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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) 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.

Color vision is based on comparing responses of photoreceptors with differing spectral sensitivities. The numbers of receptor types and their spectral sensitivities vary substantially across the animal kingdom (Kelber et al. 2003), and there are corresponding variations in color discrimination. It is therefore interesting to ask how evolutionary history and visual ecology determine an animal's complement of spectral receptors. Primates are of particular interest because they are highly variable. There is evidence for widespread and evolutionarily stable genetic polymorphism, which gives up to six types of color vision in a population (tables 1, 2).

Comparative work on visual pigments, molecular genetics, and behavioral studies of color vision shows that Old World (catarrhine) primates normally have three types of cone photopigment (rhodopsin; table 1; fig. 1; Jacobs 1993; Nathans 1999). Red-green color-blind individuals are an exception (Birch 2001; Hanazawa et al. 2001). Color-normal individuals have the three pigments with sensitivity maxima (λ_{max}) close to 425 nm (short wavelength; S), 535 nm (medium wavelength; M), and 562 nm (long wavelength [L]; fig. 1; Dartnall et al. 1983; Jacobs and Deegan 1999). Note that λ_{max} values used in the text and tables 1 and 2 are typical and not necessarily the precise values published in the cited references; these vary by a few nanometers due to experimental method and error. An autosomal gene codes the S photopigment, while adjacent M and L genes on the X chromosome originate by duplication of a single ancestral gene (Dulai et al. 1999; Nathans 1999). Three visual pigments allow catarrhines to have trichromatic color vision, meaning that a mixture of three primary colors is needed to match any color (Kelber et al. 2003; Surridge et al. 2003).

The uniform set of visual pigments and "routine trichromacy" of Old World monkeys and apes can be contrasted with the diversity in New World (platyrrhine) monkeys and prosimians (tarsiers and strepsirhines). Howler monkeys (*Alouatta*) had a gene duplication, independent of that in the Old World, to give them separate M and L loci, and they too are trichromats (Jacobs et al. 1996; Dulai et al. 1999). Other genera have one M/L gene

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

Suborder, family, genus	Number of genes	λ_{max} of known pigments	Source
Catarrhini:			
Human	2	535, 562	Dartnall et al. 1983; Jacobs and Deegan 1999
Platyrrhini:			
Atelidae:			
Alouatta	2	535, 562	Jacobs et al. 1996
Ateles	1	550, 562	Jacobs and Deegan 2001
Cebidae:			
Saimiri	1	535, 550, 562	Jacobs and Neitz 1987
Aotus[a]	1	540	Jacobs et al. 1993
Saguinus	1	540, 555, 562	Jacobs and Deegan 2003
Strepsirhini:[b]			
Lemuridae:			
Propithecus	1	545, 562	Jacobs et al. 2002

Note: The pigment is designated by the wavelength of the absorbance maximum, λ_{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 λ_{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 λ_{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).[1] 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

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[1] Statistical comparison of M/L pigment allele frequencies in callitrichines 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 : 1.0, 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 chysomelas*, *Leontopithecus rosalia*.

Table 2: The six color vision phenotypes, with M/L pigment λ_{max} values, for squirrel monkeys and tamarins

Squirrel monkey, λ_{max}	Tamarin, λ_{max}	Visual phenotype	Abbreviation
535	543	Protanopic dichromat	D_M
550	556	…	D_A
562	562	Deuteranopic dichromat	D_L
535, 562	543, 562	Normal trichromat	T_{LM}
535, 550	543, 556	Protoanomalous trichromat	T_{MA}
550, 562	556, 562	Deuteroanomalous trichromat	T_{LA}

Note: Names are based on those used for human color deficiencies (Birch 2001). The abbreviations are those used in the text.

phenotypes is frequency dependent; that is, relative fitness of a phenotype decreases with increasing frequency in the population. This frequency dependence could arise perhaps because they can exploit different types of food. Alternatively, trichromacy may give an advantage to heterozygous females over all homozygous phenotypes (overdominance). These two possible explanations are not mutually exclusive, but the possibility of overdominance is of particular interest because there are few clear examples of this phenomenon, especially where more than two alleles are involved (Futuyma 1998; Crow 2000).

