# Efficient coding, natural colour statistics and photoreceptor responses

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## ABSTRACT

We investigate how the amount of information about colours in natural scenes available to the visual system depends on the spectral sensitivities of the three types of cones. In contrast to most trichromatic animals, humans and other old-world primates have a large overlap in the sensitivities of their M- and L-cones, which have peak sensitivities at approximately 540nm and 565nm. As a result, the activations of L- and M-cones are strongly correlated, which reduces the signal to noise ratio and so is apparently not ideal for colour vision. We find that a significant increase in colour information could be achieved, but only if the L-cone were sensitive to even longer wavelengths. However, this might lead to a reduction in spatial acuity and to the information available in dim lighting conditions.

## 1. INTRODUCTION

The M- and L-cones in the primate retina have peak sensitivities at about 540nm and 565nm, while the S-cone sensitivity peaks at about 445nm (figure 1). These sensitivities have been stable across many species for a long period of evolutionary time[2], which is strong evidence that they are optimal for primate vision. If the cone sensitivities were adapted to give the best possible colour vision, we might expect them to give the maximum possible information about reflectances of surfaces in a natural environment. However, the spectral sensitivities of the M- and L-cones have a considerable overlap, which must lead to a high degree of correlation in the activities of M- and L-cones, and as a result much of the information in the cones' activities is redundant. It is also possible that cones are not adapted for colour vision in general, but for a specific task such as finding coloured fruit[2,3]. The cone sensitivities might then give the maximum possible information about edible fruit but not about all colours in natural scenes.

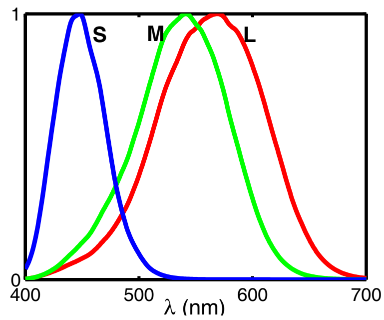


**Figure 1:** Spectral sensitivities of the three cone types[1].

We will compute the amount of information about colours in cone responses, using two estimates of the statistics of surface reflectances in natural scenes, and also using an estimate of the statistics of reflectances of fruit eaten by primates. We find that both for natural scenes in general, and for fruit, more information would be given if the L-cone were sensitive to the longest possible wavelength. We also discuss possible disadvantages that this would entail for spatial vision and vision in dim light.

## 2. COLOUR STATISTICS AND MUTUAL INFORMATION

If the cone sensitivities have been adapted to optimally identify the reflectances of surfaces, with no constraints on the possible values of $\lambda_{max}$ of the cones, we would expect the cone outputs to give the maximum possible information about the reflectance in natural scenes. That is, the cone sensitivities would maximise the mutual information between cone outputs and reflectances in natural scenes. To compute this mutual information, we need to know the distributions of reflectances, and of cone responses to the reflected light.

We represent reflectances $S(\lambda)$ by a linear combination of three principal components

$$S(\lambda) = S_0(\lambda) + \sum_{i=1}^{3} W_i s_i(\lambda) \quad (1)$$

where $S_0$ is the mean reflectance, and $s_i$ are the principal components. We obtain the principal components, and estimate the distribution of the weights $W_i$, for three sets of data: Vrhel et al's database of reflectances of 170 surfaces[4], Nascimento et al's hyperspectral images of rural scenes[5], and Sumner and Mollon's reflectances of tropical fruit[6]. For each set of data, we fitted a truncated Gaussian distribution which takes account of the fact that $S(\lambda)$ must lie between 0 and 1 for all values of $\lambda$; ie. For a reflectance with $\mathbf{W}=(W_1,W_2,W_3)$, $p(\mathbf{W})=0$ if $S(\lambda)<0$ or $S(\lambda)>1$ for any $\lambda$; otherwise $p(\mathbf{W})=\exp[\Sigma_i(W_i-m_i)^2/2v_i]$, where $m_i$ and $v_i$ are chosen to give the distribution the same mean and variance as the data.

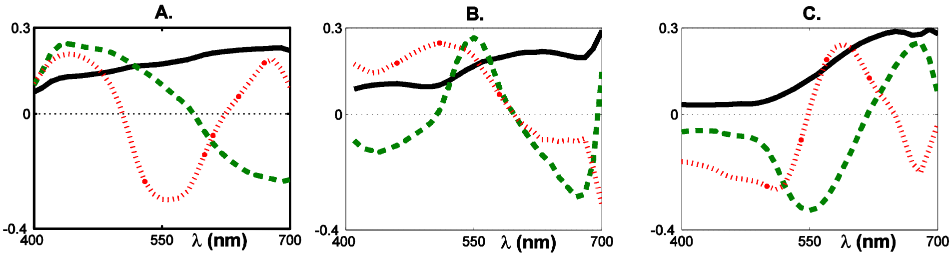


**Figure 2:** Principal components for **A.** the Vrhel et al reflectances; **B.** the Nascimento et al images; and **C.** the Sumner & Mollon fruit reflectances. In each case the 1st P.C. is the solid line, the 2nd P.C. is the dashed line and the 3rd P.C. is the dotted line; the first three P.C.s account for approximately 98% of the variance of each set of data.

