Review

Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision

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This review outlines how eyes of terrestrial vertebrates and insects meet the competing requirements of coding both spatial and spectral information. There is no unique solution to this problem. Thus, mammals and honeybees use their long-wavelength receptors for both achromatic (luminance) and colour vision, whereas flies and birds probably use separate sets of photoreceptors for the two purposes. In particular, we look at spectral tuning and diversification among ‘long-wavelength’ receptors (sensitivity maxima at greater than 500 nm), which play a primary role in luminance vision. Data on spectral sensitivities and phylogeny of visual photopigments can be incorporated into theoretical models to suggest how eyes are adapted to coding natural stimuli. Models indicate, for example, that animal colour vision—involving five or fewer broadly tuned receptors—is well matched to most natural spectra. We can also predict that the particular objects of interest and signal-to-noise ratios will affect the optimal eye design. Nonetheless, it remains difficult to account for the adaptive significance of features such as co-expression of photopigments in single receptors, variation in spectral sensitivities of mammalian L-cone pigments and the diversification of long-wavelength receptors that has occurred in several terrestrial lineages.

Keywords: colour vision; evolution; ecology; retina; photoreceptor

1. INTRODUCTION

Thomas Young (1802) observed that jointly sampling spatial and spectral signals with a single array of photoreceptors presents a problem, because there cannot be an ‘infinite number’ of detectors for different frequencies of light at each point on the retina. He suggested that humans have three. The potential difficulties are illustrated when, in TV pictures, fine luminance patterns, such as pinstriped cloth, are aliased to appear as coloured Moiré patterns. Humans are indeed trichromatic, but it remains uncertain how much we suffer from aliasing between spatial and spectral signals, and whether photoreceptor spectral sensitivities and spatial layout reflect a compromise between their conflicting requirements (Williams *et al.* 1993; Osorio *et al.* 1998; Williams & Hofer 2004).

The distinction between spectral and spatial signals is inherent to image physics, but this does not specify how information should be coded. Many animals use achromatic (e.g. luminance or brightness) and chromatic signals for separate purposes (Srinivasan 1985; Livingstone & Hubel 1988; Giurfa *et al.* 1996, 1997; Schaerer & Neumeier 1996; Jones & Osorio 2004). Monochrome pictures can be enjoyed almost as much as a colour, because achromatic intensity represents most signal power, and hence visual information (Osorio *et al.* 1998; Ruderman *et al.* 1998; van Hateren *et al.* 2002). Primates

use luminance signals for tasks such as motion, form and texture perception. Spectral information is represented by chromatic signals, which are based on differences between receptor quantum catches rather than absolute values. Chromaticity is probably relatively stable (constant) in natural illumination, so that it gives information about surface reflectance, pigmentation and other material properties (Rubin & Richards 1982; Gegenfurtner & Kiper 2003). Colour vision is therefore likely to be important for object detection or classification.

Available evidence suggests that most species resemble humans in using chromatic and achromatic signals for separate tasks (§2), but there are substantial differences in retinal sampling. For instance, primate luminance mechanisms combine outputs of long (L; red) and medium (M; green) cones, while chromatic mechanisms compare responses of all three cones (Wyszecki & Stiles 1982; Livingstone & Hubel 1988). Honeybees (*Apis mellifera*) also use all three of their spectral receptors for colour vision, with the long-wavelength receptor providing a ‘luminance’ signal that is used for motion and form perception (Backhaus 1991; Giurfa *et al.* 1997; Vorobyev *et al.* 2001). In contrast to primates and bees, cyclorhaphid flies (Diptera) and birds probably have separate sets of photoreceptors for luminance and colour vision (figure 1; Hardie 1986; Strausfeld & Lee 1991; Osorio *et al.* 1999; Anderson & Laughlin 2000; Jones & Osorio 2004). In birds, these are double and single cones, and in the flies, short and long visual fibres, respectively. This dual arrangement has obvious costs, but avoids compromises