Selection of cone pigments depends upon the fitness of the different visual phenotypes and hence the animal's visual ecology, that is, the spectra of interest to the animal, behavioral uses of color and achromatic (i.e., luminance) information, and the light levels when activity takes place. One consideration is that trichromacy comes at a cost to achromatic vision. In trichromatic primates, the nervous system combines M and L cone signals to give a luminance signal, which is used for "color-blind" tasks such as motion detection and shape recognition (Livingstone and Hubel 1988; Mollon 1989). Differing spectral inputs could corrupt this luminance signal, much as TV signals are corrupted when fine patterns such as striped clothing are rendered as shimmering colored moiré patterns (Williams et al. 1993). This problem may result in the spectral separation of the M and L pigments being limited to a value below the optimum for color vision (fig. 1; Osorio et al. 1998). According to this argument, differences between species in the costs and benefits of trichromacy could account for their having different sets of M/L photopigments (table 1) and ultimately for dichromacy being favored over trichromacy. However, a trade-off between color and luminance vision is not sufficient to account for polymorphism because this requires frequency-dependent selection for different types of color vision. In this context, an interesting suggestion is that dichromats may have an advantage over trichromats in defeating camouflage by use of visual texture perception (Morgan et al. 1992). This advantage might arise either if color competes with texture information or if trichromats simply learn to rely on color at the expense of texture. It is therefore conceivable that dichromats and trichromats within a population could exploit different food sources, leading to frequency-dependent selection.

An alternative to invoking compromises between color and luminance vision in selection of primate visual pigments follows Allen's (1879) proposal that animal color vision evolved for finding fruit and flowers among leaves (Mollon 1989; Regan et al. 2001). Experiments support this suggestion for primates: trichromatic marmosets (*Callithrix geoffroyi*) and tamarins (*Saguinus* spp.) both have an advantage over dichromats in finding colored food in seminatural foraging conditions (Caine and Mundy 2000; Smith et al. 2003). Likewise, models suggest that trichromacy, in particular the red-green (L-M) chromatic signal using 535- and 562-nm pigments, is superior to dichromacy and may indeed be optimal for finding or recognizing edible fruit and leaves (table 1; Osorio and Vorobyev 1996; Sumner and Mollon 2000*a*; Dominy and Lucas 2001; Parraga et al. 2001; Regan et al. 2001). If color vision is indeed optimal, there is no need to invoke a compromise between demands of chromatic and luminance vision in selection of the visual pigments. However these arguments are generally applied to routine trichromacy of catarrhines and do not deal with M/L polymorphism. An exception is the review by Regan et al. (2001) who, in addition to an extensive discussion of visual ecology and eye design, discuss polymorphic color vision of New World primates. In particular, they suggest that frequency-dependent selection may be important, with different color vision phenotypes specializing on different types of food.

Regardless of whether the routine trichromacy of Old World primates is optimal for finding fruit or represents a trade-off between different demands of luminance and color vision, one lesson from previous work on primate visual ecology is that to make sense of the function of color vision requires data on the spectra that primates see in their daily lives. Here we investigate the selective influences on primate photopigments, based on a model of color signals for more than 100 species of food plant consumed by tamarins in the Peruvian Amazon (app. A in the online edition of the *American Naturalist*).

