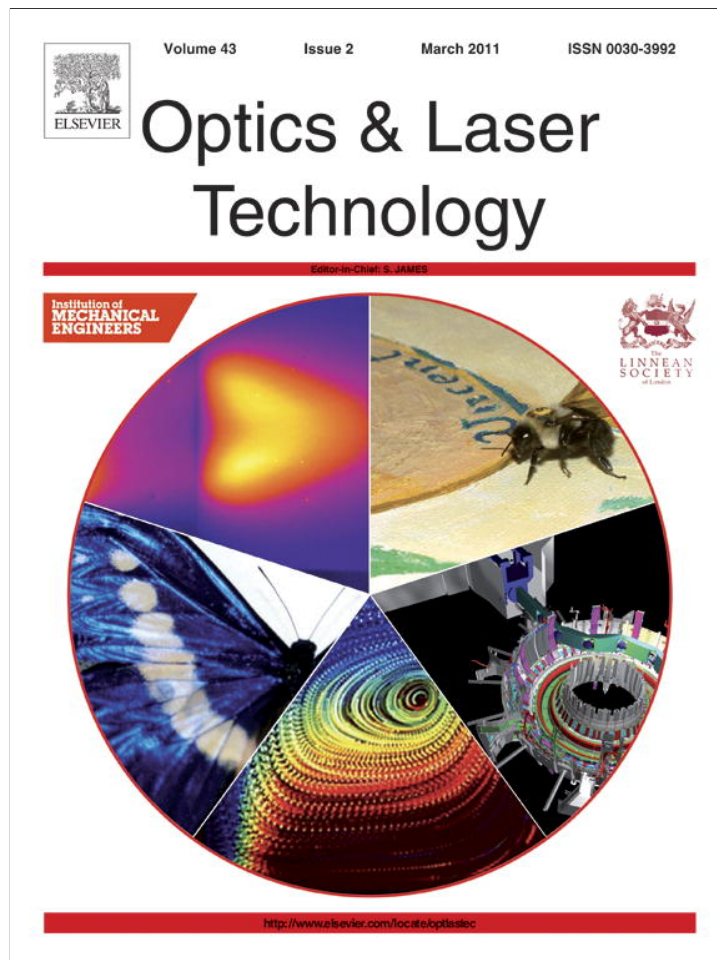


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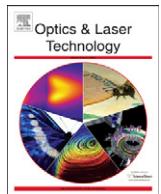
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Is colour cognitive?

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ABSTRACT

In recent years, colour-vision abilities have been rather generously ascribed to various invertebrates and even bacteria. This uncertainty of when to diagnose colour vision stems in part from confusing what colour vision can do with what it is. What colour vision can do is discriminate wavelength independent of intensity. However, if we take this as a definition of what colour vision is, then we might be obliged to conclude that some plants and bacteria have colour vision. Moreover, there is a similar confusion of what are necessary and what are sufficient mechanisms and behavioural abilities for colour vision. To humans, seeing in colour means seeing an image in which objects/lights have chromatic attributes—in contrast to the sensation that we have when viewing monochrome movies, or our experience in dim light when only rod vision is possible. The necessary basic equipment for this is to have at least two types of photoreceptors that differ in spectral sensitivity, and at least one type of spectrally opponent cell to compare the signals from the photoreceptors. Clearly, however, a necessary additional prerequisite for colour vision is to have vision, which entails the identification of shapes, sizes and locations of objects in the world. Thus, if an animal has colour vision, it should see an image in which distinct objects/lights have colour attributes. This distinguishes colour vision from wavelength discrimination, but also from what has historically been called wavelength-specific behaviour: a type of behaviour triggered by fixed configurations of spectral receptor signals; however, we discuss difficulties in diagnosing wavelength-specific behaviour as an indicator of the absence of colour vision. Finally, we discuss whether colour vision, by definition, contains a cognitive dimension for ordering and classifying perceptual experience.

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1. Introduction

What is colour vision? For humans, this question might appear easily answerable—since by introspection, we can appreciate what it means to see colours, and moreover, what it is like *not* to see colour, since at night we become monochromats. But how can we decide whether an animal has the ability to see the world in colour? According to a recent review [1], “an animal has colour vision if it can discriminate two lights of different spectral composition, regardless of their relative intensity” (see also Refs. [2,3]). Our purpose in this essay is to disentangle operational criteria for colour vision from what colour vision really is. There is no doubt that colour vision entails the ability to discriminate the wavelength of light (rather than just its intensity). However, if we use this criterion as a *definition* of colour vision [1], then we might find that plants and even bacteria have colour vision. For example, cyanobacteria have molecular photosystems with different spectral sensitivities [4] and can respond to wavelength independent of intensity via ‘neural network-like’ biochemical interactions

downstream of the photosensors [5]. Shade avoidance in plant growth, in some species, is not strictly driven by light intensity, but guided by the ratio of red to far red light [6]. To complicate matters further, machines that sort fruits by spectral properties (e.g. Ref. [7] – while obviously having no perceptual experience of colour – might behaviourally qualify for colour vision by the criterion above.

Moreover, there is compelling neuropsychological evidence for a dissociation between wavelength discrimination and colour vision in humans. Patients with cerebral achromatopsia (an acquired loss of colour vision due to damage in certain areas of visual association cortex, without damage to early retino-cortical processing) report complete loss of phenomenal colour experience. Such patients can nevertheless detect borders between fields of illumination adjusted for intensity in such a way that wavelength differences provide the only cue for distinguishing the fields [8,9].

There are good reasons to feel uncomfortable with ascribing colour-vision abilities to bacteria and machines, related to the fact that colour vision, perhaps trivially, involves *vision*, and vision is more than sensitivity to light. Vision, or to see, is to “have or use the power of discerning objects with the eyes” [10], which implies that the visual system must form images of objects in the world.

