Detection of Fruit and the Selection of Primate Visual Pigments for Color Vision

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Abstract: Primates have X chromosome genes for cone photopigments with sensitivity maxima from 535 to 562 nm. Old World monkeys and apes (catarrhines) and the New World (platyrrhine) genus Alouatta have separate genes for 535-nm (medium wavelength; M) and 562-nm (long wavelength; L) pigments. These pigments, together with a 425-nm (short wavelength; S) pigment, permit trichromatic color vision. Other platyrrhines and prosimians have a single X chromosome gene but often with alleles for two or three M/L photopigments. Consequently, heterozygote females are trichromats, but males and homozygote females are dichromats. The criteria that affect the evolution of M/L alleles and maintain genetic polymorphism remain a puzzle, but selection for finding food may be important. We compare different types of color vision for detecting more than 100 plant species consumed by tamarins (Saguinus spp.) in Peru. There is evidence that both frequency-dependent selection on homozygotes and heterozygote advantage favor M/L polymorphism and that trichromatic color vision is most advantageous in dim light. Also, whereas the 562-nm allele is present in all species, the occurrence of 535- to 556-nm alleles varies between species. This variation probably arises because trichromatic color vision favors widely separated pigments and equal frequencies of 535/543- and 562-nm alleles, whereas in dichromats, long-wavelength pigment alleles are fitter.

Keywords: primate, color vision, modeling, balancing selection, evolution.

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Table 1: M/L pigment genes present in various primate genera

<table>
<thead>
<tr>
<th>Suborder, family, genus</th>
<th>Number of genes</th>
<th>( \lambda_{\text{max}} ) of known pigments</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Catarrhini:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Human</td>
<td>2</td>
<td>535, 562</td>
<td>Dartnall et al. 1983; Jacobs and Deegan 1999</td>
</tr>
<tr>
<td>Platyrrhini:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Atelidae:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alouatta</td>
<td>2</td>
<td>535, 562</td>
<td>Jacobs et al. 1996</td>
</tr>
<tr>
<td>Ateles</td>
<td>1</td>
<td>550, 562</td>
<td>Jacobs and Deegan 2001</td>
</tr>
<tr>
<td>Cebidae:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saimiri</td>
<td>1</td>
<td>535, 550, 562</td>
<td>Jacobs and Neitz 1987</td>
</tr>
<tr>
<td>Aotus^</td>
<td>1</td>
<td>540</td>
<td>Jacobs et al. 1993</td>
</tr>
<tr>
<td>Saguinus</td>
<td>1</td>
<td>540, 555, 562</td>
<td>Jacobs and Deegan 2003</td>
</tr>
<tr>
<td>Strepsirhini:^b</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lemuridae:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Propithecus</td>
<td>1</td>
<td>545, 562</td>
<td>Jacobs et al. 2002</td>
</tr>
</tbody>
</table>

Note: The pigment is designated by the wavelength of the absorbance maximum, \( \lambda_{\text{max}} \). The apparent absence of an allele from a species simply may mean that it has been overlooked, especially where samples are drawn from a small number of individuals or an inbred group. At present, there is no clear evidence for differences in the alleles present between species within a genus.

^a Owl monkeys (Aotus spp.) have a defective S cone pigment and so are cone monochromats.

^b Some tarsiers and strepsirhines may have only one allele (Tan and Li 1999).

on the X chromosome, but often this gene is polymorphic and has alleles for two or three spectral types of photopigment (table 1). Behavioral studies confirm that heterozygous females, which express two M/L pigments, are trichromats, whereas males and female homozygotes are dichromats (Jacobs and Blakeslee 1984; Mollon et al. 1984; Jacobs 1993). In addition to polymorphism within species, the sets of alleles vary between species (table 1).

To our knowledge, all have a 562-nm allele, but \( \lambda_{\text{max}} \) of the shorter wavelength variants ranges from 535 to 556 nm (Jacobs and Deegan 2003). A polymorphic population with three alleles can have six visual phenotypes, which we denote according to the type of M/L pigments present (table 2); three dichromatic, \( D_M \), \( D_A \), \( D_L \), and three trichromatic, \( T_{ML} \), \( T_{MA} \), \( T_{LA} \). In this article, “M” refers to pigments with \( \lambda_{\text{max}} \) of 535 or 543 nm, “A” (anomalous) refers to 550- or 556-nm pigments, and “L” refers to the 562-nm pigment.