There are considerable differences between the three datasets (figure 2). The Vrhel et al. reflectances include the widest variety of surfaces. Nascimento et al.'s images of rural scenes are dominated by greens and reds, while the reflectances of fruit are even more dominated by reds. In addition, the 1st P.C., which corresponds roughly to luminance as it is always positive, has 81% of the variance for the Vrhel et al. data, 89% for the Nascimento et al. data and 72% for the Sumner & Mollon fruit data. This indicates that the rural images have the lowest proportion of chrominance to luminance information, and the fruit reflectances the highest proportion.

The mean quantum catch $Q_i$ of a cone with spectral sensitivity $g_i(\lambda)$, for light reflected by a reflectance $S(\lambda)$ in an illuminant $E(\lambda)$, is

$$Q_i = \int_{400}^{700} E(\lambda)[S_0(\lambda) + \sum_{i=1}^{3} W_i s_i(\lambda)] g_i \, d\lambda \qquad (2)$$

and we use CIE65 daylight as $E(\lambda)$. The cone responses are subject to various sources of noise. In low levels of light, when cones are close to threshold, dark noise in the cones is most important. However, in most conditions, quantum noise is much greater than the dark noise, and when quantum noise is dominant the probability distribution for the cone output $O_i$ given a reflectance ($\mathbf{W}$), $p(O_i|\,\mathbf{W})$, is a Poisson distribution with mean $Q_i$. In this case the signal to noise ratio for each cone type will depend on the range of quantum catches, which in turn depends on $\lambda_{max}$. In very bright light (or for vision at low spatial frequencies, when the outputs of many cones are combined), quantum noise becomes insignificant compared to post-receptor sources of noise, and we take $p(O_i|\mathbf{W})$ to have a Gaussian distribution. In this condition we expect the gain of the cone output to adapt to maintain a constant signal to noise ratio. However, we obtain similar results for both types of noise.

Given $p(\mathbf{W})$ and $p(O_i|\mathbf{W})$, we can compute the mutual information between reflectances and cone outputs

$$I_M = \int p(\mathbf{O},\mathbf{W}) \log[\frac{p(\mathbf{O},\mathbf{W})}{p(\mathbf{W})p(\mathbf{O})}] d\mathbf{W} d\mathbf{O} \qquad (3)$$

where $p(\mathbf{W})$, $p(\mathbf{O})$ and $p(\mathbf{W},\mathbf{O})$ are respectively the distributions of $\mathbf{W}=(W_1,W_2,W_3)$, $\mathbf{O}=(O_1,O_2,O_3)$ and jointly ($\mathbf{W}$ and $\mathbf{O}$), with $p(\mathbf{W},\mathbf{O})= p(\mathbf{O}|\mathbf{W})\, p(\mathbf{W})$.

## 3. RESULTS

We evaluated the information given by equation (3) using the Stockman & Sharpe spectral sensitivity curves, but varying $\lambda_{max}$ by shifting the whole curve to longer or shorter wavelengths. The total information (in bits/cone integration time) increases as the variance of the noise in the cone responses decreases, and hence as the intensity of the illuminant increases. However, the variation of $I_M$ with $\lambda_{max}$ does not depend strongly on noise variance, or on whether the noise is Poisson or Gaussian, provided the signal to noise ratio is much greater than 1.

Figure 3 shows how the information varies with $\lambda_{max}$ for the L-cone, when the S- and M-ones are unchanged. The total information would be greater if $\lambda_{max}$ were larger. Similarly, the total information would increase if the M-cone were sensitive to longer wavelengths than the L-cone (figure 4). If we assume that the M-cone is constrained to have $\lambda_{max}$ at a shorter wavelength than the L-cone, then it is close to its optimum position, although a small increase in information can be obtained by increasing the separation of M- and L-cones by about 20nm. We also find that the information would be slightly increased if the S-cone were sensitive to even shorter wavelengths, but this last result does not take account of the increased absorption of light by the lens and macular pigment at short wavelengths. The results for each cone type are very similar for all three sets of statistics.

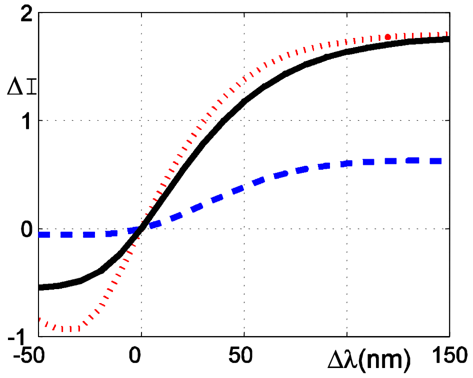


**Figure 3:** Change in information in cone responses, in bits, when $\lambda_{max}$ for the L-cone is changed by $\Delta\lambda$ relative to the Stockman & Sharpe spectral sensitivity, with the S- and M-cones unchanged. Solid line: Vrhel et al reflectances. Dashed line: Nascimento et al images. Dotted line: Sumner & Mollon fruit reflectances.