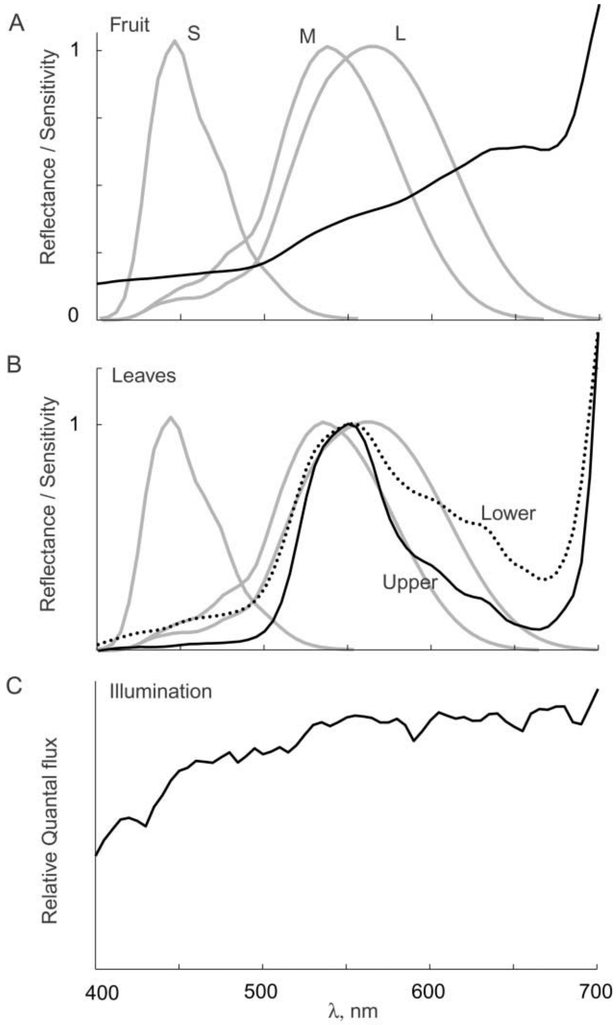

Figure 1: *A*, *Black line* = mean reflectance of all species of fruit consumed by tamarins in this study (online app. A). The reflectance of each sample was normalized to the value at 700 nm. *Gray lines* = normalized spectral sensitivities of human S, M, and L cone photoreceptors (Smith and Pokorny 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 ΔI 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 $\Delta I_{th}/I$ 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 illumination, is “dark noise” due to either thermal isomerization (i.e., without absorption of a photon) of photopigment molecules or other metabolic activity, which limits sensitivity (Koskelainen et al. 2000; Rieke and Baylor 2000). Second, at low light levels, variation in photon catch is likely to be the main source of noise. The laws of physics dictate that the variances in the number of quanta absorbed from a fixed light source have Poisson statistics; that is, the noise is proportional to the square root of the number of absorbed quanta. This means the contrast threshold should fall with the square root of intensity, a relationship known as the DeVries-Rose law (Barlow 1964; Rovamo et al. 2001). Third, in bright illumination, noise is proportional to signal intensity, leading to contrast thresholds being independent of intensity, as predicted by Weber’s law.

It is likely that in normal conditions color discrimination operates under both DeVries-Rose (dim illumination) and Weber’s law (bright illumination). In human color vision, Rovamo et al. (2001) find that the transition from a photon noise limit to Weber’s law occurs at about 160 trolands (a troland is a measure of illumination of the retina), which corresponds to moderate daylight. Although color thresholds are dependent on pooling multiple receptor signals and are affected by object size, this transition point is apparently independent of spatial scale (Rovamo et al. 2001).

As we have mentioned, this is not the first modeling study to evaluate color signals of natural primate foods. The principle that performance is limited by receptor noise is similar to that used by Regan et al. (1998, 2001) and by Sumner and Mollon (2000*a*), but their models differ from ours, chiefly because we are looking at different questions. We assume that in a trichromat, all three spectral types of cones are used together for color discrimination (app. B), whereas the latter papers consider two separate (photon noise–limited) dichromatic mechanisms, namely blue-yellow ($S - [L + M]$) and red-green ($L - M$). Modeling separate dichromatic signals is appropriate if the two types of signal are used for separate visual tasks and in particular if the red-green mechanism is used alone for finding food (Mollon 1989). In addition, there are differences in the measures used to evaluate the detectability of fruit against leaves. In this study, a fruit is assumed to be detectable when its difference from the most similar leaf of the same species exceeds a specific threshold. The alternative approach (Sumner and Mollon 2000*a*; Regan et al. 2001) uses the spectra of many species of leaf from the field site and evaluates the difference in red-green signals between the fruit and the mean leaf. The signal-to-noise ratio is defined as the ratio of this chromatic difference to the standard deviation of the leaf distribution added to photon noise.

