratios within each chromatic channel and their subsequent integration across the entire visual field. This is achieved by either sequential integration of local contrasts (Land 1986) or using a large-scale spatial average as a reference, and to assume that this average is neutral ('grey world assumption') (Helson 1964; Buchsbaum 1980; Land 1986; Ebner 2007). An alternative retinex computation is the 'white patch algorithm', which works by identifying the brightest patch in a visual scene, and to assume that this is white, and to calibrate the visual system accordingly (Land and McCann 1971; Ebner 2007).

For either computation, the underlying neuronal processes would have to employ spatially extensive operations. Colour-coding neurons with wide-field input have been identified at several stages of the visual pathway of honeybees and bumblebees, i.e. in the medulla (Kien and Menzel 1977; Hertel 1980; Hertel and Maronde 1987; Paulk et al. 2009b), lobula (Hertel 1980; Riehle 1981; Yang et al. 2004) and the central and lateral protocerebrum (Paulk

et al. 2009a; Mota et al. 2013). It is noteworthy that the majority of colour-coding neurons that have been identified in bees have exceedingly large receptive fields, and often receive input from entire eye regions, and sometimes the entire visual field of an eye, or indeed wide-field input from both eyes (Hertel 1980). In principle, such neurons might thus be well suited to integrate spectral information from across the visual scene, and for a ‘grey world’ calibration. However, a direct neurophysiological correlate for colour constancy has not been identified. Possible candidates might have a combined spatial and chromatic antagonism in their receptive fields, comparable to that of double opponent cells of goldfish retina (Daw 1968) or primate visual cortex (Michael 1978). Such neurons might support colour constancy because any changes in the stimulation of their receptive field centre would potentially be cancelled out by corresponding changes in the stimulation of the surround. In bees, colour-coding neurons in the optic lobes and the protocerebrum exhibit a large range of complex combinations of spatio/chromatic and temporal responses (Kien and Menzel 1977; Hertel 1980), but not ‘tidy’ centre-surround organisations. The functional role of such neurons in the processing of chromatic information, including colour constancy, remains poorly understood. It is noteworthy that retinotopic projections from colour-coding neurons in the visual periphery to centres involved in learning and memory (the mushroom bodies) have not been found altogether (Ehmer and Gronenberg 2002), though there appears to be a coarse segregation between projections from the ventral and dorsal halves of the visual field to the collars of the mushroom bodies (Ehmer and Gronenberg 2002), mediating perhaps the independent assessment of spectral information from the illumination above and the visual scene beneath the flying insect (Dyer 2006).

Modelling the quantitative benefits of various colour constancy algorithms

We have seen that bees do not entirely ‘discount’ the illuminant and indeed the spectral quality of natural illumination holds important information about, for example, weather conditions and time of day (Chittka et al. 2013). Therefore, animals face the challenge of remaining colour constant and yet to also be able to perceive changes to the light (Skorupski and Chittka 2011). While some authors have held that colour constancy needs to be essentially perfect for colour vision to be at all useful (Land 1977), the penalties for departures from perfect colour constancy paid under natural conditions need to be quantified on a case-by-case basis, depending on the actual variation of the illumination, and colours that need to be distinguished (Faruq et al. 2013). The question we ask in this section is

how effective various computational colour constancy algorithms are under biologically relevant, natural conditions.

In a recent modelling study, the quantitative benefits of various colour constancy algorithms were explored using an agent-based model of foraging bees, where agents select flower colour based on reward. Each simulation was based on 100 ‘meadows’ with five randomly selected flower species with empirically determined spectral reflectance properties, and each flower species was associated with realistic distributions of nectar rewards. Simulated foraging bees memorised the colours of flowers that they had experienced as most rewarding, and their task was to discriminate against other flower colours with lower rewards, even in the face of changing illumination conditions. Two classical retinex algorithms in computational colour constancy were applied to the scenes in our experiments. These were (1) the grey-world assumption which is the assumption that the colour components of the scene in average to grey (Helson 1964; Buchsbaum 1980; Land 1986; Ebner 2007); (2) the white patch calibration which uses the most intense region of the scene as a reference point and assumes that this point must be white (Land and McCann 1971; Ebner 2007).