Figure 5 shows the change in total information when the sensitivities of the L- and M-cones are varied together, keeping their separation fixed. In this case, in contrast to figures 3 and 4, the maximum information is not achieved when $\lambda_{max}$ is as large as possible. Under this constraint, the cone sensitivities are very close to the optimal values for the statistics of the Nascimento et al hyperspectral images, although an increase of approximately 40nm would give maximum information for the Vrhel et al reflectances.

## 4. DISCUSSION

We have found that the amount of information about colour encoded in cone outputs would be considerably greater if one cone type were sensitive to longer wavelengths. This is true both for natural scenes, and for colours of edible fruit. A simple explanation for this is that, in all three of the sets of statistics we used, there is considerable variation in the reflectances at long wavelengths. Thus, the output of the L-cone would be less strongly correlated with that of the M-cone if the L-cone were sensitive to longer wavelengths. Changing the sensitivity of the M-cone so that it is mid-way between the L- and S-cones would not give a large increase in information.

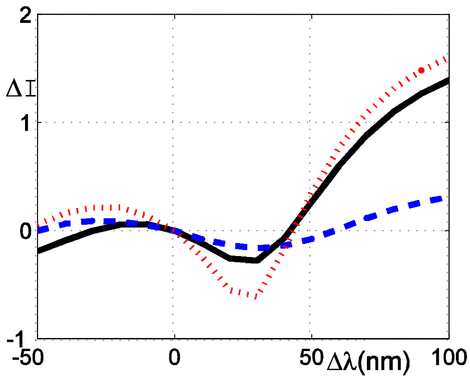


**Figure 4:** Change in information in cone responses, in bits, when $\lambda_{max}$ for the M-cone is changed by $\Delta\lambda$ relative to the Stockman & Sharpe spectral sensitivity. Solid line: Vrhel et al reflectances. Dashed line: Nascimento et al images. Dotted line: Sumner & Mollon fruit reflectances.

In varying the spectral sensitivity of the cones, we have implicitly assumed that $\lambda_{max}$ can take any value between 400nm and 700nm, and that the optimal values are those that give most information in photopic conditions. Our results also show that if the maximum value of $\lambda_{max}$ for the L-cone, or the maximum separation of the M- and L-cones, or both, are constrained by other factors, the human cone sensitivities could be optimal for colour vision. Such constraints could arise from the impact on spatial vision of changing the cone spectral sensitivities.

In bright light, the limit of resolution of the eye is determined by diffraction at the pupil. The size of the pointspread function due to diffraction is proportional to the wavelength of the light, and so an increase in $\lambda_{max}$ for the L-cone would lead to an reduction in the maximum spatial frequency to which the eye is sensitive, and consequently to a reduction in spatial information which may be greater than the increase in colour information. Similarly, an increase in the separation of L- and M-cones would lead to increased chromatic aberration, which again would lead to a reduction in spatial information.

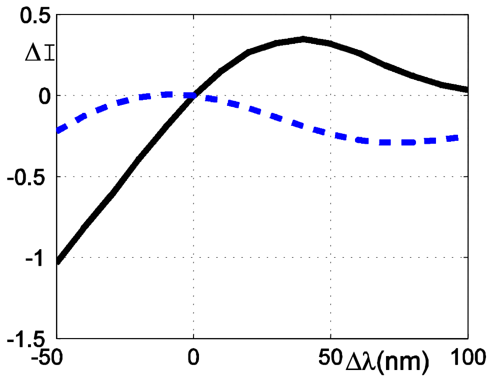


**Figure 5:** Change in information in cone responses, in bits, when $\lambda_{max}$ for the L- and M-cones is changed by $\Delta\lambda$ relative to the Stockman & Sharpe spectral sensitivities, with the separation between the two cone types fixed. Solid line: Vrhel et al reflectances. Dashed line: Nascimento et al images.

In very dim light, when cones are only slightly above threshold, the signal to noise ratio for cones is much lower than in brighter light and correlations between cones become less important. The maximum information in cone outputs is then achieved when the quantum catch of each cone type is maximized. This requires $\lambda_{max}$ for the L- and M-cone to be the same, and thus any increase in their separation would lead to a loss of information in dim light.

These results do not contradict the theory that primate cones are specifically optimized for finding fruit, or for detecting coloured targets against a background of leaves[6,7]. However, our results are consistent with cone sensitivities simply being adapted to give maximum possible information about natural scenes across all spatial scales and all levels of illumination.

## References

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