

Eye design for coding natural spectra

D. Osorio

School of Life Sciences, University of Sussex. Brighton, BN1 9QG. UK
d.osorio@sussex.ac.uk

ABSTRACT

Reflectance spectra of natural objects are produced by a limited range of pigment molecules, and hence fall into a small number of distinct classes. Terrestrial scenes are dominated by the green of chlorophyll and spectra that increase approximately linearly with wavelength that are produced by otherwise unpigmented plant material. On this background of greens and browns, both animals and plants display colours produced by carotenoids, anthocyanins and a few other types of molecule. This limited spectral palette may have influenced sampling of chromatic and spatial information, affecting both photoreceptor spectral sensitivities and the layout of receptors in the retina.

1. INTRODUCTION

Thomas Young¹ advocated his theory of trichromacy on the grounds that it was 'inconceivable' that an eye could sample each wavelength at each point in the retinal image. Nature suggests that there is no simple solution or universal optimum to the problem of sampling of space and the spectrum with a single retina. Animals have anything from one to 16 different spectral types of receptors². Some have intraocular spectral filters that narrow spectral tuning, whilst receptor arrays ranges from being highly orderly to random. Some eyes have colour vision across the visual field, whilst in others it is restricted to a specialized region. How might natural signals influence the evolution leading to this biological diversity?

Following workers such as Barlow³, who drew attention to information as a measure of performance and proposed that efficiency as a key function of sensory coding, a range of models have been proposed to account for spectral sampling and neural coding of colour by visual systems. These evaluate performance according to criteria such as: matched sampling⁴, minimizing redundancy^{5,6}, maximizing information capacity⁷, or maximising discriminability of spectra⁸. Related models that have been applied to spatio-chromatic coding include the objective of identifying independent components⁹, or minimising corruption of luminance information¹⁰. Regardless of the criterion, signals and noise (or uncertainty due to variable illumination) affect performance. This article deals with receptors themselves, where efficiency may be especially important¹¹. I outline how natural spectra may have influenced the evolution of spectral sensitivities and retinal arrays in primates and other species.

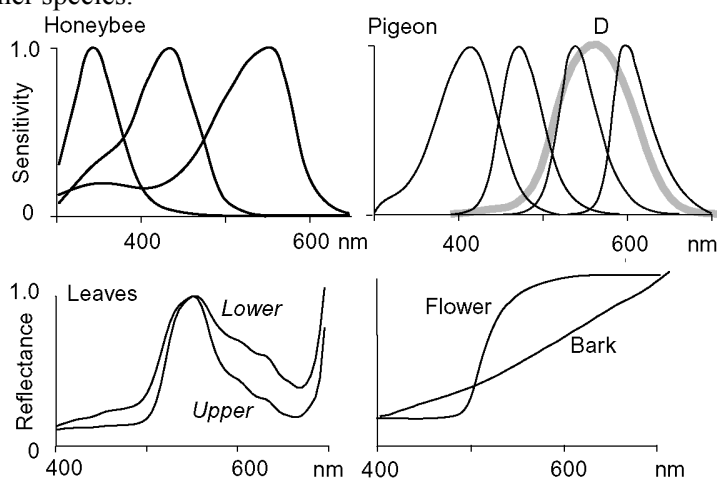


Figure 1: Above: Spectral sensitivities of honeybee and chicken photoreceptors. Avian double cones (D) comprise about 50% of the total and may be used for luminance vision, whilst the remaining four more narrowly tuned cone types serve colour vision (see ref. 2).

Below: Normalised spectral reflectances of mean upper and lower leaf surfaces from about 200 species of Amazonian tree, and examples of bark and a carotenoid pigmented flower.

2. SPECTRAL SAMPLING THE NUMBER OF RECEPTOR TYPES.

Diurnal vertebrates generally use from two to four types of cones for colour vision, and invertebrates a similar range of photoreceptors, but 12 in the exceptional case of some stomatopod crustaceans². Barlow⁴ drew an analogy between optical blur in spatial sampling, and the tuning curve of rhodopsin, which limits spectral resolution. He went on to apply sampling theory to colour vision, estimating the range of the spectral (as opposed to spatial) frequencies that could be represented by a rhodopsin based system, and concluded that four or five spectral types would suffice for the visible spectrum, but three is too few. One might expect a greater number of receptor types if tuning curves are narrower than that of rhodopsin, and animals with larger numbers of receptor types such as reptiles, birds and certain invertebrates do indeed narrow spectral photoreceptor tuning with colour filters. These animals almost certainly use >3 spectral receptors for colour vision² (figure 1).

However it is readily apparent⁴ that the optimal sampling strategy is dependent not only upon limitations of the sensors, but also signal to noise ratio in the stimuli. There would be no benefit in encoding fine spectral detail if signals are below the noise level. In practice natural spectra are restricted to a small part of the human colour gamut¹², and also they vary quite smoothly. Thus Maloney¹³ found that three principal components can represent >98% of the variation in natural spectra (a dataset of 'natural formations' the Soviet Union). Thus, unlike spatial sampling where it generally pays to improve resolution, there may be little benefit from increasing spectral resolution. Subsequently van Hateren⁷ used a frequency domain based model to predict the sampling strategy that maximises information coded in the presence of noise. For spectra from an ensemble of natural images and realistic noise levels, he found that three receptor types, with spectral tuning functions resembling that of rhodopsin, are close to optimal.

Models such as those outlined indicate that a trichromatic system can represent a large proportion of the chromatic information in nature. They do not however predict the diversity of eye design in diurnal animals (e.g. Figure 1), including the specific spectral locations of receptors. Nor do they take account of rare but biologically important colours used for communication within and between species, such as fruit, flowers, and bird plumage.