Three benchmark models of vision were used to evaluate the performance of the colour constancy methods in comparison; (1) colour blind bees foraged from all flower species indiscriminately, as if they were members of the same species. Such bees made adaptive spatial foraging movements, but could not choose the most rewarding species by colour. (2) Perfect-colour-constancy bees were modelled as making no mistakes induced by changes in illumination; they experienced no perceptual colour shift, but still made the usual colour discrimination errors based on their ability to discriminate colours, i.e. similar colours were confused with a certain probability, but independently of illumination changes. (3) ‘No-colour-constancy bees’ were simulated by assuming fixed adaptation states for the three colour receptor types, independently of the illumination. Nectar foraging success in the simulated flower meadows was used as a quality indicator of the various algorithms.

Perhaps unsurprisingly, bees with perfect colour constancy performed significantly better than colour blind bees. However, a bee equipped with trichromatic colour vision but no colour constancy performed only ~20 % better than a colour blind bee (relative to a maximum improvement at 100 % for perfect colour constancy). This demonstrates that without a suitable correction mechanism in conditions of changing illumination, colour vision is only of limited value. Interestingly, the improvements provided by simulating various (imperfect) colour constancy mechanisms under such naturalistic conditions, compared with colour blind bees or bees with no colour constancy, were relatively moderate. A simple von Kries photoreceptor adaptation mechanism resulted in a further improvement of

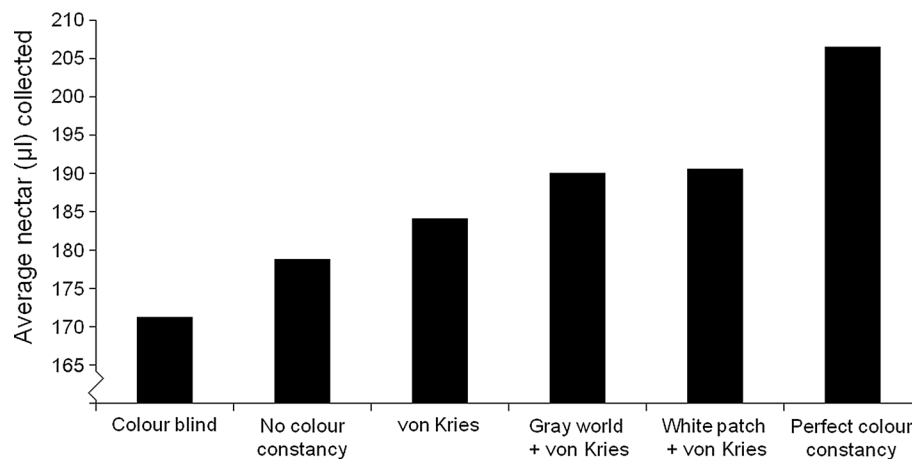


Fig. 7 Modelled foraging performance of bees foraging from coloured flowers in agent-based model, as a function of colour constancy algorithm, and under realistic illumination changes. Success is measured as average nectar collected by a bee agent from various realistic sets of flower species under changes of illumination (for details see Faruq et al. 2013). Because most flower species contain some amount of nectar, even a colour blind bee (that visits all species indiscriminately) collects a reasonable amount of nectar. Only a

moderate improvement is provided by a bee with colour vision but no colour constancy (second column from *left*). Adding a von Kries-type adaptation mechanism results in a substantial enhancement of foraging performance, and combining such a mechanism with white patch or grey-world retinex colour constancy algorithms results in a further improvement (though none of these result in foraging performance near a hypothetical perfect recovery mechanism)

15 % in nectar collection. The most efficient recovery of reflectance in the face of changing illumination was generated by a combination of von Kries photoreceptor adaptation and a white patch calibration closely followed by the grey-world condition (Fig. 7). While these two mechanisms did not convert into significantly different nectar collection performances, they substantially outperformed the colour blind bee, the colour vision system without colour correction, as well the bee equipped with only von Kries receptor adaptation. This shows that there is substantial adaptive value to colour constancy under biologically realistic conditions. However, it is also remarkable that none of the correction mechanisms explored here resulted in performance anywhere near perfect colour constancy, which is still substantially better than the best colour constancy algorithm that we tested (Faruq et al. 2013).