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Rather than attempting to define colour vision in terms of basic operational criteria, we discuss here a cognitive view of colour vision, where colour is used in learning about and classifying regularities in an organism's environment [11,12].

On the other hand, some views of colour vision imply a definition that may be too restrictive. For example, some scholars have viewed colour vision as the ability to detect the invariant physical surface properties of light-reflecting objects in the world [13], in which case colour vision is simply the output of the processes that compute colour constancy (see Section 4), and colour constancy will be an essential defining feature of colour vision [14–16]. Although some degree of colour constancy is a by-product of basic receptor properties, it is not an essential prerequisite of colour vision, since colour vision continues to function even in the face of failures of colour constancy.

2. Spectral sensitivity and wavelength discrimination

The biologically relevant information in light energy may vary along several dimensions, including direction, intensity, wavelength and polarization. Colour vision involves sensitivity to information contained in variations in the spectral content of light. Therefore, wavelength discrimination, defined as sensitivity to changes in the spectral composition of light independent of intensity, is a prerequisite for colour vision.

Wavelength discrimination requires the presence of at least two types of photoreceptor with different (but overlapping) spectral sensitivities. A single photoreceptor is colour blind, since its signal confounds wavelength and intensity (a given signal could result from lower-intensity wavelengths near the peak sensitivity, or higher-intensity wavelength further away from the region of maximal spectral sensitivity); this is the principle of univariance [17]. However, given two photoreceptors with different (but overlapping) spectral sensitivities, most wavelengths will excite the two receptors to different degrees, and the ratios of receptor excitations can provide a colour signal. The term opponent processing, broadly defined, refers to any mechanism that extracts chromatic signals by comparing input channels from different photoreceptors, or different combinations of photoreceptors [2,18–21].

The presence of more than one spectral class of photoreceptor, then, is an essential criterion for colour vision. By this criterion alone the number of candidate organisms for colour vision is rather large, with representatives present from almost all major phyla, including the Cnidaria [22] and most major phyla from the Bilateria [1,2]. However, additional evidence would be required to show that two or more photoreceptor spectral classes are actually involved in wavelength discrimination. It is possible, for example, that they could simply be used to broaden the available sensitivity spectrum; photoreceptor signals could theoretically be pooled rather than compared, maximizing sensitivity to intensity at the expense of wavelength [18,23]. Since anatomical and physiological evidence for opponent processing is sometimes not readily available, it is often inferred from behavioural experiments [21,24,25].

There are many examples of different behavioural responses to different wavelength bands, often termed wavelength-specific behaviour [2], or wavelength-dependent behaviour [18]. Whiteflies, *Trialeurodes vaporariorum*, for example, are strongly attracted to UV–violet light, which induces migratory behaviour, while green–yellow light promotes landing [26]. Could such behaviours occur without wavelength discrimination? In principle, it seems that pathways from photoreceptors to motor pattern generators could be hard-wired in such a way that different behaviours are triggered by different wavebands, without the

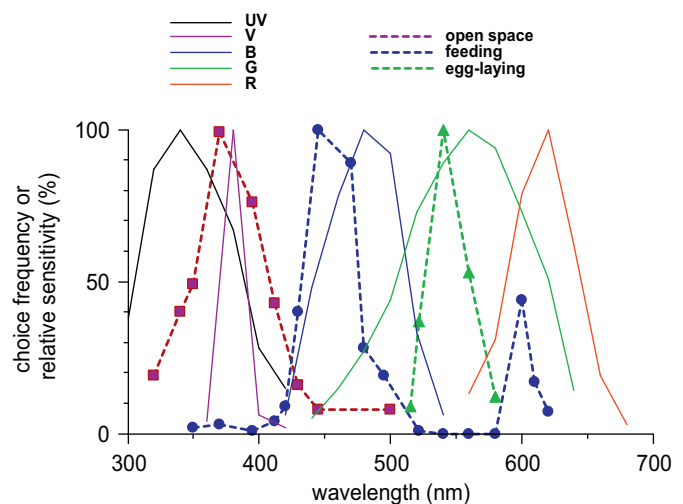


Fig. 1. Wavelength-dependent behaviour in the butterfly *Pieris rapae* cannot be explained in terms of simple driving of behaviour by unique photoreceptor outputs. Action spectra for three stereotyped behavioural responses (dashed lines): the open space reaction (violet), the feeding reaction (blue) and egg-laying (green). Solid lines plot electrophysiological measurements of five classes of photoreceptor, with peak sensitivities around 340 nm (UV), 380 (V), 480 (B), 560 (G) and 620 nm (R). Action spectra re-plotted from Scherer and Kolb [27] photoreceptor spectral sensitivities from Shimohigashi and Tominaga [98].

need to extract a chromatic signal by opponent processing. In such cases, the observed behavioural action spectra would be expected to conform to the sensitivity spectra of the photoreceptors concerned. Often this is not the case: action spectra peaks may, for example, be more narrowly tuned to wavelength than the underlying photoreceptor spectral sensitivities (Fig. 1) [27]. In such cases, the principle of univariance is no longer maintained and interactions between photoreceptors can be inferred [18] (see also Fig. 3).