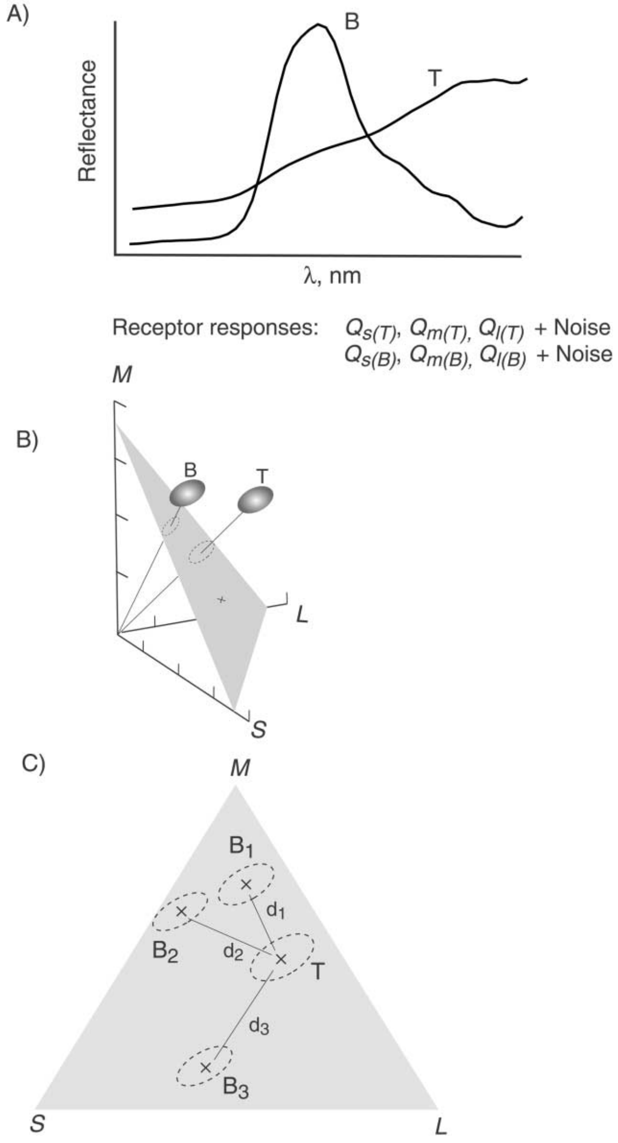

Figure 2: Summary of the method used to estimate the color signal for target fruit against a background of leaves (online app. B). *A*, Estimates of photoreceptor quantum catches and noise are obtained for target (*T*) and background (*B*) spectra (online eqq. [B1]–[B4]). *B*, Loci of target and background 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_{1-3}) 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. 1*C*). 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).

The model predicts the discriminability of any two spectra, but fruit and leaf spectra of a given species of plant vary. To evaluate the average visibility of fruit, we first calculate the color distance (online eqq. [B5], [B6]) between each fruit spectrum (the target) and each leaf spectrum (the background) from that species (fig. 2). Colors of upper and lower leaf surfaces differ substantially and consistently (fig. 1*B*), and the tasks of finding fruit from above (against upper leaves) and from below are treated separately. Given that fruit are relatively rare among leaves, a reasonable estimate of visibility is the minimum difference between a fruit spectrum and all leaf spectra (fig. 2). Because there are at least three fruit samples from each species, the color signal for a given species is the median of these minima. The median gives an indication of when 50% of the fruit will be visible. It should be noted that color signals are not normally distributed (M. Vorobyev, unpublished observations) and that the main conclusions are not affected by choice of a different statistic such as the mean.

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

Table 3: Performance of different types of color vision

	Dichromats			Trichromats		
JND	D_M	D_A	D_L	T_{ML}	T_{MA}	T_{LA}
Tamarin:						
Bright:						
1	56	58	59	93	87	76
2	40	38	36	74	60	44
3	26	22	24	53	38	28
4	14	14	16	34	23	16
Dim:						
1	5	5	6	58	32	10
Squirrel monkey:						
Bright:						
1	53	58	58	94	90	86
2	37	39	35	81	66	61
3	24	24	22	67	44	36
4	17	14	15	48	26	22
Dim:						
1	6	7	8	71	40	36

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 trichromacy over dichromacy is greater under dim illumination. JND = just noticeable difference.