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Figure 1. Vertebrate cone and insect photoreceptor spectral sensitivities, normalized to $\lambda_{\max}$. (a), (b) Humans and honeybees have three spectral types of photoreceptor, and trichromatic colour vision. Human M and L cones, and the bee's long-wavelength receptor also provide luminance signals. (c), (d) In birds and flies, respectively, the double cone (D) and short visual fibre (SVF) signals are used for luminance, while the bird's four types of single cone and the fly's long visual fibres (LVFs) give chromatic signals. The fly photoreceptors are named according to their location in the rhabdom (R7 or R8), and by their colour pale (p) or yellow (y). The five types of fly receptor illustrated are found across most of the eye, but in specialized regions are replaced by others (Hardie 1986). Vertebrate and bee visual photoreceptors contain only a single type of photopigment, but flies also have a UV sensitive antennal pigment, which accounts for their complex spectral sensitivity (Hardie 1986; Stavenga 2004).

between the competing demands of coding chromaticity and luminosity. For instance, narrowing photopigment spectral tuning with coloured filters probably benefits colour vision, but reduces absolute sensitivity (Douglas & Marshall 1999; Hart 2001; Stavenga 2002; Vorobyev 2003). Flies tailor further features of receptor physiology, such as response speed and gain to the specific needs of chromatic and luminance coding (Anderson & Laughlin 2000). For instance, at any given adapting intensity, short visual fibres have faster responses than long visual fibres. This is expected because chromatic signals have a lower signal-to-noise ratio (SNR) (van Hateren 1993).

The diversity of retinal designs implies that there is no universal solution to jointly sampling spatial and spectral information. To begin to understand this diversity, we start with the relatively simple question of spectral tuning of photoreceptors. In a world where evolution had optimized performance, one could identify the function of a system by establishing what it did best. Species differences would depend upon their sensory ecology. The real world is not optimal, but adaptive variation in photopigment and receptor spectral sensitivities, and its molecular basis is relatively easy to understand. Models of visual coding can then propose a criterion for evaluating performance, based on (noisy) receptor responses to natural stimuli.

(a) Photopigment spectral sensitivities

The wealth of data on photoreceptor spectral sensitivities and the phylogeny of photopigment proteins (opsins) is an excellent basis for comparative studies (figure 1). In addition, the spectral sensitivity of a photopigment is determined by its peak ($\lambda_{\max}$; Govardovskii *et al.* 2000), which makes it easy to model receptor sensitivities and to simulate the effects of evolutionary change. Vertebrates have five genetic classes of visual photopigment (Hisatomi *et al.* 1994; Yokoyama 1994), of which four emerged

before the divergence of cyclostomes and fishes (Collin *et al.* 2003). Several groups, including birds and many lizards, retain all five classes. These gene families are generally known (Yokoyama 1994) as: RH1, which are rod pigments with $\lambda_{\max}$ from approximately 460 to 530 nm, and cone pigment classes, RH2, $\lambda_{\max}$: 460–530 nm; SWS1, $\lambda_{\max}$: 350–440 nm; SWS2, $\lambda_{\max}$: 430–470 nm and LWS/MWS $\lambda_{\max}$: 495–575 nm (Bowmaker & Hunt 1999; the spectral ranges include fishes). The LWS/MWS family is so named because it includes primate medium- (M) and long- (L) wavelength sensitive cone pigments, but these latter pigments are genetically closely related, and we refer to the family simply as LWS. Arthropod photopigments evolved independently from those of vertebrates. They fall into three families—'UV', 'blue' and 'green'—which diverged before the radiation of insects (Briscoe 2000; Briscoe & Chittka 2001).