Male fireflies and glow-worms, for example, are attracted to the green–yellow bioluminescent signals of the females, in the region of 545–575 nm [28]. This has been interpreted as a wavelength-dependent behaviour driven by a single photoreceptor. The peaks of the emission spectra vary with the species-typical time of activity after sunset, with nocturnal species favouring shorter peaks than twilight-active species, and the photoreceptor sensitivity spectra of the males appear to be adaptively tuned to the females' emission spectra [29]. However, in at least one species, male glow-worms' preference for green (555 nm) light is markedly inhibited by adding a weaker blue (485 nm) component to the signal. Males prefer a brighter green light to a dimmer one with the same spectral peak, but will choose the dimmer green light if the brighter one is mixed with the inappropriate blue light (Fig. 2) [30]. This result is compatible with opponent-type processing generating a signal along a blue–green chromatic axis. Comparable results have been obtained from a variety of species. For example, hawkmoths feed predominantly on white, UV absorbing flowers, and feeding behaviour can be elicited in the laboratory by white artificial flowers with broadband reflectance limited to the (human) visible range above 400 nm, but not by artificial flowers (equally white to human eyes) with an additional reflectance component below 400 nm [31]. Similarly, experiments with horseshoe crabs under natural daylight conditions indicate that positive phototaxis, mediated specifically by the median dorsal ocellus, can be elicited by daylight transmitted through a UV-pass filter, but not by the natural broadband (i.e., unfiltered) daylight [32]. All of the examples reviewed above could be interpreted as evidence for

colour vision, if colour vision is defined purely in terms of opponency: inhibitory interactions between the outputs of different spectral classes of receptor. The common theme is that a behaviour reliably elicited by one waveband may be inhibited by the admixture of light from another waveband, even when the intensity of the normally effective waveband is increased [1,25,30,31]. The addition of the inhibiting wavelength has the effect of changing the chromaticity signal: in human terms, male fireflies (for example) will see the “wrong” colour when the normally attractive green light is mixed with blue; increasing the intensity of the green component is irrelevant, since the behaviour

is not purely intensity-driven. Using this technique, it is straightforward to show the modification of unlearned behaviour by chromatic information, which means that some form of wavelength discrimination is present. However, whether we should take this as a demonstration of colour vision is open to question.

First, additional evidence would be required to establish the presence of physiological mechanisms for opponent processing. Where an unlearned behaviour is modified by chromatic information, the possibility exists that the underlying mechanism depends on inhibitory interactions in motor rather than visual systems (Fig. 3). Given the ubiquity of reciprocal inhibition in even the simplest motor systems [33–35], this caution seems warranted; behavioural criteria alone are insufficient to distinguish between the schemes of Fig. 3B and C. Second, even if opponency is involved (meaning in sensory processing rather than indirect effects via reciprocal inhibition in the motor system) the behaviour may still be wavelength-dependent in a rather fixed and inflexible way. Wavelength-dependent behaviour and colour vision may exist in parallel. For example, in many insects, UV light can trigger flight, escape, or ‘open space’ reactions, which are considered examples of wavelength-dependent behaviour [2,3]. However, in many hymenopteran and lepidopteran species where colour vision has been extensively studied, the UV receptor contributes chromaticity signals based on opponent processing [29]. The notion of wavelength-dependent behaviour implies ‘hard-wired’ neural circuitry, linking detected wavelengths to the relevant motor circuits. Theoretically, such circuitry could exist in the absence of any system for perceptual processing of colour, or it could simply by-pass such a system. However, an additional possibility is that the output of a wavelength-discrimination system (based on opponent processing at the post-receptoral level) could be used to drive both hard-wired, relatively inflexible behaviour patterns, but also be used in a colour vision system for

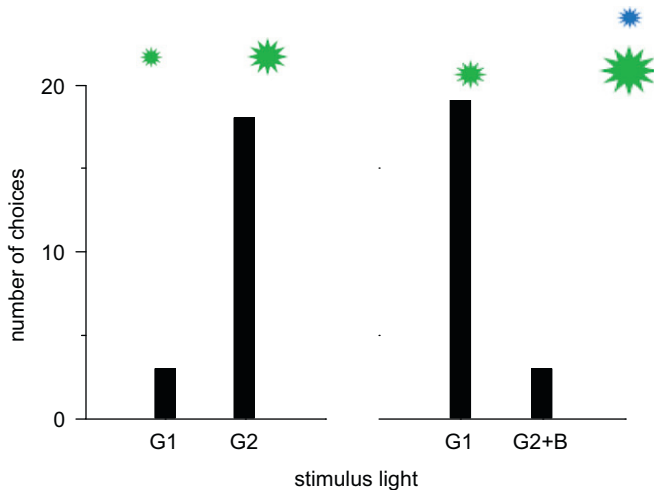


Fig. 2. Colour opponent processing in wavelength-dependent behaviour? Male fireflies (*Lampyris noctiluca*) prefer a brighter (G2) to a dimmer (G1) green light (top), but will choose the dimmer if the brighter light is mixed with blue (G2+B). Data from Ref. [30].