Conclusions and outlook

From numerous independent studies and on several species, it is clear that insects typically cope well with the challenges related to target identification under changing illumination conditions (Werner et al. 1988; Kinoshita and Arikawa 2000; Balkenius and Kelber 2004; Dyer and Chittka 2004). According to some authors, the central function of colour vision is detection of surface spectral reflectance (SSR) of objects in the world; the colour of an object simply is its SSR (Hilbert 1992; Hurlbert 1998; Byrne and Hilbert 2003). This view obviously requires colour

constancy as a central mechanism of colour vision. Since the perceived SSR depends on both the actual SSR and the spectral quality of the illuminating light, it follows that the computation of the actual SSR is only possible if the illuminant can somehow be discounted. Colour vision might then be construed as the output of computations that ‘correct’ the apparent SSR (by discounting the illuminant) to estimate the actual SSR. Given near-perfect colour constancy mechanism, such a system would seem to lead to constant perception of colours, systematically related to real-world SSRs. However, as reviewed above, there is clear evidence, both from modelling and from an empirical perspective, that colour constancy in bees is not perfect (Neumeyer 1981; Werner et al. 1988; Dyer and Chittka 2004; see Jameson and Hurvich 1989 for similar evidence from humans). Furthermore, colour constancy can be impaired in humans with extrastriate cortical lesions, even though such subjects can still name colours and report colour experience (Clarke et al. 1998). This shows that colour constancy can be dissociated from colour experience, at least to some extent, and would appear to be direct evidence against the view that colour constancy is integral to colour experience. The same is likely to apply in other species. Bumblebees, for example, when faced with a colour discrimination task under varying illumination conditions, far from discounting the illuminant, can actually use it as a contextual cue (Lotto and Chittka 2005). On the other hand, some degree of constancy will be inextricably tied to any colour vision system by virtue of adaptational properties of the receptors themselves. Since chromaticity depends on ratios of

photoreceptor signals, adaptation of photoreceptors with sensitivities in spectral regions containing more ambient light can provide a mechanism for maintaining these ratios reasonably constant as spectral illumination conditions change. Such receptor-level mechanisms can explain, at least to some extent, colour constancy under a variety of experimental conditions, in both humans (Zaidi et al. 1997) and insects (Balkenius and Kelber 2004; Dyer and Chittka 2004). Some form of colour constancy will almost certainly be present in any animal with colour vision (Neumeyer 1998; Kelber et al. 2002; Balkenius and Kelber 2004). This is in part due to a basic cellular electrophysiological property: receptors often respond best to changing signals and adapt to static ones. However, this does not mean that colour constancy is a necessary requirement for colour vision (Skorupski and Chittka 2011).

Insects such as bumblebees and some species of Lepidoptera offer outstanding opportunities for exploring the influence of individual experience on colour constancy performance, since they can be raised entirely in controlled laboratory conditions under restricted and controlled lighting conditions, and with fewer ethical concerns than might be the case in vertebrates. It is conceivable that, in addition to hard-wired receptor and more central nervous processing to compensate for changes in illumination, there might also be cognitive aspects to deducing object reflectance (Land 1986; Bloj et al. 1999; Lotto and Chittka 2005; Smithson 2005). For example, humans know from experience that illumination at dusk and dawn can be red-shifted, and that a sheet of papers that appears pink at these times of day might in fact be white, but illuminated with reddish light. In the same vein, it is possible that animals learn what colour shifts of natural objects are contingent with certain (familiar) shifts in lighting conditions. It should be possible to test this by raising insects in laboratory conditions in which target colour shifts are associated with shifts in illumination conditions that are physically impossible under natural conditions, so that, for example, more long-wavelength shifted light is reliable associated with scene reflectance properties shifted to shorter dominant wavelengths. In this view, it should be possible to disentangle hard-wired from cognitive components of colour constancy, and to explore the extent to which animals such as bees might use individual experience to resolve the stimulus ambiguities that come with identifying colour targets, such as flowers, under varied illumination.

Finally, the influence of shape in identifying coloured objects under conditions of changing illumination deserves further attention. Mondrian-type displays are of course designed to eliminate the possibility to identify targets by shape, but under natural conditions, even where colour constancy fails, target shape (such as in flowers) still provides unambiguous cues for target identity (Dyer and Chittka 2004). Moreover, familiar shapes could actually

assist animals in learning the rules of perceived changes that come with familiar illumination shifts of illumination. In the example in the previous paragraph, experience helps us in identifying an object as a sheet of paper (by its shape); knowing that paper is typically white means that we can deduce that a spectral shift in the illuminant has taken place if papers appear in a colour other than white. This paired knowledge of object shape and colour thus allows the deduction of the properties of the illuminant, and identification of other objects by reference. Such a cognitive version of the ‘white patch algorithm’ could in principle work for any colour. If an object is identified by its shape under familiar lighting conditions, this allows the deduction of the nature of an illumination shift even when colour constancy fails, which in turn allows identification of other objects that might appear different as well (Wicklein and Lotto 2006). Some insect species should be useful to explore these possibilities, because of the feasibility to fully control the coloured world to which subjects are exposed during ontogeny.

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