Color vision is an attractive subject for investigating the evolution and ecology of a sensory system, in part because of the straightforward relationship between the genotype and spectral phenotype of visual photopigments (Yokoyama and Radlwimmer 2001). Spectral sensitivity differences between M/L pigments are primarily caused by amino acid substitutions at only three sites on the opsin protein (Neitz et al. 1991; Asenjo et al. 1994). Genetic sequence data and the fact that many species are polymorphic strongly imply that the polymorphism of the M/L gene in New World primates is maintained by balancing (i.e., frequency-dependent) selection, and that stabilizing selection conserves the spectral sensitivities of the pigments encoded by the different alleles (table 1; Boissinot et al. 1998; Cropp et al. 2002; Surridge and Mundy 2002; Surridge et al. 2003). Data on allele frequencies are clearly relevant to understanding selective basis for the M/L polymorphism, and here there are two relevant studies. First, in seven callitrichine (marmosets and tamarins) species, the 556-nm allele is significantly rarer than the 562-nm allele (Surridge and Mundy 2002). By comparison in three species of squirrel monkey (Saimiri spp.) the mean frequencies of 535-, 550-, and 562-nm genes are, respectively, 0.64 : 1.0 : 0.88 (sample size = 257 alleles; Cropp et al. 2002). Thus, the 550-nm allele is most common and the 535-nm least common. The 535-nm allele’s absence from callitrichines and rarity or absence from other groups (table 1) are additional evidence suggesting that it is at a selective disadvantage when there is a single M/L gene.

Why should M/L polymorphism be retained by some lineages when the gene has duplicated in others, and why are different sets of alleles present in different species (table 1)? Mollon et al. (1984) pointed out that two main types of explanation for the polymorphism are possible. One possibility is that the fitness of various color vision was made by ranking the relative frequencies of M/L alleles (0, commonest; 2, rarest) in the species for which Surridge and Mundy (2002) sampled >10 alleles (total 207 sequences). The mean ranks are 543 : 10, 556 : 1.6, and 563 : 0.4. The 562-nm allele is significantly more common than the 556-nm allele (Wilcoxon signed rank test \( Z = -2.38; P = .017 \)). Species: Saguinus labiatus, Saguinus fuscicollis, Saguinus imperator, Saguinus mystax; Callimico goeldii; Leontopithecus chrysomelas, Leontopithecus rosalia.
Table 2: The six color vision phenotypes, with M/L pigment $\lambda_{max}$ values, for squirrel monkeys and tamarins

<table>
<thead>
<tr>
<th>Squirrel monkey, $\lambda_{max}$</th>
<th>Tamarin, $\lambda_{max}$</th>
<th>Visual phenotype</th>
<th>Abbreviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>535</td>
<td>543</td>
<td>Protantopic dichromat</td>
<td>D_M</td>
</tr>
<tr>
<td>550</td>
<td>556</td>
<td>...</td>
<td>D_A</td>
</tr>
<tr>
<td>562</td>
<td>562</td>
<td>Deuteranopic dichromat</td>
<td>D_L</td>
</tr>
<tr>
<td>535, 562</td>
<td>543, 562</td>
<td>Normal trichromat</td>
<td>T_{LM}</td>
</tr>
<tr>
<td>535, 550</td>
<td>543, 556</td>
<td>Protoanomalous trichromat</td>
<td>T_{MA}</td>
</tr>
<tr>
<td>550, 562</td>
<td>556, 562</td>
<td>Deuteroanomalous trichromat</td>
<td>T_{LA}</td>
</tr>
</tbody>
</table>

Note: Names are based on those used for human color deficiencies (Birch 2001). The abbreviations are those used in the text.
Figure 1: A. Black line = mean reflectance of all species of fruit consumed by tamarins in this study (online app. A). The reflectance of each sample was normalized to the value at 700 nm. Gray lines = normalized spectral sensitivities of human S, M, and L cone photoreceptors (Smith and Pokorny 1975). Normalization of reflectance spectra here and in figure 2 is for the purposes of these illustrations only; we did not normalize reflectances when calculating receptor excitations. B, Mean reflectance of all upper leaf surfaces (solid lines) and lower leaf surfaces (dotted line) from plants consumed by tamarins in this study. The reflectance of each sample was normalized to the value at 550 nm. Gray lines = human spectral sensitivities as above (see also fig. 4). C, Illumination spectrum used for the model. The spectrum was recorded at the field site.

