

## The spectral distribution of primate cones and of the macular pigment: Matched to properties of the world?

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We have asked quantitatively whether the spectral positions of primate photopigments are optimized for discovering fruit signals against a background of foliage. In primary tropical rain forest, we have measured the spectral reflectances of fruits observed to be taken by a particular species of monkey (*Alouatta seniculus*) and have also measured the foliage background against which the signal must be discriminated. In the case of trichromatic monkeys, the actual positions of the long-wavelength and middle-wavelength photopigments (which lie in the range 530 to 560 nm) can be shown to maximize the signal-to-noise ratio of fruits to foliage in the newer subsystem of color vision. The latter subsystem compares the quantum catches in the long- and middle-wavelength cones and enjoys much better spatial resolution than the older subsystem (which compares the short-wavelength signal with the other two). The advantage, however, may extend to a wider range of signals than fruits: modelling shows that the spectral positions of the long- and middle-wavelength photopigments are such as to minimize the variance of vegetable greens in the newer subsystem of color vision. The degree to which this variance is minimized depends also on the optical density of the pre-receptoral, macular pigment of the retina; and the optimal positions of the photopigments vary according to the density of the macular pigment. © 1999 *The Optical Society of America*. [S1070-9762(99)00110-4]

### INTRODUCTION

Why are our cone photopigments asymmetrically placed in the spectrum? There is an interval of more than 100 nm between the peak absorbance of the short-wavelength pigment (420 nm) and that of the middle-wavelength pigment (530 nm), but the latter lies only 30 nm from the peak of the long-wavelength pigment (560 nm).<sup>1</sup> The origins of this asymmetry, we suggest, lie in the arboreal world in which our visual system evolved.

### THE SUBSYSTEMS OF PRIMATE COLOR VISION

The early mammals were probably dichromatic, as most mammals are today.<sup>2,3</sup> For the main business of vision—the detection of movement, flicker and form—they depended on a single class of cone with its peak sensitivity in the range 530–560 nm; and they gained a basic color vision by comparing the quantum catch in those cones with the quantum catch in a sparse population of short-wavelength cones. During the evolution of the primates, as the result of the duplication of a gene on the X chromosome, a second pigment arose in the 530–560 nm range, and the two X-linked pigments diverged to give the present long- and middle-wavelength pigments.<sup>4,5</sup>

There remain in the human and primate visual systems two distinct subsystems of color vision.<sup>6</sup> The phylogenetically older subsystem compares the signal of the short-wavelength cones with some combination of the long- and

middle-wavelength cone signals. Its spatial resolution is poor, peaking close to 1 cycle per degree.<sup>7</sup> The newer subsystem compares the signals of the long- and middle-wavelength cones, and it exhibits a much better spatial resolution. The two subsystems have different morphological substrates and remain relatively independent in the early stages of the primate visual system.<sup>8</sup> The signals of the older subsystem are carried by the blue cone bipolar cell and the small bistratified ganglion cell, which project to koniocellular laminae 3 and 4 of the lateral geniculate nucleus (LGN), and thence directly to layers 2 and 3 of the striate cortex.<sup>9,10</sup> In contrast, the signals of the newer subsystem are carried by the midget bipolar cell and the midget ganglion cell, which project to the parvocellular laminae of the LGN and thence to layer 4C $\beta$  of the striate cortex.

The differentiation of the long- and middle-wavelength pigments in our primate ancestors may have been associated with frugivory. In the natural world, there are rather few tasks that challenge color-deficient members of our own species, but one of these is picking fruit. We need color vision when the background varies randomly in form and in luminance, conditions where only chromaticity differentiates the target.<sup>6</sup> The hypothesis that primate trichromacy evolved for finding fruit, and judging its ripeness, can be traced to Grant Allen's "Colour-Sense" of 1879,<sup>11</sup> but it draws modern support from ecological evidence that certain trees explicitly use color to signal to monkeys. In the rain forests of both the Old and the New World there exist species of tree whose seeds

