



Contents lists available at ScienceDirect

## Optics &amp; Laser Technology

journal homepage: [www.elsevier.com/locate/optlastec](http://www.elsevier.com/locate/optlastec)

## Is colour cognitive?

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## ARTICLE INFO

Available online 13 February 2009

## Keywords:

Colour vision  
Wavelength discrimination  
Colour constancy

## 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.

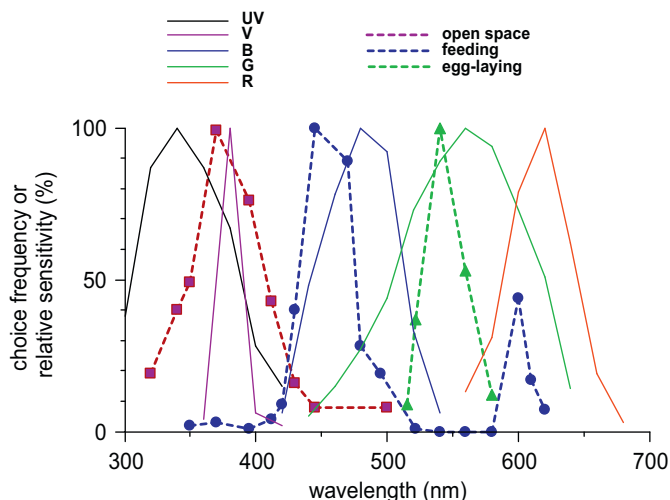
## 2. Spectral sensitivity and wavelength discrimination

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 nm (V), 480 nm (B), 560 nm (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

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