Modeling Color Signals

We seek to establish how different types of color vision will serve in detecting fruit against a background of leaves. Measurement accuracy, whether by biological or artificial sensors, is limited by noise (i.e., fluctuations that mask the signal; Cohn 2004). This means that a model of discrimination requires knowledge of signals and noise. To predict discriminability of pairs of colors (i.e., fruit against leaves) this study uses a three-stage model (fig. 2; app. B in the online edition of the American Naturalist): first, receptor responses to fruit and leaf spectra are calculated; second, noise is added to the receptor signals; and third, we specify how these noisy signals are used for color discrimination. Models of this kind have been applied to human data since the nineteenth century, chiefly to help understand the mechanisms of color vision (Kelber et al. 2003). The model used here assumes that full use is made of information about chromaticity (i.e., hue and saturation) present in noisy receptor responses and that differences in achromatic intensity (i.e., brightness) are ignored. This model has two advantages. First, it predicts color discrimination thresholds of humans and many other animals within experimental error (Sperling and Harwerth 1971; Osorio and Vorobyev 1996; Vorobyev and Osorio 1998; Vorobyev et al. 2001; Goldsmith and Butler 2003; Kelber et al. 2003). Second, the model is simple in terms of its implications for the underlying physiology because it is specified entirely by measurements of receptor sensitivities and makes minimal assumptions about subsequent neural processing (e.g., color opponency).

As is usual in visual science, signals are specified by their contras, that is, the ratio of intensities, rather than absolute differences. Contrast is defined as $\Delta I/I$, where $I$ is the mean or background intensity and $\Delta I$ the change in intensity. Contrast is a useful parameter because it is dependent on reflection of surfaces and independent of illumination intensity. In addition, Weber’s law—perhaps the best known of all psychophysical laws—states that contrast threshold $\Delta I/I$ is constant and independent of $I$. Weber’s law holds over a wide range of conditions but not universally, especially at relatively low intensities (Barlow 1972). The failure of Weber’s law is manifest by the fact that faint or fine patterns are best viewed under bright light. Because light levels in tropical forest vary widely, even during the daytime, it is necessary to take account of such intensity effects on contrast sensitivity in comparing different types of color vision.

Intensity dependence of contrast sensitivity arises because whereas contrast is unaffected by illumination intensity, noise is intensity dependent. Photoreceptors suffer from three main sources of noise, which dominate at different intensity ranges (Barlow 1964). The first, in dim
Figure 2: Summary of the method used to estimate the color signal for target fruit against a background of leaves (online app. B). A, Estimates of photoreceptor quantum catches and noise are obtained for target (T) and background (B) spectra (online eqq. [B1]–[B4]). B, Loci of target and background stimuli in a Cartesian space whose axes are given by the responses of S, M, and L cones. For T and B spectra, the estimated cone excitations locate the centers of ellipsoids whose dimensions are given by the standard deviation of noise in each cone mechanism. The model of discriminability projects the ellipsoids onto a two-dimensional chromatic surface (C), which represents differences in hue and saturation but not brightness. C, Color distances (ΔS) separating a target from three background spectra are given by the distance between ellipse centers divided by the noise (online eqq. [B5], [B6]). The minimum value of ΔS was used as an estimate of the visibility of a given fruit spectrum. With multiple fruit samples, the average signal was given by the median of these minima.
Methods

Data Collection

From January to December 2000, we measured some 3,000 reflectance spectra from 179 food-plant species (app. A) consumed by two species of tamarin (Saguinus fuscicollis and Saguinus mystax) at the Estación Biológica Quebrada Blanco II (4°21’S, 73°09’W) in northeastern Peru (for details see Heymann and Hartmann 1991). Although, strictly speaking, not all consumed foods were fruit, most were, and all foods hereafter are described simply as “fruit.” Reflectance spectra were from at least three fruits and three mature leaves of each species; spectra were recorded, where possible, from fruit discarded by tamarins as they fed and from both the upper and undersides of leaves. Spectra were recorded on the day of collection under an HL-2000 halogen lamp (Ocean Optics, Dunedin, Fla.) relative to a barium sulphate standard. We used an S2000 spectrometer (Ocean Optics), which was frequently recalibrated to minimize drift. To standardize records and to minimize specular reflection, spectra were recorded in a special-purpose holder with a fixed geometry between the light source, object surface, and radiometer (Lucas et al. 2001).