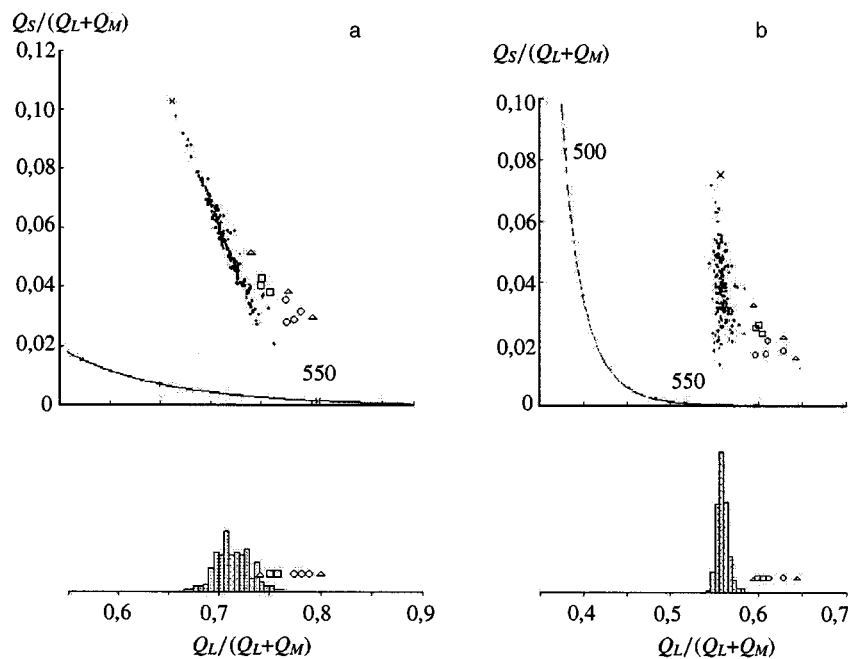


FIG. 1. Chromaticity diagrams analogous to that of MacLeod and Boynton,<sup>19</sup> constructed for different sets of photopigments. (a) pigments 430, 485, and 540 nm. (b) 430, 530, and 562 nm. See text for explanation.

are disseminated almost exclusively by monkeys.<sup>12–15</sup> Examples are trees of the Sapotaceae family in South America. Such trees typically have fruits that weigh between 5 and 50 g, have a hard outer coat, and are yellow or orange in color when ready to be dispersed. Against a foliage background, the signal is easily visible to a trichromatic disseminator, but not to a typical mammalian dichromat. The tree offers to the monkey a nutritious pulp, and in return the monkey either spits out the seed at a distance or defecates it later with fertilizer.

#### FORAGING FOR FRUIT AS A SIGNAL DETECTION TASK

We have recently made expeditions to French Guiana in order to quantify the signals that fruits present to monkeys.<sup>16</sup> Using a portable spectroradiometer (PhotoResearch 650), we have measured the spectral reflectance curves of fruits actually observed to be eaten by particular species of monkeys in the rain forest. We have also measured the spectral reflectances of the foliage background from which the fruit must be discriminated. We treat the discrimination of fruit against foliage as a signal detection task, with the fruit as signal and the foliage as noise. We ask whether the retinal photopigments are placed in the spectrum so as to maximize the signal-to-noise ratio. We also ask whether the macular pigment enhances or reduces the signal-to-noise ratio.

We give here results for the red howler monkey, *Alouatta seniculus*, observed at the Nouragues field station (45' N, 52°40' W). In this species, both males and females are known to be trichromatic, and in this they are unusual among platyrrhine monkeys.<sup>17</sup> By following troops of howlers, we secured fresh samples of fruits, or fragments of fruits, that were actually harvested by the monkeys.

To estimate the spectral radiance stimulus reaching the eye of a monkey from a particular surface, we multiplied each reflectance spectrum by an illuminant spectrum. We measured the latter in the forest canopy at noon under typical

overcast conditions; the use of alternative illuminants has little effect on the results. To estimate the spectral stimulus reaching the retina, we modified the radiance spectrum to allow for absorption by the lens and by the macular pigment. Below, we discuss the effects of assuming different optical densities for the macular pigment.

The modified spectra were then multiplied by the spectral sensitivities of the retinal photopigments to estimate the quantum catches in individual classes of cone. The absorbance spectra of cones were generated by the polynomial formula of Baylor, Nunn, and Schnapf,<sup>18</sup> assuming an axial optical density of 0.3. We have repeated this analysis not only for the triplet of photopigments actually thought to be present in *Alouatta seniculus* but also for many other possible sets of pigments: we fix the peak of the short-wavelength pigment always at 430 nm, but, in iterated analyses, allow the “middle-wavelength” and “long-wavelength” pigments to occupy all possible positions between 490 and 640 nm. For any given triplet of photopigments, we can express the results in an analog of the MacLeod–Boynton chromaticity diagram for human observers.<sup>19</sup> Examples are shown in Fig. 1. If we denote the quantum catches in the short-, middle-, and long-wavelength cones as  $Q_S$ ,  $Q_M$ , and  $Q_L$ , the abscissa of the diagram corresponds to  $Q_L/(Q_L+Q_M)$  and the ordinate corresponds to  $Q_S/(Q_L+Q_M)$ . Thus the ordinate represents the input to the phylogenetically ancient subsystem of color vision, whereas the abscissa represents the input to the newer subsystem.