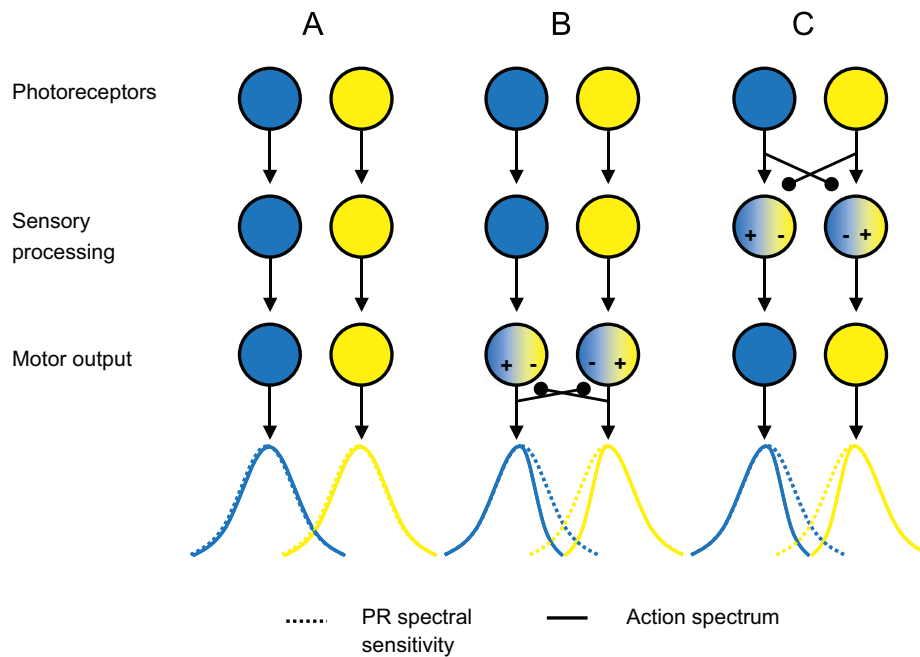


Fig. 3. Simplified schemes to illustrate wavelength-dependent behaviour with and without chromatic interactions. (A) In the simplest case, photoreceptors with peak sensitivities in different wavebands could drive different motor patterns independently. In such cases the behavioural action spectra should be explainable in terms of the sensitivity spectra of the relevant photoreceptors (bottom). (B) In practice, mutual incompatibility between different behavioural outputs and reciprocal inhibitory interactions in motor circuits could lead to opponency-type effects, where light from waveband exerts an inhibitory effect on the behaviour normally evoked by light from another waveband. In such cases the behavioural action spectra would deviate from photoreceptor spectral sensitivities, showing a narrowing in regions of spectral overlap. The behaviour would now be expected to show some chromatic sensitivity, rather than being purely intensity-driven. (C) A chromatic signal is extracted by opponent processing early in the visual system, which is then used to drive different motor output patterns. Such wavelength-dependent behaviours would be expected to show chromatic sensitivity. The chromatic signal could also be used by a cognitive system for colour learning and memory.

learning about regularities in the visual environment and guiding behaviour in a much more flexible manner. Given that detailed evidence concerning structure and function of the relevant neural circuits is often not available, the distinction between wavelength-specific behaviour and colour vision might be difficult and arbitrary in many cases.

A number of physiological responses to colour are known even in human subjects [36]. The difficulty in diagnosing an animal as having “only” wavelength-dependent behaviour (rather than colour vision) becomes clear from the following dramatic example, in which one might erroneously conclude that humans are ‘merely’ exhibiting wavelength-dependent behaviour. In December 1997, when red and blue frames of the popular *Pokemon Pocket Monsters* cartoon, flashed briefly on screen in alternation at 12 Hz, epileptic seizures were induced in 685 Japanese children and some adults (ca. 75% of these had not had seizures ever before). A subsequent study measuring photo-induced abnormalities in the electroencephalogram concluded that the effect was wavelength-dependent (specifically wavelengths in the region of 650 nm), since variations in luminosity at the same frequency were without effect [37]. Note that the apparent “stimulus–response” association, i.e. a certain receptor signal configuration triggering a certain involuntary behaviour pattern, fits the notion of a wavelength-specific behaviour perfectly. Thus, the wavelength-discrimination ability of the human visual system, which undoubtedly is used for colour vision, could also in certain circumstances be used to trigger responses that we would not normally consider under colour vision.

Taken together, these examples indicate that there is a risk of false-negative diagnoses – not awarding colour vision to an animal that indeed has this capacity – when quantifying wavelength-specific behaviours. The absence of flexibility, or trainability, of responses to spectral stimuli might not be conclusive evidence against colour vision. To sum up: if a visual system is capable of disentangling intensity and wavelength, is it by definition a colour vision system? On the basis of the above discussion we would argue that the answer is no. This condition is necessary, but cannot be considered sufficient for colour vision. If an unlearned and relatively unmodifiable behaviour can be manipulated by chromatic intervention, then this is evidence that this condition has been met. However, it is not strictly evidence for colour opponent processing, since the effect could occur via reciprocal inhibition in the motor system. Moreover, even if

opponent mechanisms are implemented just downstream of photoreceptor spectral sampling, this cannot be considered definitive evidence of colour vision, since wavelength discrimination can be involved in releasing or triggering fixed and inflexible behaviours and physiological responses.

3. Is colour cognitive?

In classic experiments by von Frisch, the honeybee’s associative learning ability was used to probe its wavelength-discrimination ability—the claim of colour vision rested on the bees’ ability to learn. Bees that had learned to feed on cards of a particular colour could later select the trained colour from among multiple shades of grey [38]. The assumption here is that a sufficient number of grey cards will provide a range of intensity signals encompassing the intensity reflected from the trained colour, so that at least one card would potentially be confused with the coloured one if discrimination was only based on intensity [1,38].

Is the grey-card experiment a demonstration of colour vision? If an animal can learn a rule, choose colour x , where x is any colour that can be coded within the animal’s wavelength-discrimination capabilities, then in some sense colour is already being abstracted, and available as a variable in a wider cognitive space to guide recognition, learning and categorisation. In other words, colours will be *colours of things*. Bees and wasps, for example, can simultaneously learn colour and shape and respond accordingly [39,40]. Trained to find a reward on a blue but not yellow square, they will reliably choose a blue triangle in transfer tests. However, if confronted with uncoloured (black) stimuli differing in shape (triangle or square) they will then choose the square rather than the triangle [40]. Different colours can also be learned simultaneously and applied in different contexts (for example, according to spatial location [41] and colour itself can be learned as a contextual cue [42–44]).

All of these results require more than just wavelength discrimination. The ability to arbitrarily associate a colour with a reward requires that colours are learned and compared, which in turn implies organizing and categorizing along dimensions of perceptual similarity. Colour itself becomes a perceptual category. This type of evidence inevitably involves training experiments, possibly followed by transfer tests. It may be objected that this criterion will have the effect of making the colour-seeing animals a rather exclusive club. However, the danger of false-negatives can



Fig. 4. What is colour vision? A good way of approaching this question intuitively is by appreciating what it is like not to have colour vision. When viewed in black and white, these three London icons, the mail box, the double-decker bus and the phone booth, share no commonalities. This changes when they are seen in colour (see subsequent page). Photos are by ©Patrick Hudepohl (post box), ©Greg Gayden (London bus), ©Jason Kottke (phone booth); all reproduced with permission.