Adaptive variation of visual pigments is well known, especially among fishes whose receptor sensitivities tend to match the ambient illumination spectrum as it varies with water depth and quality (Lythgoe 1979; Bowmaker 1995). Shifts in spectral sensitivity are caused by amino acid substitutions at a few specific sites in the opsin molecule, so that point mutations can substantially affect visual phenotype (Yokoyama & Radlwimmer 1999; Briscoe 2001; Hunt *et al.* 2001; Yokoyama & Radlwimmer 2001). Best known are primate LWS pigments, where substitutions at three sites shift $\lambda_{\max}$ from 535 to 560 nm (Neitz *et al.* 1991; Asenjo *et al.* 1994; Nathans 1999). Almost certainly, these critical sites have been subject to stabilizing selection (and convergent selection) in separate primate lineages (Deeb *et al.* 1994; Surridge *et al.* 2003). At a broader phylogenetic scale, there are parallels between groups. For example, the amino acid substitutions that differentiate pigments in the long-wavelength range ($\lambda_{\max} > 510$ nm) are alike in mammals, fishes and

butterflies (Yokoyama & Yokoyama 1996; Briscoe 2001; Yokoyama & Radlwimmer 2001).

In the face of the simple relationship between photopigment genotype and spectral phenotype, and for adaptive variation in fishes, several workers have commented on the uniformity of pigment spectral sensitivities within certain taxonomic groups of land animals. Examples include bees and wasps, anole lizards, birds and Old World (catarrhine) primates (Peitsch *et al.* 1992; Jacobs & Deegan 1999; Briscoe & Chittka 2001; Hart 2001; Loew *et al.* 2002). Within each of these groups, receptor sensitivities vary little (figure 1), and seem to be unaffected by habitat, feeding behaviour or the species' own colours. This uniformity is consistent with the view that signalling colours, such as those used in sexual displays, exploit a fixed sensory system (Allen 1879; Ryan 1990). However, as Wallace (1879) pointed out, there is little support for the prediction (Allen 1879) that species feeding on fruit and flowers should have superior colour vision, and more colourful displays than others. Primates may be an exception, in that by comparison with other mammals, they have superior colour vision, a preference for feeding on fruit and are relatively colourful.

The evolutionary conservatism of photoreceptor spectral sensitivities should not be exaggerated. For instance, the shortest wavelength (SWS1) pigments of birds have repeatedly switched from an ancestral form, $\lambda_{\max}$ ca 410 nm, to a 365 nm form (Odeen & Håstad 2003). $\lambda_{\max}$ of mammalian LWS pigments varies from 495 to 565 nm (Jacobs & Deegan 1994; Yokoyama & Radlwimmer 1999). Meanwhile, long-wavelength pigments have diversified by gene duplication in groups such as Primates and Lepidoptera, a subject to which we return below.

2. LUMINANCE SPECTRAL SENSITIVITY

Although not directly concerned with spectral information, the spectral sensitivity of achromatic signals is likely to be affected by two main considerations: (i) the SNRs in signals from absorbed photons and (ii) the rate of thermal isomerization of photopigment. Thermal isomerization is indistinguishable from photon absorption and hence is a source of noise.

In principle, achromatic signals might be derived by summing the outputs of any number of different spectral types of photoreceptor, but normally, outputs of a single type of photoreceptor are used for tasks such as motion perception and form vision. By analogy with human vision, this can be called a 'luminance signal' (Wyszecki & Stiles 1982; Livingstone & Hubel 1988).¹ Mammals use long-wavelength sensitive (L) cones (Jacobs 1993), while birds and fishes probably use double cones (which contain the LWS pigment; Schaerer & Neumeier 1996; Jones & Osorio 2004). Amongst insects, bees use their long-wavelength receptor (Srinivasan & Lehrer 1988; Giurfa *et al.* 1996, 1997), and flies, the short visual fibres (Hardie 1986; Heisenberg & Buchner 1977; Anderson & Laughlin 2000). These luminance receptors are generally the most abundant type (excluding vertebrate rods), which allows high sensitivity and spatial resolution. The relatively recent evolutionary divergence of primate M and L cones may explain why their outputs are combined (Mollon 1989).