The right-hand panel of Fig. 1 gives the results of such an analysis for the triplet of photopigments actually thought to be present in the retina of the howler monkey. The small solid circles show the chromaticities of foliage, and the open symbols the chromaticities of the three fruits most commonly observed to be eaten by *Alouatta seniculus* at the field site: *Bagassa guianensis* (open triangles), *Chrysophyllum lu-*

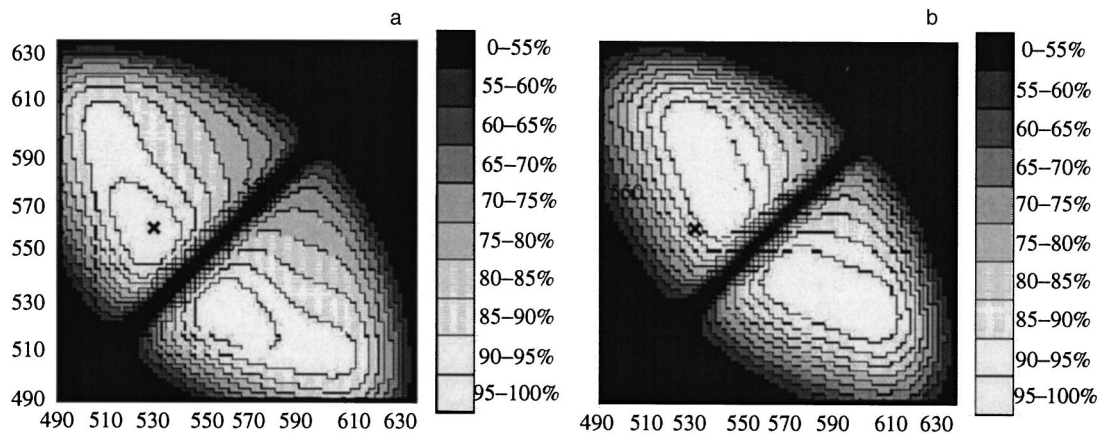


FIG. 2. Signal-to-noise ratios for detecting fruits against a background of foliage. Values have been calculated for all possible pairings of photopigments in the range 490 to 640 nm. The vertical axis represents the spectral position of one pigment in nanometers and the horizontal axis represents the spectral position of the second pigment. (a) screened, (b) without screening by macular pigment.

*centifolium* (open circles), and *Vouacapoua americana* (open squares). The small crosses represent the chromaticity of the illuminant. The left-hand diagram is for a triplet of pigments with peak sensitivities evenly spaced in the spectrum, at 430, 485 and 540 nm (a set never observed in primates), and the right-hand diagram is for the set of pigments thought to be present in *A. seniculus*—430, 530 and 562 nm. Notice that the foliage distribution is tilted in the left-hand diagram but is close to perpendicular in the right-hand diagram. The small histograms below each diagram show the distribution of foliage chromaticities when projected onto the abscissa. Notice that the fruit and foliage are better separated in the right-hand case.

For both the left-hand and right-hand panels of Fig. 1, we have projected the foliage distribution onto the abscissa, thus showing the inputs that the leaves offer to the phylogenetically newer subsystem. In the case of the triplet of pigments actually thought to be present in *Alouatta* (right-hand panel), the projected distribution is very narrow, whereas the imaginary but symmetrically placed triplet (left-hand panel) yields a much broader distribution.

We have systematically calculated where the long- and middle-wavelength photopigments should be placed in the spectrum to maximize the mean signal-to-noise ratio for all the fruits in the diet of *Alouatta*.<sup>16</sup> For each individual fruit sample, we calculate the signal as the difference between the fruit chromaticity and the mean chromaticity of the foliage distribution, where chromaticity is  $Q_L / (Q_L + Q_M)$ , the input to the newer subsystem of color vision. The signal-to-noise ratio is then this signal divided by the noise, which is constituted primarily by (1) the variance of the foliage distribution and secondarily by (2) the expected variance due to stochastic variation in the quantum catch. When this analysis is repeated for each possible spectral position of the long- and middle-wavelength pigments, the maximum signal-to-noise ratio coincides almost exactly with the photopigments actually found in *Alouatta*. In the contour plot of Fig. 2a, the ordinates are the spectral positions of the two possible pigments, and the lighter the area, the higher the signal-to-noise ratio. The cross marks the combination of pigments thought

to be present in the howler monkey, and they are clearly near-optimal. The lighter the shading, the closer is the signal-to-noise ratio to its maximum value. The cross represents that combination of long- and middle-wave pigments thought to be present in *A. seniculus*. In the case of Fig. 2a, we have assumed that the photoreceptors are screened by macular pigment of the optical density observed in Man. In the case of Fig. 2b, the density of the macular pigment was set to zero.