Fig. 5. When viewed in colour, the post box, the London bus and the phone booth fall into a common category, the category of red objects. In a cognitive definition, colour vision requires seeing coloured images, in which objects have colour attributes, and where an organism is able to disentangle colour from shape, so that colour can be extracted from an object and be applied to arbitrary new objects. Photos are by ©Patrick Hudepohl (post box), ©Greg Gayden (London bus) and ©Jason Kottke (phone booth); all reproduced with permission.

be minimized with mechanistic data concerning photoreceptor spectral sensitivities [18], models enabling predictions of an animal's perceptual space [45] and sufficient ecological information to devise realistic training regimes. In this more restrictive view, colour vision involves the ability to extract colour as an attribute of an object, and to apply this attribute to a differently shaped object (Figs. 4 and 5).

It is important that the experimental paradigm uses shapes that can actually be discriminated by the animal in question—so that an apparent categorisation of objects by colour is not a result of failure to discriminate the objects. It is clear that this requires image-forming eyes [46], and the neuronal “hardware” to analyse images [47]. But what counts as an image? Given the variety of eye designs, the only objective criterion seems to be spatial comparison of sensory signals concerning light in a sensory surface—i.e., a photoreceptor array. Interestingly, this criterion turns out to be the same for both spatial (image formation) and wavelength processing. We will return to this point later, since it has bearing on the evolutionary and developmental origins of colour vision.

4. Colour constancy

If wavelength discrimination is too loose a definition for colour vision, then is it possible that other definitions are too rigid? According to some views, colour constancy is fundamental to colour vision (e.g. [14–16]). The physical property of an object that most influences its colour appearance (at least for non-transparent objects with definable surfaces) is its surface spectral reflectance: a function describing the proportion of light reflected over all wavelengths of the visible spectrum [13,48,49]. This is where the issue of colour constancy arises. Since an object can only reflect light with which it is illuminated, and since the spectrum of the illuminating light can vary quite significantly (in natural daylight, for example, with the time of day, under direct sunlight or in shadow, with weather conditions, and so on) then it follows that the actual spectrum reflected from the object will deviate from its idealized surface spectral reflectance. The fact that colour appearances do not fundamentally change under such shifting illumination conditions is referred to as colour constancy [15,50–52].

Should we require colour constancy as an additional criterion for the possession of colour vision? According to some views a

major function of colour vision is detection of surface spectral reflectance (SSR) of objects in the world (e.g. [13,48,53]). Since the apparent SSR (the perceived reflectance) is inherently ambiguous, as it confounds the actual SSR with the spectral quality of the illuminating light, it follows that the illuminant must somehow be discounted if the ultimate task is to compute the actual SSR. If colour vision is construed in this way, then colour constancy would certainly be integral to colour vision. But then, do imperfections of colour constancy render an animal colour blind (Fig. 6)? It is obvious that human colour constancy is not perfect [54]; in fact it is precisely the imperfection of colour constancy that makes colour vision the deliciously subtle experience it often is (Fig. 6). In bees, likewise, colour constancy is only approximate [50]. This fact alone would seem to argue against any view of the nature of colour vision that depended too heavily on colour constancy. If colour vision is viewed as being constituted in the output of computations that ‘correct’ the apparent SSR (e.g. by discounting the illuminant) in order to estimate the actual SSR, how much failure of colour constancy can we tolerate for an organism to still qualify as having colour vision?

Remarkably, while colour constancy may have a cognitive component in some species [15,43,55], some form of colour constancy will simply come ‘for free’ with colour vision, because of the basic electrophysiological properties of the receptors themselves. Photoreceptors are not static quantum counters; they adapt to steady-state signals and respond best to changing ones. It has been proposed, originally by von Kries [56], that independent adaptation by different spectral photoreceptors could provide an automatic mechanism for discounting the illuminant at least to a certain extent [50]. Since chromaticity depends on the ratios of photoreceptor signals, adaptation (decreasing responsiveness in photoreceptors with sensitivities in spectral domains containing more ambient light) provides a mechanism for maintaining these ratios reasonable constant under varying spectral illumination conditions. Under a variety of experimental conditions, in both humans [57] and insects [50,51] such low-level, early visual mechanisms can explain observed colour constancy to a considerable degree. This means that some form of colour constancy will be present in all animals with colour vision [23,51,52], as a simple by-product of how receptors function—but this should not be mistaken to mean that colour constancy is a necessary criterion for colour vision.

Furthermore, human neuropsychological studies, as well as experiments on nonhuman primates, show that colour constancy



Fig. 6. Is colour constancy a necessary criterion for colour vision? A Colorado landscape photographed at different times of day. Traditional cameras do not have a colour-constancy mechanism, and therefore the colours seen vary even more drastically than perceived by human observers (although the photos largely reflect the photographer's (LC) subjective experience). Notice how the shrub land near the river and the dry grassland beyond seem to have the same shade of green in twilight (top figure), but broad daylight reveals the relative aridity of the grassland (i.e. biologically useful information). Nonetheless, this failure of colour constancy does not mean that the image ceases to be in colour. While colours change in a manner that, by experience, is consistent with the lighting at various times of day, these changes are rarely so drastic under natural conditions that they might compromise object identification.

can be dissociated from colour experience, at least to some extent. Colour constancy can be impaired in humans with extrastriate cortical lesions, even though such subjects can still name colours and report colour experience [58]. This would appear to be direct evidence against the view that a colour-constancy mechanism is integral to colour experience—colour perception is independent of full colour constancy, in primates at least. The same is likely to be true for 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 [43,44].