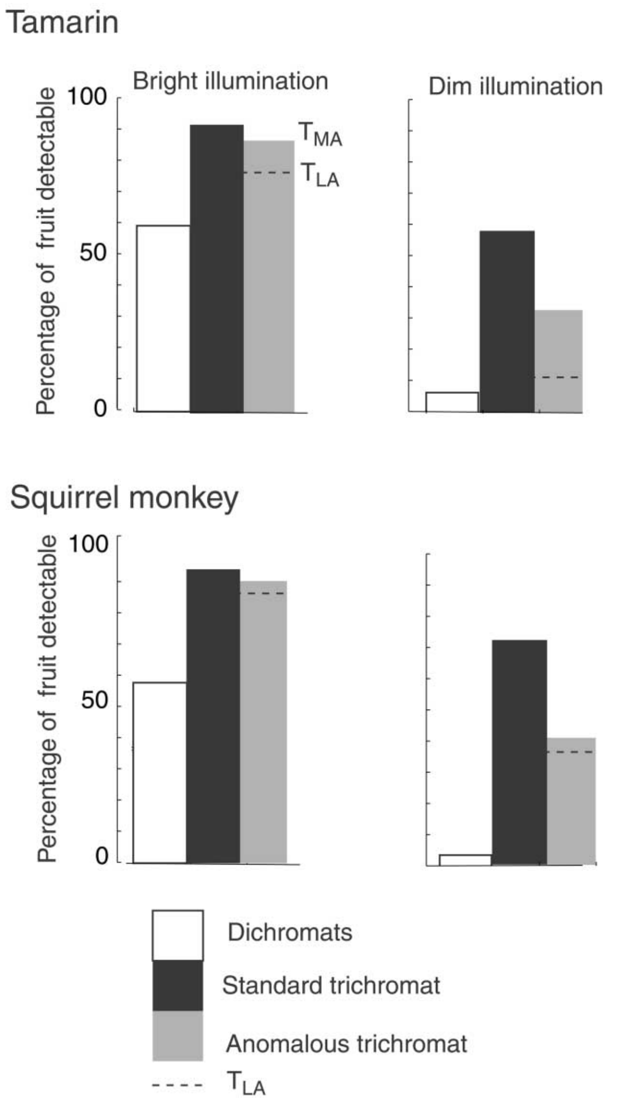

Figure 3: Overall performances of the different types of color vision (table 2), showing the percentage of fruit signals that exceed 1 JND (just noticeable difference) in bright and in dim illumination (table 3). Data for dichromats are averages for all three phenotypes. For anomalous trichromats, the T_{LA} (deuteroanomalous) type (*dashed line*) performed less well than the T_{MA} type (*gray bar*).

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 eqq. [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_L and D_M. The most interesting observation is that the difference between the D_M and D_L phenotypes exceeded 1 JND in ∼23% of cases for the tamarin and 40% for the squirrel monkey (table 5). Although D_L 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_L by >1 JND, and it was 16% for the squirrel monkey (table 5). This finding leads to the prediction that

Table 4: Comparison of fruit detectability for the main types of color vision in tamarin and squirrel monkey (table 2)

	Bright illumination						Dim illumination					
	Dichromats			Trichromats			Dichromats			Trichromats		
	D_M	D_A	D_L	T_{ML}	T_{MA}	T_{LA}	D_M	D_A	D_L	T_{ML}	T_{MA}	T_{LA}
Tamarin:												
D_M	…	55	54	97	96	67	…	52	53	100	99	96
D_A	44	…	55	98	89	90	42	…	54	100	100	98
D_L	45	44	…	95	79	78	44	41	…	100	100	99
T_{ML}	3	2	5	…	3	3	0	0	0	…	0	0
T_{MA}	3	10	21	95	…	21	0	0	0	100	…	0
T_{LA}	31	7	21	96	79	…	3	0	0	100	100	…
Squirrel monkey:												
D_M	…	54	54	98	97	79	…	52	51	99	100	10
D_A	46	…	56	98	94	94	43	…	54	99	99	100
D_L	45	43	…	99	81	89	42	40	…	100	100	100
T_{ML}	2	3	2	…	4	2	0	1	0	…	1	2
T_{MA}	3	6	19	97	…	29	1	0	0	99	…	23
T_{LA}	22	5	11	98	69	…	0	0	0	98	73	…

Note: Each cell gives the percentage of occasions where the signal of the column type exceeds that of the row type. The sums of complementary pairs of cells may be <100 because discriminability values are treated as equal when they differ by <0.01 JND. JND = just noticeable difference.

some fruit are most detectable to D_L 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_L 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. 1*B*, 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. 4*B*).