Among mammals, the spectral sensitivity of L cones varies; primates have 560 nm LWS pigments, while sheep and cows have a 555 nm pigment (Jacobs *et al.* 1998), owl monkeys (*Aotus* spp.) have a 545 nm pigment (Jacobs *et al.* 1993), ground squirrels (*Spermophilus* spp.) have a 520 nm pigment (Kraft 1988), rats, mice and rabbits have a 510 nm pigment (Yokoyama & Radlwimmer 2001) and the Mongolian gerbil (*Meriones unguiculatus*) has a 495 nm pigment (Jacobs & Deegan 1994). Amniotes have rod pigments with $\lambda_{\max}$ close to 500 nm. By comparison, in birds and anole lizards, the LWS pigment $\lambda_{\max}$ is nearly always 565 nm (Hart 2001; Loew *et al.* 2002; although some lizards, including *Anolis carolinensis*, have a 620 nm (A2) pigment, Provencio *et al.* 1992).

For rhodopsins with a retinal (A1) chromophore, 565 nm is close to the longest known value of $\lambda_{\max}$, and this may be an upper limit imposed by photopigment chemistry. Below this (hypothetical) limit, the $\lambda_{\max}$ for mammalian LWS pigments is unlikely to be selectively neutral between 500 and 560 nm (Yokoyama & Radlwimmer 1999, 2001). New World monkeys (Platyrrhini) provide direct evidence for selection because they have a single LWS opsin gene that is polymorphic for the M/L pigments in the 535–560 nm range. Longer wavelength (L type) pigments appear to be selectively favoured in homozygous monkeys, which are dichromats. Genetic equilibrium is maintained because 535 nm pigments confer an advantage to heterozygous individuals, which are trichromats (Surridge *et al.* 2003; Osorio *et al.* 2004).

(a) Terrestrial spectra, thermal isomerization and luminance spectral sensitivities

Where SNR is determined by photon absorption (as opposed to thermal isomerization), the optimal value of $\lambda_{\max}$ will tend to favour maximizing photon catch. Presumably, this is why fish photopigment sensitivities match illumination spectra. Celestial illumination has a comparatively broad spectrum (figure 2a), but in light reflected from or transmitted through leaves, chlorophyll produces a relatively narrow spectrum (figure 2b; Endler 1993). For standard daylight, quantum catch of visual photopigments will increase with $\lambda_{\max}$ (figure 2c), but for green forest light, quantum catch is practically independent of $\lambda_{\max}$ in the range of 500–560 nm. Thus, maximizing sensitivity may explain why luminance mechanisms tend to use receptors with $\lambda_{\max} > 500$ nm, but variation in illumination spectra is unlikely to account for the differences among land animals.

An alternative and long-standing proposal is that the spectral sensitivity reflects a compromise between the need to maximize photon catch and the effects of dark noise, which favours short-wavelength receptors (Barlow 1957). Illumination spectra at night are much like those of daylight (Henderson 1977), and given that a 560 nm pigment maximizes photon catch (figure 2c) it is a puzzle why rod sensitivity peaks at 500 nm. The difference between photopic (light adapted) and scotopic (dark adapted) spectral sensitivities is known as the Purkinje shift. Barlow (1957) suggested that the rate of spontaneous activation of photopigment molecules by thermal isomerization, or 'dark light' increases with $\lambda_{\max}$, because the energy barrier for thermal isomerization falls with $\lambda_{\max}$ (see also Ala-Laurila *et al.* 2004). Dark noise raises absolute threshold (i.e. the weakest light detectable over