On the other hand, patients rendered colour blind by cerebral damage (achromatopsia) can still discriminate on the basis of wavelength, and apparently show at least some colour constancy, despite reporting no experience of colour whatsoever [59]. Finally, visual experience of colour has been reported in a few patients who are otherwise almost completely blind (no form vision); at least one such patient also shows severely impaired, but not abolished colour constancy [60]. It seems that colour constancy

can be *degraded*, but no lesion or brain damage has resulted in completely abolished colour constancy while leaving wavelength discrimination and other aspects of vision completely intact. This is to be expected to the extent that basic receptor mechanisms contribute to colour constancy [50].

To sum up, we argue that colour constancy is not a defining feature of colour vision. In part, it is in fact an integral feature—some degree of constancy will be inextricably tied to any colour vision system by virtue of adaptational properties of the receptors themselves (we do not, however, consider this to be an *a priori* requirement: if an animal did happen to have photoreceptors with the properties of static wavelength meters this does not rule out the possibility of colour vision). On the other hand, colour constancy is also at least partly dissociable from colour vision. In those cases where colour constancy fails, surely we do not cease to see colour. In other words, the claim that colour constancy is a defining criterion for colour vision would have to quantify how much colour constancy would be required for an animal to qualify. Since this seems both arbitrary and unrealistic, we do not consider colour constancy, in itself, to be a defining criterion for colour vision.

5. Is colour vision secondary to perceptual constancy?

A variant of the question of whether colour constancy is a necessary component of colour vision is the question of whether colour vision is actually *subservient* to the more general need for perceptual constancy (see also [52,61]). A monochromatic organism (which would have only one spectral receptor class, and therefore be incapable of wavelength discrimination and colour vision) can only detect changes in the intensity of light reflected from objects; in human terms we might be tempted to say that it only sees in black and white. But this is not strictly true: although such an organism would perceive surfaces as having different lightnesses, it is difficult to see how they could have the properties 'black' and 'white' as colours, in the way that black and white are colours to us, unless the illuminant is constant either in time or across the visible spectrum. If it is not constant along either of these axes then, for a monochromat, the 'blackness or 'whiteness' of objects will vary with illumination conditions: a monochromat cannot achieve lightness constancy [61]. For example, unripe green fruit under a clear blue sky close to midday would most likely reflect more light than ripe red fruit viewed under the same conditions (because the illuminating light would be relatively rich in shorter wavelengths). Viewed at sunset, where there would be a shift in the spectral composition of the illuminant towards longer wavelengths, the ripe red fruit might reflect more light than the unripe green [62]. A monochromat, therefore, would be incapable of learning about colours in any way that would be useful in visual object recognition. A rule such as, "choose the black ones" could be correct at noon but incorrect at sunset, unless the organism had some way of compensating for spectral changes in the illuminant. And detection of such spectral changes would require more than one spectral class of photoreceptor, which is, of course, also a prerequisite for colour vision (and colour constancy). An important advantage, therefore, of having more than one spectral class of photoreceptor is that it improves detection of permanent features of objects. It allows changes over time to be disentangled from changes in illumination as opposed to changes in object properties. Colour vision could thus be a by-product of wavelength discrimination in the service of perceptual constancy. More information about the visual world is obtained from sampling the spectral quality of light, as well as its sheer radiant quantity [63]. Wavelength discrimination can make a difference, especially if the overall intensity in a visual scene

varies significantly and perhaps randomly [64], where intensity varies more randomly than wavelength, then colour pops out [65]. So too do objects and states (such as fruit ripeness), if colour is cognitive.

6. Is colour “inevitable”?

Given the advantages for perceptual constancy of a visual system that is at least dichromatic, and given that a dichromatic visual system is the minimal requirement for the most basic form of colour vision, should we then expect (at least rudimentary) colour vision to be the norm among animals that are both cognitive and visual (that is in animals that use vision in learning about and identifying objects)? Is colour vision inevitable, as Jacobs asks [66]? The question suggests itself because a basic requirement for both spatial and colour vision is the same; namely comparison of adjacent neural samples in a spatial array of receptors (Fig. 3). Furthermore, the basic requirements for lightness constancy and wavelength discrimination are inextricably linked (see above). However, the extent to which this extends into colour vision will be a matter of degree, depending on an animal's cognitive and sensory ecology. Wavelength discrimination comes with a cost—a trade-off between spatial and spectral sampling. Nevertheless, in so far as perceptual constancy is important in visual function, a basic requirement for colour vision (wavelength discrimination) is likely to be in place. This suggests that some degree of colour vision, while perhaps not inevitable, is at least likely in animals that are both visual and cognitive.

What then of potential counter-examples of animals with image-forming eyes, but without colour vision? Are there really monochromats in the strict functional sense of only sampling the quality of light along a single dimension (radiant intensity)? It has recently been established that marine mammals are cone monochromats [67]. They possess a single spectral class of cone (medium to long wave-sensitive) unlike the majority of mammals, which possess two, and are therefore dichromats. However, even so-called cone monochromats have available a second spectral receptor class, namely rods. Rod-cone interactions are well known to influence chromatic discrimination in humans under mesopic viewing conditions and the same seems likely for ‘monochromatic’ marine mammals [68]. Perhaps a more serious objection might be raised from considering the cephalopods, a class which appear to be mainly monochromatic [69,70], but which includes active, highly visual animals [71]. Octopuses, for example, can be trained to recognize particular patterns and then transfer this information in visual object discrimination tasks [71]. In an interesting recent twist, however, Cronin et al. have demonstrated sophisticated visual discrimination abilities in the octopus, based on polarization sensitivity. These authors argue that polarization sensitivity may be incorporated into high-level visual perception permitting scene segmentation and facilitating object detection in a manner analogous to colour vision in other animals [72,73]. This result would seem to broaden questions about the function of colour vision into more general ones about the dimensionality of vision.