Notice that this result has its origins in the perpendicularity of the foliage distribution in the right-hand panel of Fig. 1; and thus, by placing both the long- and the middle-wavelength pigments beyond 530 nm, the primate observer may maximize the detectability of other biological targets besides fruits. A perpendicular line in the MacLeod–Boynton space and its analogs is a tritanopic confusion line, representing a set of chromaticities that would be confused by an observer who lacked the short-wavelength cones. That foliage is distributed along a tritanopic confusion line can be seen in the data of Hendley and Hecht published in 1949.<sup>20</sup>

## THE ROLE OF MACULAR PIGMENT

A yellow pigment, a mixture of the carotenoids lutein and zeaxanthin,<sup>21,22</sup> is present in the central region of the primate retina, particularly in the fibers of Henle and the inner plexiform layer.<sup>23,24</sup> Its peak absorption lies in the region of 460 nm. Higher animals cannot synthesize carotenoids, and the main dietary source is plants.<sup>25</sup>

Several explanations have been offered for the presence of the macular pigment:

(1) It may counteract the chromatic aberration of the eye and enhance acuity by reducing the sensitivity of the long- and middle-wavelength cones to the short-wavelength component of the image.<sup>26–28</sup> The emmetropic eye is typically focused for the yellow region of the spectrum, and is about 1 diopter myopic for short-wavelength light.

(2) The contrast of natural scenes is degraded by scattered light, which is maximal at short wavelengths. The

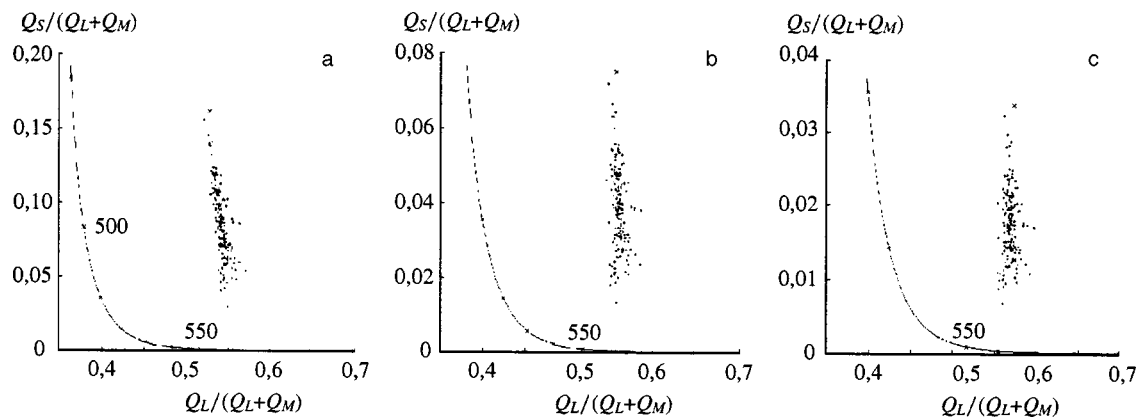


FIG. 3. Chromaticity diagrams as in Fig. 1, but for three different optical densities of the macular pigment. (a) without screening by macular pigment, (b) macular pigment of usual density, (c) macular pigment of double density.

macular pigment may enhance visibility by screening the long- and middle-wavelength photopigments from this component of the image.<sup>26</sup>

(3) By selective absorption, the macular pigment may protect the most strongly illuminated retinal region against the tissue-damaging effects of short-wavelength light.<sup>29</sup>

(4) The macular pigment may have anti-oxidant properties, quenching activated oxygen-free radicals.<sup>29,30</sup>

Here we examine a further possible function.

In the analysis of the preceding section, we assumed that the spectral signal reaching the photoreceptors is filtered by macular pigment of a fixed density, comparable to that found in Man. This is a reasonable assumption: although there is not direct report of macular pigment in the retina of *Alouatta seniculus*, the macular pigment is known to be present in other platyrrhine primates, such as *Saimiri* and *Cebus*.<sup>24</sup> However, what happens if we apply our model to the same set of spectral reflectance measurements but now manipulate the optical density of the macular pigment?