Figure 2. (a) Illumination spectrum of standard daylight in quantum units. Illumination spectra contain differing proportions of direct sunlight, blue skylight, and light filtered through leaves, which resembles the leaf reflectance spectrum. (b) Here, illustrated by the average from a large sample of rainforest species. Leaf spectra peak at 555 nm, and increase sharply beyond 680 nm. (c) Dependence of quantum catch on the wavelength position of the photopigment containing A1 pigments. A2 pigments, which can peak at up to 620 nm, give very similar curves. Illumination is assumed to be either standard D65 daylight (*ca* figure 2a) or forest light. Calculations assume the receptor views a surface whose reflectance is uniform across the spectrum, and that the absorption at the peak does not depend on $\lambda_{\max}$. Forest light is assumed to be the product of D65 illumination with the reflectance of leaves, which is an extreme green light. Quantum catch is normalized to that for a receptor peaking at 645 nm. The quantum catch in forest light increases sharply at the peak wavelengths greater than 600 nm. Ordinarily visual pigments contain a vitamin A1 chromophore (or in some insects, a chromophore based on xanthophylls; Hardie 1986), which allow $\lambda_{\max}$ to reach about 570 nm. However, the lizards use vitamin A2 as a chromophore (Provencio *et al.* 1992), which gives an LWS pigment with $\lambda_{\max}$ 620 nm. A2 pigments are common in fishes and it unclear why they are rare in amniotes.

a dark background), and so is most important in dim light. In fact, thermal isomerization rates are affected by $\lambda_{\max}$, but other causes underlie the 10^4 fold difference in rates of spontaneous isomerization between rod and cone pigments (Ala-Laurila *et al.* 2004). Thus, the Purkinje shift may be attributable to the wavelength-dependence of thermal isomerization, but there is no clear evidence that

Figure 3. Effects of mixing long- (L) and short- (S) wavelength sensitive pigments on quantum catch. Dependence of the quantum catch on the ratio L : S in a cone containing a mixture of an L pigment peaking at 565 nm and an S pigment peaking at 435 nm. Calculations are for two optical densities. The solid line corresponds to a receptor with a peak absorbance of 0.4, and the dashed line a peak absorbance of 0.99. This shows that even for very long receptors (with high optical density), the quantum catch for a cone containing only L pigment exceeds that for a receptor with a mixture of visual pigments.

this effect accounts for the diversity of mammalian LWS pigments. The simplest prediction being that $\lambda_{\max}$ should be lower in species that use cones in dim light.

(b) Broadening spectral sensitivity: mixtures of visual pigments and antennal pigments

Some groups including rodents and butterflies co-express short- (S) and long- (L) wavelength sensitive opsins within photoreceptors (Szel *et al.* 2000; Arikawa *et al.* 2003), which broadens spectral sensitivity. Often, the L : S ratio varies systematically across the retina, to form gradients. Typically, the proportion of short-wavelength pigment is greatest in the receptors that view the sky (Szel *et al.* 2000; Briscoe *et al.* 2003). This arrangement seems logical (because the sky is blue), and might maximize the contrast of objects seen in silhouette. However, using the best single type of pigment (figure 3) nearly always maximizes photon catch, and the advantage of mixing pigments is unclear.

In dipteran flies, UV sensitivity of the main type of photoreceptor (R1-6) is often enhanced by an antennal pigment, which transfers light energy to the rhodopsin (figure 1; Hardie 1986). This pigment is thought not to reduce the rhodopsin concentration, and may increase quantum catch by up to 20% depending on the stimulus spectrum (Stavenga 2004).

3. COLOUR VISION

Colour vision can be defined as the ability to discriminate variation in the spectrum of light from changes in overall intensity (Kelber *et al.* 2003). This requires comparison of responses in two or more spectral types of photoreceptor, but how many types are needed to code natural spectra? The broad spectral tuning of visual photopigments limits their spectral resolution (Barlow 1982), which means that eyes cannot discriminate two closely spaced wavelengths from a single intermediate spectral line. Whether broad tuning is a limitation depends on the spectral signals, and ordinary reflectance spectra tend to vary relatively

smoothly. As with a scene viewed through fog, the absence of fine spectral detail means there may be no benefit from high resolution.