We recorded illumination spectra in the forest with the S2000 spectrometer calibrated by a standard lamp (LS-1-Cal, Ocean Optics). This study uses one of these illumination spectra for modeling spectral signals (fig. 1C). In nature, illumination spectra vary between sunlight and shadow and under foliage (Endler 1993). However, we restrict ourselves to the single illuminant because previous work (Vorobyev et al. 1998; Regan et al. 2001) shows that variations have minor effects on discriminability and would not affect our conclusions.

Modeling Discriminability of Fruit against Leaves

The model of color discrimination (fig. 2; app. B) predicts the discriminability of any two spectra measured in units of just noticeable difference (JND). The value of 1 JND is based on data from a laboratory observer required to detect a target against a background under specific viewing conditions with a specified accuracy (e.g., Sperling and Harwerth 1971). Ideally, a stimulus that exceeds 1 JND is detectable and one that falls below this threshold is not. In practice, animals are unlikely to be operating under laboratory conditions. Nonetheless, the model clearly indicates performance of color vision close to the threshold. To take account of the effects of varying viewing conditions (e.g., stimulus size) we tabulate performance in bright light with nominal thresholds ranging from 1 to 4 JNDs (table 3).

<p>| Table 3: Performance of different types of color vision |</p>
<table>
<thead>
<tr>
<th>JND</th>
<th>Dichromats</th>
<th>Trichromats</th>
</tr>
</thead>
<tbody>
<tr>
<td>T_{ML}</td>
<td>T_{MLA}</td>
<td>T_{LA}</td>
</tr>
<tr>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Bright</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>56</td>
<td>58</td>
</tr>
<tr>
<td>2</td>
<td>40</td>
<td>38</td>
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<tr>
<td>3</td>
<td>26</td>
<td>22</td>
</tr>
<tr>
<td>4</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td>Dim</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>5</td>
<td>5</td>
</tr>
</tbody>
</table>

Note: Percentages of fruit color signals that exceed a specified threshold for the main types of tamarin and squirrel monkey color vision (table 2) under both bright and dim illumination. For bright illumination where the contrast threshold is fixed, predictions are for nominal thresholds from 1 to 4 JNDs and for dim illumination where photon noise dominates at 1 JND. The predicted relative advantage of trichromy over dichromy is greater under dim illumination. JND = just noticeable difference.

Results are tabulated in two ways. The first (table 3; fig. 3) is as the percentage of signals that exceed a specified threshold from 1 to 4 JNDs. Roughly speaking, 1 JND corresponds to performance under ideal conditions, and higher thresholds correspond to the effects of deteriorating conditions. Therefore, the range of thresholds shows how varying the difficulty of the task will affect performance of different types of eye. Second (tables 4, 5), to compare...
different types of color vision, A and B, without regard to actual value of discrimination thresholds, we assume that type A detects a fruit better than type B if the signal for A exceeds that for B.

**Dark Fruit**

Many fruit are "black" and shiny and as such are detected by their luster rather than their chromaticity. Accordingly, where the mean quantum catch of 535- and 562-nm cones viewing a fruit was <0.05 relative to a 100% white reflectance standard, the species was not used in this article. This limit was chosen because it accords with our subjective judgement as to when chromaticity (i.e., color) ceases to be useful.

**Results**

We estimated the visibility of 103 fruit species against upper and lower leaf backgrounds for the main types of color vision in New World monkeys (tables 1, 2). The two representative species were squirrel monkey (Cebinae) and tamarin (Callitrichinae), each of which has six color vision phenotypes. Although the spectra were from fruit eaten by tamarins, the squirrel monkey is also frugivorous and sympatric at the study site. Visibility of a fruit was defined as the median of the minimum signals in just noticeable differences between each fruit sample and the leaves (fig. 2). A fruit was deemed to be detectable if this value exceeded a threshold specified in units of human JND (app. B). We consider both "dim illumination," where photon noise dominates so that contrast sensitivity is intensity dependent, and "bright illumination," where the sensitivity asymptotes to a maximum (online eqs. [B2]–[B4]). Table 3 gives the proportion of suprathreshold signals for different types of eye, and for bright conditions, it shows nominal thresholds from 1 to 4 JNDS. Tables 4 and 5 compare different types of color vision using absolute chromatic signals (table 4) and where the differences between these signals exceeded 1 JND (table 5).