3. BIOLOGICAL SIGNALS AND PHOTORECEPTOR SPECTRAL TUNING

To understand the spectral tuning of receptors in dichromatic eyes on land and underwater Lythgoe and Partridge^{14,15} measured spectra of woodland and aquatic objects, to predict the best pair of receptor sensitivities for discriminating amongst them. Increasing the spectral separation of the pigments generally increases the amplitude of the signal, but this is offset by the low photon flux at short-wavelengths on land, and both long and short wavelengths in water. Similar models have been used to estimate the discriminability of objects such as flowers visited by bees, fruit eaten by primates, bird plumage and coral reef fishes. These models vary in how they estimate colour thresholds², and treat suprathreshold differences. There are now substantial datasets of spectra, which often include the UV (300nm - 400nm). The availability of low-priced, portable spectrometers has been a major factor stimulating this enterprise.

How then are pigment sensitivities matched to natural spectra? It is well known that biological pigments are predominantly from a fairly small number of chemical families¹⁶. The main types include: *i*) melanins used in animal pigments; *ii*) photosynthetically active plant structures (leaves) dominated by chlorophyll (with variant types in the marine algae); *iii*) carotenoids that produce bright yellow to red colours of many fruit and flowers, and are also used by many animals; *iv*) anthocyanins in plants including in immature leaves; *v*) otherwise unpigmented plant material, including dead leaves and bark. Finally, *vi*) structural colours are common in animal integuments, especially of birds and insects.

The pigment families tend to have characteristic spectra. For example: chlorophyll has a reflectance peak close to 555nm, and absorbs strongly below 500nm (Figure 1); carotenoids absorb strongly from about 400nm up to some point between 500nm and 600nm, where there is a steep

rise in reflectance; while reflectance of melanin and 'unpigmented' plant material increases roughly linearly with wavelength between 400 and 700 nm to give a range of greyish to reddish colours.

These characteristic features mean that the amount of variation is not uniform across the spectrum. This could influence the spectral location of receptors, and means that chromatic signals may not have Gaussian statistics (as assumed by some models of coding). For example, it has been observed that the tuning of human M and L receptors *minimises* the range of red-green signals presented by leaves. This arrangement may serve to simplify the task of detecting fruit among leaves¹⁷, or minimise the red-green signal in natural scenes and hence limit corruption of the luminance signal¹⁸. More generally, reflectance (and perhaps variation in reflectance) is greater above 500nm than below, which may favour evolution of multiple long-wavelength receptors, as has occurred in various lineages of terrestrial animals, including primates and butterflies.

4. SPATIAL AND CHROMATIC SAMPLING BY PRIMATES

Whereas conventional reflectance and illumination spectra are sufficient to investigate spectral coding, understanding the joint sampling of spatial and spectral signals¹ requires hyperspectral (or spatio-chromatic) images. In principle one might evaluate the total spatio-chromatic information in a natural images, but in practice it is often convenient to treat luminance and chromatic information separately. Primates use chromatic and luminance signals for different types of visual task, and other animals are probably similar. Some, such as birds and flies, may well have entirely separate sets of receptors and neural pathways for chromatic and achromatic/luminance vision (Figure 1). Others such as bees use the certain receptors (typically long wavelength sensitive) for both purposes. Trichromatic primates are unusual in combining the outputs of two cone types to produce a luminance signal. This allows trichromacy without compromising spatial resolution, but risks aliasing between luminance and chromatic signals^{19,20}. The aliasing is perhaps best understood as noise in the luminance signal, but does it matter, and could it account for the relatively large spectral overlap of the M and L cones? There is little direct psychophysical evidence on this point. Williams and his collaborators¹⁹ point to the faint 'Brewster's colours' seen in fine high-contrast patterns, but otherwise it is uncertain whether dichromats outperform trichromats in any psychophysical task²¹.

An alternative to psychophysical tests is to estimate luminance and chromatic signals in natural images. A good starting point is to describe spatial frequency power spectra for luminance and chromatic signals^{10,22,23}. These spectra obey a power-law, with the signal power approximately proportional to $1/f^2$, where f is spatial frequency. Roughly speaking, power in the luminance signal is about 10 times that in human a blue-yellow signal and 100 times that in the red-green signal at all spatial frequencies^{6,10,22}. The wide applicability of this power-law relationship means that deviations are indicative of the effects of noise and blur in hyperspectral images. More importantly, if noise (e.g. cone mechanisms) is taken in to account, we can estimate spatio-chromatic information as a function of spatial frequency, or predict signals in retinal ganglion cells.

We used hyperspectral images to examine the effects of altering the spectral tuning of the L and M cones¹⁸. Red-green signals increase rapidly with spectral separation, but perhaps more surprisingly for a given spectral separation the actual cone sensitivities appear to *minimise* the average signal across natural images. This latter observation is consistent with the notion that the red-green mechanism is adapted for detecting rare but important colours, such as ripe fruit, with minimal cost to 'general-purpose' luminance vision. We subsequently estimated the effects of having separate cone inputs to the primate magnocellular (M) system¹⁹. The M-system is spectrally unselective and is thought to encode much of the luminance signal in primate vision. Assuming equal numbers of M and L cones in a random retinal array the mean level of chromatic noise for natural images is equivalent to a luminance contrast signal of about 0.01 at the optimum spatial frequency for the M- system. This value is approximately equal to the psychophysical luminance contrast threshold, which implies that chromatic noise is roughly equivalent to other sources of noise. Any increase in the magnitude of the red-green signal would swamp other sources of noise, and become deleterious to luminance vision. This problem could be avoided, for example by having a retina of alternating L and M cones, but it does seem possible that a trade-off between luminance and chromatic coding in has influenced the evolution of primate trichromacy.

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