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

	Bright illumination						Dim illumination					
	Dichromats			Trichromats			Dichromats			Trichromats		
	D_{M}	D_{A}	D_{L}	T_{ML}	T_{MA}	T_{LA}	D_{M}	D_{A}	D_{L}	T_{ML}	T_{MA}	T_{LA}
Tamarin:												
D_{M}	…	6	12	56	36	18	…	0	0	37	10	1
D_{A}	6	…	0	54	37	4	0	…	0	37	11	1
D_{L}	11	2	…	54	37	8	0	0	…	38	10	0
T_{ML}	0	0	0	…	0	0	0	0	0	…	0	0
T_{MA}	0	0	0	17	…	0	0	0	0	1	…	0
T_{LA}	2	0	0	48	15	…	0	0	0	12	1	…
Squirrel monkey:												
D_{M}	…	8	24	74	44	47	…	0	0	56	21	12
D_{A}	8	…	3	72	42	37	0	…	0	58	19	13
D_{L}	16	6	…	70	43	36	0	0	…	57	16	10
T_{ML}	0	0	0	…	0	0	0	0	0	…	0	0
T_{MA}	0	0	0	52	…	0	0	0	0	17	…	0
T_{LA}	0	0	0	58	6	…	0	0	0	25	0	…

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.

tion for the different color vision phenotypes is important, there should be occasions when dichromats outperform trichromats. In practice, dichromat advantages can easily be contrived in the laboratory, but it is not certain when these arise in nature (Mollon et al. 1984; Morgan et al. 1992; Williams et al. 1993; Osorio et al. 1998). This study deals with color discrimination, so it would be surprising if any advantages of dichromacy came to light. Nonetheless, modeling of the signals that distinguish fruit from leaves together with an understanding of allelic variation in New World monkeys and prosimians (table 1) gives useful insights.

First, for dichromats, longer-wavelength alleles are, on average, advantageous for detecting fruit. An observable advantage of D_{L} color vision might be expected because of the larger spectral separation of the S and L pigments (Sumner and Mollon 2000*a*), but in practice it is rather small and inconsistent (tables 3–5). Many species of fruit are more detectable to D_{M} eyes than to D_{L} eyes (tables 4, 5). This could lead to different types of dichromat specializing on different types of fruit and could support frequency-dependent selection for the homozygous phenotypes, as suggested by Mollon et al. (1984).

Second, trichromacy is favored over dichromacy, and in trichromatic individuals, the standard 535-nm (M) and 562-nm (L) pigment pairs are better than the intermediate variants (tables 2, 4, 5). For detecting fruit, it is therefore unlikely that frequency-dependent selection amongst the trichromatic phenotypes favors the 550- and 556-nm alleles. More generally, it is unlikely that there is any significant task where the anomalous trichromats (T_{MA}, T_{LA}) have an advantage over the T_{ML} form. This is because receptor noise will always be the major constraint on performance of anomalous trichromats, outweighing any possible advantages such as dealing with the effects of variable illumination (Regan et al. 2001). This implies that the presence of the 550- and 556-nm alleles in primates with a single M/L gene is more likely to be because they increase the likelihood of females being heterozygous and hence having some type of trichromacy. This conclusion is consistent with the 535-nm allele being the norm in routine trichromats—catarrhines and howler monkeys—even though intermediate pigments arise commonly (at least in humans; Deeb et al. 1994; Nathans 1999). If the anomalous trichromats were at an advantage when rare, we would expect 550-nm pigment alleles to occur fairly commonly in catarrhine and howler monkey populations. In practice, the 550-nm allele is unknown in routine trichromats other than humans, where it is likely to be mildly deleterious. Similarly, it is likely that the 556-nm allele occurs at a relatively low frequency in callitrichines (Surridge and Mundy 2002) because the two trichromat phenotypes with this allele have inferior color vision to the standard T_{ML} phenotype.