**Dichromats**

Dichromats have a fixed S cone pigment and a single M/L pigment whose peak sensitivity lies between 535 nm and 562 nm (table 1). There are three possible effects of varying this peak: first, that signals are unaffected by varying the M/L pigment; second, that one type of M/L pigment is always best; or third, that no one type of M/L pigment is best for finding all fruit species.

Under bright illumination, for all types of dichromat, 50%–60% of signals exceeded 1 JND (table 3; fig. 3). On average, the proportion of detectable fruit is similar for all three dichromat phenotypes (table 3), and the $D_A$ signals were invariably intermediate between the $D_M$ and $D_M'$. The most interesting observation is that the difference between the $D_A$ and $D_1$ phenotypes exceeded 1 JND in ~23% of cases for the tamarin and 40% for the squirrel monkey (table 5). Although $D_1$ phenotypes were best overall, for many individual fruit species, $D_M$ phenotypes have the advantage. For the tamarin eye, 11% of $D_M$ signals exceeded $D_1$ by >1 JND, and it was 16% for the squirrel monkey (table 5). This finding leads to the prediction that...
some fruit are most detectable to D_s eyes and others to D_M eyes, which is consistent with the third effect listed above, namely, that different phenotypes will be best for different fruit. Invariably, the D_M phenotype was best where the fruit were “bluer” than leaves, and the D_s phenotype was best where the fruit were less “blue” (yellower) than leaves. (Blueness is defined as \( S/(L + M) \), where \( L \), \( M \), and \( S \) are absorptions of the L, M, and S receptors normalized to the white standard; online eq. [B1].)

### Trichromats

Under both bright and dim illumination, standard trichromacy (T_ML) was best overall, and there were very few cases where it was inferior to any other type of color vision (tables 3–5; fig. 3). On average, but not invariably, the anomalous trichromat (T_MA, T_LA) signals were larger than dichromat signals (table 4). Where dichromats were better, their advantage never exceeded 1 JND (table 5) and hence might be considered negligible. A key point here is that the absolute and relative performance of different types of color vision is strongly dependent on the magnitude and type of noise. In particular, the relative advantage of trichromacy over dichromacy was greatest in dim illumination (table 3; fig. 3).

### Lower versus Upper Leaves

As is obvious from casual observation, upper leaf surfaces are greener and darker than lower leaves, and this difference is apparent when we plot luminance \((M + L)\) and red-green \((L/L + M)\) signals for leaves (figs. 1B, 4). Not unexpectedly, the model predicts substantial differences in the average detectability of fruit against upper and lower leaves, but the effect of intensity is interesting. For most types of color vision, fruit are most detectable against the upper leaves in bright light, when the larger color difference is advantageous, but in dim light, where photon noise is important, the advantage shifts by up to 30% toward detection against lower leaves (fig. 4B).

### Discussion

The salience of color in daily life belies its minor role in much of visual perception (Livingstone and Hubel 1988); we enjoy monochrome movies, and people may be unaware of their red-green deficiency (color blindness) until specifically tested. The fact that we can manage well without raises the question, What is the function of color vision? Discoveries during the 1980s of genes for human visual photopigments (Nathans 1999) and polymorphism of the M/L gene in New World monkeys stimulated interest (Jacobs and Blakeslee 1984; Bowmaker et al. 1987; Jacobs and Neitz 1987; Travis et al. 1988), but fundamental questions remain about the selective basis for gene duplication and allelic variation (Mollon et al. 1984; Cropp et al. 2002; Surridge and Mundy 2002; Surridge et al. 2003). For instance, if polymorphism is maintained mainly by heterozygote advantage, why have all primates not benefited from gene duplication? If, instead, frequency-dependent selec-
Table 5: Comparison of fruit detectability for the main types of color vision in tamarin and squirrel monkey (table 2), where the differences between phenotypes exceed 1 JND

<table>
<thead>
<tr>
<th></th>
<th>Bright illumination</th>
<th>Dim illumination</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dichromats</td>
<td>Trichromats</td>
</tr>
<tr>
<td>Tamarin:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DM</td>
<td>...</td>
<td>6</td>
</tr>
<tr>
<td>DA</td>
<td>6</td>
<td>...</td>
</tr>
<tr>
<td>DL</td>
<td>11</td>
<td>2</td>
</tr>
<tr>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>TMA</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>TL A</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Squirrel monkey:</td>
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<td></td>
</tr>
<tr>
<td>DM</td>
<td>...</td>
<td>8</td>
</tr>
<tr>
<td>DA</td>
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<td>DL</td>
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<td>TML</td>
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<td>0</td>
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<tr>
<td>TMA</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>TL A</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Note: Each cell gives the percentage of occasions where the signal of the column type exceeds that of the row type by 1 JND. JND = just noticeable difference.