Maloney (1986) used principal components analysis to show that within the visible spectrum three components are sufficient to represent most of the variation in spectra of 'natural formations' from the Soviet Union. The smallest signals that can usefully be coded depend upon the level of noise, and when this effect is taken into account trichromacy and rhodopsin tuning curves (with a half-width of about 100 nm) may be well matched to natural spectra (van Hateren 1993). The model predicts a smaller number of more broadly tuned receptors as the SNR falls (e.g. in dim light).

Given that the relatively small number of receptor types found in animal eyes are more or less sufficient to encode natural spectra we can go on to ask what factors may underlie differences between species; for example, in the spectral locations of receptors, or the narrowing of spectral tuning with coloured filters (figure 1). Work on the number of receptors has used sampling and information theory and considered a wide range of spectra (Barlow 1982; van Hateren 1993), but clearly, the particular objects of interest and the behavioural uses of colour vision may be significant. One can estimate receptor responses to object spectra, and simulate performance of colour vision in a plausible task, such as finding fruit, identifying the maturity of leaves or selecting mates (Vorobyev & Osorio 1998; Kelber 1999; Sumner & Mollon 2000a,b; Regan *et al.* 2001). To test a hypothesis about evolutionary adaptation, a hypothetical set of receptors that is predicted to be optimal for a given purpose can be compared with reality. There are studies on spectra from woodlands viewed by dichromatic eyes (Lythgoe & Partridge 1989; Chiao *et al.* 2000); fruit and leaves consumed by primates (Osorio & Vorobyev 1996; Sumner & Mollon 2000a,b; Osorio *et al.* 2004); flowers visited by bees (Chittka & Menzel 1992; Vorobyev & Menzel 1999); and bird plumage colours (Vorobyev *et al.* 1998).

Although these studies differ in their details, the main observations are consistent (Lythgoe & Partridge 1989; Vorobyev 1997; Vorobyev *et al.* 1998; Vorobyev & Menzel 1999; Chiao *et al.* 2000; Vorobyev 2003). Notably, they confirm that spectral information can be coded with at most five types of receptor. Increasing the spectral separation of receptors, or narrowing their sensitivities with oil droplets will generally increase the discriminability of natural spectra.

More interestingly, models make it clear that the optimal eye design is dependent upon three main factors; namely, the spectra of interest, the behavioural task and photoreceptor noise. For example, the uniformly spaced receptors of honeybees are optimal for discriminating flower colours (Chittka & Menzel 1992; Vorobyev & Menzel 1999), whereas, detection of fruit against leaves, may favour the closely spaced L and M pigments of trichromatic primates (figure 1; Osorio & Vorobyev 1996; Sumner & Mollon 2000a,b). The large spectral overlap of the L and M receptors is probably advantageous because fruit and leaves reflect more strongly, and/or exhibit greatest variation in reflectance at long wavelengths. Finally, the demands of colour constancy may favour

relatively closely spaced and narrowly tuned receptors (Osorio *et al.* 1997).

(a) *Diversification of long-wavelength receptors and foliage colouration*

Simplification is a common form of evolutionary change, and it is no surprise that nocturnal and fossorial groups, such as mammals and snakes, have lost one or more of the ancestral classes of cone pigment (Yokoyama & Yokoyama 1996; Sillman *et al.* 2001; Arrese *et al.* 2002). Increase in complexity is perhaps more interesting, and among land animals is prominent among long-wavelength receptors ($\lambda_{\max} > 510$ nm). Thus, birds and reptiles retain the five ancestral sets of visual pigments, but coloured oil droplets on the LWS single cone substantially red-shift and narrow its peak compared with the double cones, which also contain the LWS photopigment (figure 1; Hart 2001).

Mammals lack coloured oil droplets in their cones, but trichromacy has emerged in Old World monkeys (*Catarrhine*) and howler monkeys (*Alouatta*) following independent duplications of the ancestral LWS gene (Nathans 1999; Surridge *et al.* 2003). (A fruit bat *Haplonycteris fischeri*, has duplicate LWS genes, although the spectral sensitivities of the two pigments probably do not differ; Wang *et al.* 2004.)

