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Cone pigment polymorphism in New World monkeys: Are all pigments created equal?

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Abstract

Most platyrrhine monkeys have a triallelic M/L opsin gene polymorphism that underlies significant individual variations in color vision. A survey of the frequencies of these polymorphic genes suggests that the three alleles occur with equal frequency among squirrel monkeys (subfamily Cebinae), but are not equally frequent in a number of species from the subfamily Callitrichinae. This departure from equal frequency in the Callitrichids should slightly increase the ratio of dichromats to trichromats in the population and significantly alter the relative representation of the three possible dichromatic and trichromatic phenotypes. A particular feature of the inequality is that it leads to a relative increase in the number of trichromats whose M/L pigments have the largest possible spectral separation. To assess whether these trichromatic phenotypes are equally well equipped to make relevant visual discriminations, psychophysical experiments were run on human observers. A technique involving the functional substitution of photopigments was used to simulate the discrimination between fruits among a background of leaves. The goal of the simulation was to reproduce in the cones of human observers excitations equivalent to those produced in monkey cones as the animals view fruit. Three different viewing conditions were examined involving variations in the relative luminances of fruit and leaves and the spectrum of the illuminant. In all cases, performance was best for simulated trichromacies including M/L pigments with the largest spectral separation. Thus, the inequality of opsin gene frequency in Callitrichid monkeys may reflect adaptive pressures.

Keywords: New World monkeys, Opsin genes, Color vision, Cone pigments, Fruit discrimination

Introduction

A vast majority of New World monkeys have two opsin gene loci, one of which is polymorphic and located on the X-chromosome (for a review, see Jacobs, 1998). In most species, the polymorphic locus can code for any of three alleles which produce middle- or long-wavelength-sensitive (M/L) opsins. Males, being hemizygous at this locus, can have only one of these alleles. Females can have either one or two depending upon whether they are homozygous or heterozygous, respectively. In heterozygous females, random X-chromosome inactivation sorts the expression of the M/L alleles into two discrete cone types. All of these animals have a short-wavelength-sensitive (S) cone pigment gene on chromosome 7, so males and homozygous females are dichromatic while heterozygous females are trichromatic. The M/L polymorphisms lead to striking individual variations in visual capacity as animals are segregated into six different photopigment and behavioral phenotypes (three types of dichromat, and three types of trichromat).

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In an early paper in this field, it was pointed out that several different mechanisms might be invoked as possible explanations for the presence of these polymorphisms including group selection, frequency-dependent selection, and heterozygous advantage (overdominant selection) (Mollon et al., 1984). Recent evidence supports the conclusion that trichromacy *per se* may confer a fitness advantage to individual platyrrhine monkeys (Smith et al., 2003; but see Caine et al., 2003; Dominy et al., 2003), which suggests heterozygous advantage as the primary explanation for the maintenance of M/L polymorphism. Overdominance in the absence of selection for particular forms of either dichromacy or trichromacy will produce a population in which two-thirds of the females are trichromatic. Although it has long been clear that there is robust representation of trichromatic females among these platyrrhines, most studies have necessarily examined only small numbers of individuals. In cases where the samples were somewhat more extensive it appeared that, indeed, the frequency of trichromacy was close to the expected two-thirds (Jacobs et al., 1993). There have now been sufficient studies of color vision and its biology in these platyrrhines that we thought it might be useful to examine the issue of polymorphic gene frequencies more closely. Here we report the results of a literature survey of M/L opsin gene frequencies in two groups of platyrrhines and then describe a psychophysical experiment motivated by these same concerns.

M/L opsin gene frequencies in platyrrhine monkeys

Materials and methods

Two distinct triallelic patterns have been documented in platyrrhine monkeys. As illustrated in Fig. 1, animals from the subfamily Cebinae have M/L photopigments with peak absorptions of about 535, 550, and 562 nm while a number of genera from the subfamily Callitrichinae have M/L pigments with peaks of about 543, 556, and 562 nm (Jacobs, 1998). Information was accrued separately for the two cases. For the former, we surveyed results obtained from animals of only one genus, the squirrel monkey (*Saimiri*); for the sample of Callitrichinae, we included a number of different species known to be triallelic and to share the pigments listed above.