7. How “advanced” is colour vision?

As noted above, a basic requirement for colour vision (wavelength discrimination) is already likely to be in place in animals with spatial vision, since lateral inhibition in spatial localization is neurophysiologically equivalent to opponent processing of spectral information. The question thus arises as to how detailed the specification of the circuitry required for chromatic

processing needs to be, a question which obviously has bearing on the evolution of colour vision. What would it take to exploit a novel class of photoreceptor? If colour opponent mechanisms required detailed specification of connections within and between different classes of photoreceptor and specific postsynaptic neurons, then novel colour comparisons would require novel circuitry, beyond the photoreceptor level. However, as noted above, synaptic connections required for spatial and colour opponency are basically of the same type. If the nervous system is essentially designed to detect regularities in the environment (perhaps by means of general purpose decorrelation mechanisms [74,75]) then it also seems possible that there will be sufficient flexibility to immediately exploit the potential information in a novel photoreceptor channel, perhaps via correlations with novel classes of sensorimotor contingencies [12]. Circumstantial evidence for this possibility is to be found among the new-world primates, where di- and tri-chromacy exist side by side (see [64,76] for discussion). Specifically, tri-chromacy is found among a portion of the females, heterozygous for alleles of the long-middle wave-sensitive photopigment gene, alleles which exhibit sufficient differences in spectral sensitivity to generate a chromaticity signal in this part of the spectrum. The fact that such females have been shown to be functionally (as well as anatomically) trichromatic [77] argues that the nervous system can indeed make use of whatever spectral channels are available. A fundamental implication is that the neuronal circuitry underpinning colour vision should depend on the environment experienced during ontogeny [78–82], and the receptor sampling mechanisms that provide access to this environment [21].

Recently, such flexibility in wiring up the neuronal circuitry underpinning colour vision has been dramatically confirmed. Within the last few years two research groups have independently generated transgenic mice expressing the human long-wave cone pigment [83,84]. Mice, like most mammals, are dichromats, expressing the S cone pigment and a single photopigment in the longer wavelength part of the spectrum corresponding to the Old World primate M and L cones. The genetically engineered, ‘knock-in’ mice are retinally trichromatic in that the recombinant L opsin is expressed, but are they really functionally trichromatic? Can these novel photoreceptor signals be used in chromatic processing, or does this require further elaboration of postsynaptic neural circuitry? In the most impressive demonstration yet of the flexibility of post-receptor neural processing, Jacobs et al. [85] have shown that a fraction of these transgenic mice are functionally trichromatic, able to see colours in the red-green range that their dichromatic littermates cannot discriminate. Note that this is evidence for wavelength discrimination, not full colour vision, according to the cognitive view we propose here. Nonetheless, given a nervous system fundamentally designed to extract regularities and predictabilities from the environment, there are no significant barriers to colour vision in terms of neuronal wiring. To the extent that animals are cognitive [86] they will be able to exploit this for high-level visual functions such as object identification. Wavelength-dependent behaviour may in fact represent a streamlining of visual behaviour in cases where it is economical to do so, rather than being a primitive precursor of colour vision.

8. Conclusion

We have re-evaluated the current definition of colour vision for animals, attempting to assemble criteria that are neither too generous (any spectrally opponent behaviour is indicative of colour vision), nor too stringent (only humans possess true colour vision). We have discussed so-called wavelength-dependent

behaviours [2], and have pointed out that the historic distinction between such wavelength-dependent behaviour and colour vision might lead to false-negative diagnoses (of absence of colour vision). However, while wavelength-dependent behaviours might require some of the basic mechanistic components of colour vision (e.g. receptors with differing spectral sensitivity and spectral opponency), they do not require vision, i.e. seeing images. Indeed, there are cases of human patients who, as a result of cerebral damage, have lost all sense of visual shape, but retain a sense of colour [60]: such patients are formally classed as blind (i.e. *having no vision*) and cannot, therefore, be ascribed colour-vision abilities.

Thus, to prove that an animal sees in colour, we need minimally to demonstrate that it can use spectral cues (independently of intensity) in a task that involves some form of image segmentation. A number of procedures that could be expanded to test this in animals have been developed for pre-lingual infants, using pop-out tasks, target tracking, and attentional dwell times or staring as behavioural measures (see [87] for a review). A task that does not require associative learning has recently been developed for *Drosophila*, using a novelty paradigm [88] in a flight simulator [89]. While such paradigms would demonstrate wavelength discrimination abilities in conjunction with visual scene segmentation, we argue that they still might not suffice to demonstrate colour vision in a stricter sense, since colour is a perceptual attribute whereas wavelength is not. In this respect, we have referred to cases of cerebral achromatopsia, where patients are functionally colour blind, despite having intact retinæ, and crucially, can detect boundaries using wavelength discrimination [59,90]. We therefore argued that colours, crucially, are *colours of things*, and as such there has to be a (relative) permanence about them that extends beyond pop-out detection and scene segmentation. Permanence can be achieved only by memory, and it is possibly for this reason that Menzel [2] and Goldsmith [3] have demanded that colour vision needs to be demonstrated by associative learning paradigms. In our view, stronger evidence still would be the ability to learn colour in conjunction with (and disjunction from) shape, or better yet, the ability to extract chromaticity as a cue that can independently be associated with different objects, as required by a cognitive definition. We also argued that wavelength discrimination (a basic output of colour vision) is not necessarily more advanced than the “hard-wired”, stereotyped patterns that emerge from wavelength-specific behaviour, because at a basic level, the developing nervous system’s ability to decorrelate sensory input might “automatically” provide some form of colour opponency. Given that almost any set of $n-1$ colour opponent processes will unambiguously code the information from n colour receptor types [75] the large variety of opponent processes found in some animals [79,91], and the fact that variation in human retinal cone ratios appears to have only negligible effects on colour perception [92] might in fact be the result of opponent processes self-organising during development, extracting information from retinæ in which spectral receptor types are often largely stochastically distributed [93–95]. And since even animals with relatively “simple” nervous systems (such as honeybees) are capable of rule-learning and categorisation [96,97], colour vision according to a cognitive definition might be more widespread than is currently appreciated. More animal species need to be tested using paradigms that require disentangling object shape from spectral properties, as previously shown in wasps and honeybees [39,40]. In performing such tests, we need to be wary of “false-negatives”, in cases where animals with perfectly good colour vision might fail to “understand” the task, and therefore fail the desired behavioural criterion, or where stereotyped responses to certain spectral configurations might indicate a