Duplications of long-wavelength pigment genes occurred early in insect evolution (Spaethe & Briscoe 2004), and repeatedly more recently in Lepidoptera (Briscoe 2000, 2001, 2002; Wakakuwa *et al.* 2004). Butterflies have from one to three types of long-wavelength photopigment, and use coloured filters to produce photoreceptors with $\lambda_{\max}$ from 540 to 620 nm (Stavenga 2002; Arikawa 2003). Specialized 'red receptors' are known from other insect families, including Odonata, Diptera and Hymenoptera (Hardie 1986; Peitsch *et al.* 1992; Yang & Osorio 1996; Briscoe & Chittka 2001).

As we have mentioned, there is little evidence that the evolution of long-wavelength sensitive receptors occurred in response to biological signals, such as fruit, flowers or mating displays (§1; Surridge *et al.* 2003). An alternative is that receptors evolved mainly to deal with the 'common' colours of visual backgrounds. Terrestrial spectra fall into two main classes (figure 2). Leaves absorb strongly below 500 nm, and have a peak due to chlorophyll near 555 nm. Reflectance of almost all other materials (e.g. bark, dead vegetation, soil and animal melanin pigments) increases roughly linearly with wavelength (Osorio & Bossomaier 1992).

Lythgoe (1979) recognized the probable importance of foliage colouration. He suggested that leaf spectra are more variable above the 555 nm peak than below, and speculated that this is why pigeons (*Columba livia*) have a long-wavelength single cone with its sensitivity maximum near 600 nm (achieved by an LWS pigment with a red oil droplet). However, it should be noted that all birds, with the exception of penguins, probably have this type of photoreceptor (Hart 2001, 2004).

Others have drawn attention to the importance of leaf reflectance spectra in evolution of long-wavelength spectra. Kelber (1999) suggested that having multiple long-wavelength receptors allows butterflies to discriminate between different leaf greens as an aid to oviposition. Likewise, sawflies and their allies (Symphyta), with

vegetarian (and often folivorous) larvae, have a red (600 nm) receptor, in addition to the usual three that they share with other bees and wasps (Peitsch *et al.* 1992; one bee in this study of 42 species also had a red receptor).

Mollon and his collaborators (Mollon & Regan 1999; Sumner & Mollon 2000a,b; Regan *et al.* 2001) propose a rather different scenario to account for the tuning of primate L and M pigments. They note that mature leaves of different plant species give a small range of red–green (i.e. L–M) signals, and propose that the spectral tuning of the receptors may be adapted to *minimize* these signals. The small range of leaf red–green signals might simplify the task of locating ripe fruit, which tend to be reddish. Regardless of its validity, this proposal nicely illustrates how sense organs may be adapted for specific behavioural tasks, in this case classifying fruit and leaf reflectance spectra.

4. CONCLUSION

There is clear evidence for adaptive variation in visual pigments among fishes, and also New World primates (Surridge *et al.* 2003; Osorio *et al.* 2004). Models of visual coding are useful for showing how spectral signals, receptor noise and behavioural tasks can substantially influence photoreceptor spectral tuning. They do not clearly identify what eyes are adapted to see. Photoreceptor spectral sensitivities, either as adaptations for luminance or for chromatic coding, should be a straightforward problem in sensory ecology. It is perhaps salutary that there are so few answers, at least regarding diurnal land animals. Open questions include the range of sensitivity maxima among LWS pigments of rodents and other mammals, the reasons for co-expressing pigments and the gradient of co-expression that occur in rodents and butterflies and the occurrence of multiple long-wavelength sensitive receptors in primates, butterflies and other insects.

D.O. was funded by a visiting fellowship to the Centre for Visual Science at the Australian National University. We thank A. Briscoe and the referees for advice.

5. ENDNOTES

¹In insects, achromatic signals used for behaviours such as phototaxis and celestial navigation are derived from UV-sensitive receptors.

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