To generate the results of Fig. 3, we have used the same triplet of photopigments as for right-hand panel of Fig. 1, i.e., the cone pigments thought to be present in the retina of the howler monkey. The data points represent the chromaticities of individual leaf samples, and the cross represents the illuminant. The assumed set of photopigments is that thought to be present in *A. seniculus*, with peak wavelengths at 430 nm, 530 nm and 562 nm. To generate Fig. 3a, we set the optical density of the macular pigment to zero; for Fig. 3b, we set it to have the value previously assumed, and, for Fig. 3c, we set it to have double the normal density. Notice that, in Fig. 3a, the foliage distribution is tilted counterclockwise, and, in Fig. 3c, it is tilted very slightly clockwise. The effect of these tilts is to increase the variance of the foliage distribution when it is projected onto the abscissa, i.e., to increase the variance of  $Q_L/(Q_L+Q_M)$ , the input to the recent color subsystem. We have repeated the analysis for a range of macular pigment densities, and in Fig. 4 we plot the standard deviation  $\sigma$  of the foliage distribution as a function of peak optical density. The function has a clear minimum at an intermediate density. Notice that the minimum standard deviation coincides with the average optical density for Man (indicated by a vertical arrow).

middle- and long-wavelength photopigments are assumed to lie at 530 and 562 nm, respectively. Very similar results are obtained if we perform the analysis in terms of  $\log [Q_L/(Q_L+Q_M)]$ , in order to take account of small shifts in the average value of  $Q_L/(Q_L+Q_M)$ . The minimal value lies provocatively close to the value of 0.495, tabulated for the human eye by Wyszecki and Stiles.<sup>31</sup>

From Fig. 4 we might conclude that the macular pigment has evolved in primates to optimize the efficiency of the new subsystem of color vision, which extracts the ratio of the quantum catches in the long- and middle-wavelength cones. The macular pigment minimizes the noise produced in this subsystem by a background of foliage and so frees the subsystem for the detection of signals. (One could even speculate that the signalling fruits might feed the necessary carotenoids to the monkeys, thereby enhancing their own visibility.)

So, to the list of possible functions of the macular pigment, we could add the enhancement of chromatic contrast in the arboreal theater in which primates emerged. But an argument can be advanced against this being the reason why the macular pigment evolved in the first place. For the macu-

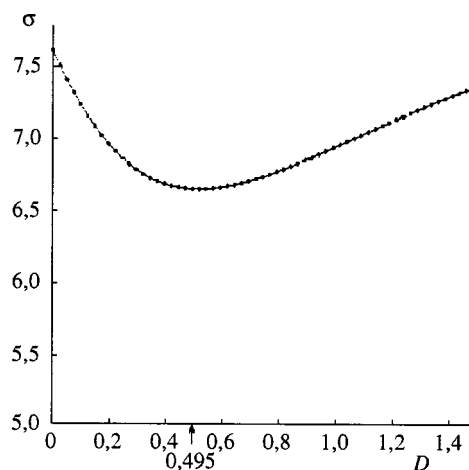
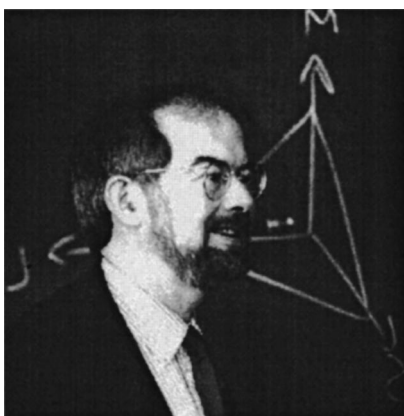


FIG. 4. The standard deviation of  $Q_L/(Q_L+Q_M)$  for the leaf distribution of Fig. 3, plotted as a function of the assumed optical density of the macular pigment that screens the photoreceptors.

lar pigment is probably universal in the diurnal primates, and it is certainly present in platyrrhines such as *Saimiri* and *Cebus*, where all the males and a subset of females are dichromats, lacking the long-wavelength/middle-wavelength subsystem of the trichromat.<sup>32,33</sup> Suppose then that the macular pigment antedates trichromacy rather than being an adaptation to an existing trichromacy. We can ask the distinct question of whether the optimal photopigments for a trichromatic primate are constrained by the presence of macular pigment. Figure 2b suggests that this is so. We have repeated the analysis of Fig. 2a, now omitting macular pigment from the model. The optimal pair of photopigments are shifted to longer wavelengths, and the long- and middle-wavelength pigments of *Alouatta* no longer fall at the very maximum. It is clear that, in judging how well the retina is matched to the task of chromatic discriminations, we must consider in conjunction the cone photopigments and the macular pigment.

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