so-called wavelength-specific behaviour. Such responses *might* indicate a “primitive” hard-wiring between spectral receptors and motor circuits, but it is also possible that colour vision and wavelength-specific behaviour are processed serially, so that stereotypic motor patterns are elicited when objects in the animal’s visual field are perceived in a certain colour.

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Glossary

Cognition (adj.: cognitive): an advanced form of information and memory processing, where information acquired in separate events is combined to generate new information and adaptive behaviour, for example, the ability to form categories of objects based on arbitrary criteria (colour, shape, etc.), rule

learning, or the formation of “cognitive maps” constructed from multiple items of memorised spatial information. The term cognition is sometimes used for *any* form of sensory processing or learning, but this is not the connotation here.

Colour: perceptual attribute of objects (or lights), based on the wavelength composition of light that reaches the eye from that object. However, colour is not a physical property of the object, but a perceptual construct that depends on many factors, including the photoreceptor spectral sensitivity (and subsequent neuronal processing) of the animal in question, and the colours' surround, recent history of surfaces viewed, and others.

Colour constancy: the spectral composition of light reflected from an object depends on the spectral composition of the light that illuminates it (imagine, for example, a white sheet of paper illuminated with blue light). Despite these physical changes, the *perceived* colour of an object tends to remain the same. This remarkable feat is referred to as colour constancy (it also means that colour cannot simply be equated with wavelength, or even combinations of wavelengths).

Colour vision: some authors define colour vision as the ability to discriminate differences in wavelength from differences in intensity, thus reducing colour vision to wavelength discrimination. We believe this is unsatisfactory because systems clearly lacking any form of visual perception (bacteria, plants) may nevertheless possess rudimentary wavelength discrimination. In this paper, we argue that image vision is an essential component of colour vision; moreover we suggest that according to a cognitive view of animal colour vision, a colour-seeing animal is capable not only of discriminating different colours, but also of abstracting colour as a category. In this view, colour becomes an additional cognitive dimension for ordering and classifying perceptual experience.

Colour opponency: the phenomenon that signals from different spectral receptor types are processed in an antagonistic fashion, based on neural mechanisms for wavelength discrimination using mutually inhibitory inputs of receptor signals (opponent processing). Requires at least two classes of receptor that sample different regions of the spectrum.

Perception: the process of constructing an internal representation of an animal's environment, integrating information from the sense organs with previous experience.

Photoreceptor: a light-sensitive cell, which generates, via a process of phototransduction, an electrical signal related to the number of photons absorbed.

Phototaxis: movement of an organism towards (positive phototaxis) or away from (negative phototaxis) light.

Phototransduction: the process of converting light energy into electrical energy, for signalling within or between cells. Based on a photon-absorbing molecular complex involving a protein photopigment.

Principle of univariance: the signal generated by a photoreceptor depends only on the number of photons absorbed, regardless of wavelength. Although the probability of absorbing a photon varies with wavelength (according to the photoreceptor's spectral sensitivity) there is no information about wavelength inherent in the absorption event. This means that a single photoreceptor is colour blind, and colour can only be extracted by comparing signals from photoreceptors with different spectral sensitivities.

Spectral sensitivity: the visible portion of the spectrum of electromagnetic radiation varies in wavelength from the near-UV (about 300 nm) to the near infra-red (about 700 nm), with different organisms sensitive to different regions of this spectrum (visible light for humans ranges from about 400–700 nm, and for bees from 300–650 nm). Since photoreceptors absorb photons of different wavelengths with different efficiencies, any light sensitive mechanism will have a spectral sensitivity, whereby it will be most sensitive to the wavelength of maximum absorption, and progressively less sensitive as the wavelength deviates from this value.

Trichromacy: the condition of having a visual system where comparisons are made (in any combination) among signals from photoreceptors divided into three classes, according to spectral sensitivity. An organism possessing such a visual system is a trichromat. Other related terms (e.g. dichromacy and tetrachromacy) refer to visual systems with different numbers of sensory input variables. A monochromat is an organism whose visual system possesses a single spectral class of photoreceptor, which (because of the principle of univariance) would be incapable of wavelength discrimination, and which would, therefore, also be incapable of colour vision.

Vision: is to “have or use the power of discerning objects with the eyes” [10], which implies that vision must form images of the environment. While the ability to recognize an object or colour on the basis of sensory information is ultimately derived from photoreceptor signals, vision is clearly more than the detection of light, and requires a neural system that can process photoreceptor inputs to provide perceptual information about objects and events in the world (spatial location, shape, motion, etc).

Wavelength-dependent behaviour: a stereotyped behaviour pattern that can reliably be evoked by light in a manner whereby certain wavelengths are more effective than others.

Wavelength discrimination: the sensory capacity to distinguish between different lights solely on the basis of differences in wavelength.