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-

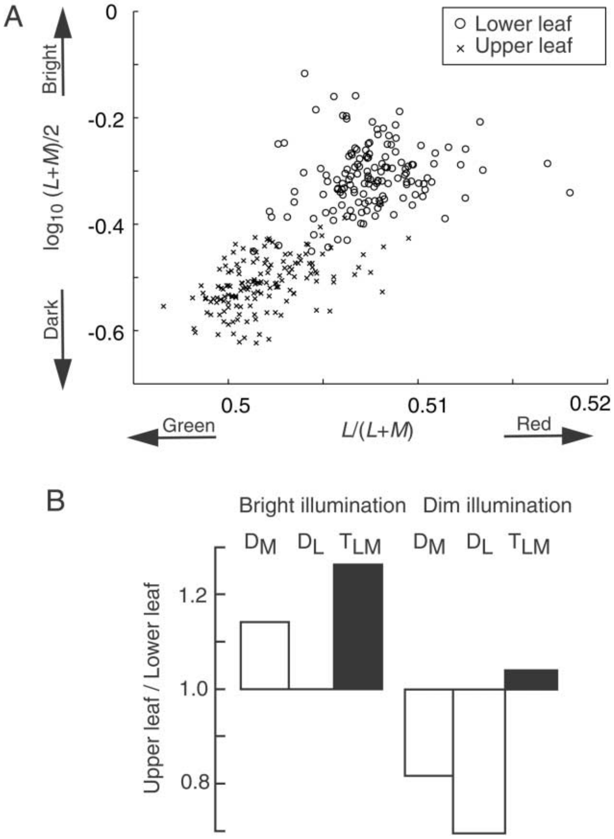

Figure 4: Differences between upper (*crosses*) and lower leaf (*circles*) surfaces. *A*, Estimated red-green ($L/[L+M]$) and luminance ($\log[L+M]$) signals for lower and upper surfaces, where L and M are responses of the squirrel monkey L and M receptors relative to a white standard (see Sumner and Mollon 2000*a*). There are no systematic differences in the blue-yellow ($S/[L+M]$) signals of upper and lower leaves. *B*, Estimated ratio of fruit detectability against upper compared with lower surfaces. Data are plotted for two types of dichromacy and normal trichromacy (table 2). It is clear that as light intensities fall from high (Weber's law) to low (photon noise limited), fruit tend to become more detectable against lower leaves. This is because lower leaf surfaces are brighter than upper leaf surfaces.

ferent species, probably at different frequencies (table 1; Cropp et al. 2002; Surridge and Mundy 2002)? As we have seen, for finding fruit and probably all other tasks, trichromatic color vision is best with 535- and 562-nm alleles (Osorio and Vorobyev 1996; Sumner and Mollon 2000*a*). It follows that 550- and 556-nm alleles may be present in species with a single M/L gene because increasing the number of alleles increases the proportion of trichromatic (heterozygote) females in a population. But although heterozygote advantage seems likely to be a major influence (tables 3–5; fig. 3), it cannot be a complete explanation for the occurrence of 550- and 556-nm alleles. If it were, the 535-nm allele should be present in all species and at least as common as 550- and 556-nm alleles. Instead the 535-nm allele is absent—or apparently absent—from several lineages and may be rare in squirrel monkeys (table 1; Cropp et al. 2002). The implication is that dichromatic individuals with the 535-nm allele are at a disadvantage, but the reason is not obvious. This could be due to their having either inferior (D_M) color vision or inferior luminance vision. One possibility is that in natural conditions, the 535-nm receptor captures 5%–10% less light than the 550/562-nm variants (D. Osorio, unpublished observations) and hence will suffer slightly worse receptor noise. In summary, it seems that the fitness of 535- to 556-nm alleles depends on a balance between the demands of trichromacy, which favors relatively widely separated pigments and equal allele frequencies of 535-nm (or 543-nm in callitrichines) and 562-nm alleles, and an advantage for long-wavelength alleles in dichromat eyes. In this context, it is of interest that although catarrhines always have a 535-nm M cone pigment, it is possible that selection against this pigment and in favor of the L cone explains the relatively low density of M cones compared with L cones in humans and perhaps other catarrhines (Deeb et al. 2000).

It may be objected that owl monkeys (*Aotus*), which are nocturnal, have a single M/L cone with a relatively short λ_{max} at 540 nm (table 1; Jacobs et al. 1993). This seems surprising because a higher photon catch would be achieved by having a longer-wavelength pigment. However, at the lowest light intensities, cone thresholds may be set by spontaneous isomerization of photopigment (dark noise), which increases with λ_{max} and so favors short-wavelength pigments (Donner 1992; Koskelainen et al. 2000; Rieke and Baylor 2000).

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; Tovée 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 sensitivity above 500 nm and hence trichromacy in primates.

If having separate M and L receptors and hence a red-green chromatic signal is especially beneficial in dim light, this may resolve an apparent inconsistency between the recent evidence that polymorphism of the M/L gene arose early in primate evolution (Tan and Li 1999; Jacobs et al. 2002) and the widely accepted notion that primates are primitively nocturnal (Ross 2000; Heesy and Ross 2001). There is then no need to assume that a red-green mechanism evolved in a predominantly diurnal animal (Tan and Li 1999); indeed, if color vision were important, the pressure would be greatest in crepuscular species.

Conclusion

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 535- 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 2000*a*, 2000*b*); 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 and 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.

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