Accounting for the Diversity of M/L Alleles in the 535–556-nm Range

All species with a single M/L gene and multiple alleles have a 562-nm allele, but why does selection maintain different ranges of shorter wavelength (535–556 nm) alleles in dif-
Did Trichromacy First Appear in Diurnal or Nocturnal Primates?

A prediction of this study is that the relative advantage of both normal and anomalous trichromacies over dichromacy is greatest in dim light where performance is limited by photon noise (fig. 3; table 3). This runs counter to the general prediction that as receptor noise rises, the relative advantage of trichromacy over dichromacy should decline (Hateren 1993). This advantage of trichromacy in dim light arises partly because of the low quantum flux below 500 nm in spectra reflected from both leaves and fruit (fig. 1); it is also partly due to absorption of short-wavelength light by the ocular media (Wyszecki and Stiles 1982; Toveé et al. 1992). Consequently, when photon catch sets thresholds, the S mechanism is more severely affected than the M/L mechanism (Vimal et al. 1989). Given that some type of color vision is beneficial, the low sensitivity of the S cones favors having separate M and L pigments with high

A prediction of this study is that the relative advantage of both normal and anomalous trichromacies over dichromacy is greatest in dim light where performance is limited by photon noise (fig. 3; table 3). This runs counter to the general prediction that as receptor noise rises, the relative advantage of trichromacy over dichromacy should decline (Hateren 1993). This advantage of trichromacy in dim light arises partly because of the low quantum flux below 500 nm in spectra reflected from both leaves and fruit (fig. 1); it is also partly due to absorption of short-wavelength light by the ocular media (Wyszecki and Stiles 1982; Toveé et al. 1992). Consequently, when photon catch sets thresholds, the S mechanism is more severely affected than the M/L mechanism (Vimal et al. 1989). Given that some type of color vision is beneficial, the low sensitivity of the S cones favors having separate M and L pigments with high
In primate M/L cone pigments, the relationship between genotype and phenotype is straightforward. Amino acid substitutions at three key sites account for almost all the spectral difference between 555- and 562-nm pigments, and a monkey’s color discrimination (or at least color matching) can be directly predicted from the complement of cones in its eyes (Jacobs 1993). That the basis for the selection of M/L pigments and genetic polymorphism remains obscure is a salutary demonstration of the difficulty of understanding the evolution and design of a sensory mechanism. Even with this simple system, many factors may be relevant. Among others, these might include the stimuli of interest, whether food or backgrounds; the noise in visual signals; the behavioral uses of color and luminance information (Livingstone and Hubel 1988; Osorio and Vorobyev 1996; Sumner and Mollon 2000a, 2000b); and the demands of higher-level vision concerned with tasks other than discrimination of spectra. One such task, for example, is to classify objects by their color, and this could have led to the selection of L and M pigment sensitivities that minimize the range of red-green (L-M) signals produced by leaves (Mollon and Regan 1999; Regan et al. 2001).

Nonetheless, given the evidence that balancing and stabilizing selection determine the pigment alleles present in those primates with a single M/L gene (Surridge et al. 2003), the aim of relating eye design to visual ecology seems worthwhile. Of particular interest is how diet affects lifestyle affect selection at this locus. For instance, selection may be strongest during food shortages when primates resort to “fallback” foods, with those that rely on leaves at these times benefiting most from trichromacy (Lucas et al. 1998, 2003; Dominy and Lucas 2001; Dominy et al. 2003). Conversely, it would be interesting to find a natural situation where dichromat monkeys or humans enjoy any advantage over trichromats. Present predictions of costs to trichromacy remain largely theoretical or confined to psychophysics laboratories (Morgan et al. 1992; Williams et al. 1993; Osorio et al. 1998). Finally, as receptor noise and hence light intensity substantially affect the relative merits of the different phenotypes, it would be useful to learn more about the light levels at which various primate species are active.

Acknowledgments

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