Information about M/L opsin gene frequencies in squirrel monkeys was derived from several published sources (Jacobs, 1984; Jacobs & Neitz, 1987; Jacobs et al., 1993; Cropp et al., 2002) and from a number of unpublished cases studied in our laboratory. Results for Callitrichid monkeys were likewise obtained from both published (Jacobs et al., 1987; Travis et al., 1988; Tovée et al., 1992; Williams et al., 1992; Caine & Mundy, 2000; Surridge & Mundy, 2002; Jacobs & Deegan II, 2003; Smith et al., 2003) and unpublished (P. Martin and E. Blessing, personal communication) sources. The primary data were derived through a number of different approaches, including direct opsin genotyping and spectral sensitivity measurements determined by microspectrophotometry, electrophysiology, and/or psychophysics. For results from spectral sensitivity measurements, genotypes were inferred from the relationships between opsin genes, photopigments, and color vision outlined above. In any cases where family relationships were made known, we included results from parents but not offspring.

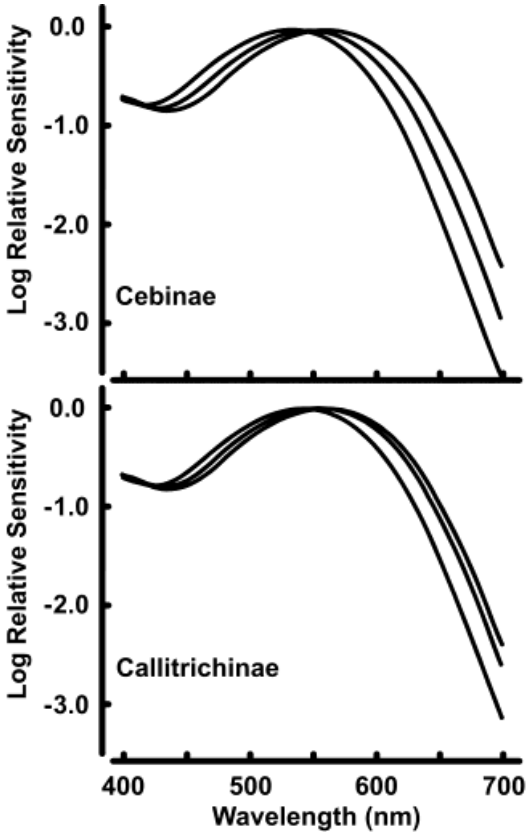

Fig. 1. Spectral sensitivities of the M/L photopigments in two subfamilies of platyrrhine monkeys.

Results and discussion

The M/L gene frequencies accumulated from the sources cited above are shown in Table 1. The relative representation of the three opsin types in the squirrel monkey do not differ from the expectation based on an assumption of equal gene frequencies ($\chi^2 = 2.94$, $df = 2$, $P > 0.05$). On the other hand, those from the Callitrichids differ significantly from what is expected if the alleles are equifrequent ($\chi^2 = 36.8$, $df = 2$, $P \ll 0.001$). Note in particular that the opsin gene allele specifying the 556-nm pigment is relatively underrepresented in this sample.

Caution is required in accepting the result that Callitrichid M/L opsin genes are not equifrequent since it is conceivable that the survey reflects some unknown sampling bias; for example, although we did not include results from closely interrelated animals where such were identified, and although the samples were drawn from a number of different colonies as well as wild populations, gene representation from small inbred groups may nevertheless be included. Although such a bias cannot be rejected out of hand, the general pattern of results summarized in Table 1 was seen in all of the larger subsamples suggesting that the disparities in gene frequencies are real.

One possible explanation for the disparity in M/L gene frequency in the Callitrichids might be that the 556-nm opsin allele has evolved more recently than the other two and that, consequently, the three alleles have not had time to reach an equilibrium state. The evidence on allele evolution is mixed. Shyue et al. (1995) compared intron 4 gene sequences for squirrel monkeys and marmosets (a Callitrichid). For the squirrel monkeys, they argue that the divergence of the three genes was nearly a trichotomy while the evidence for the marmoset was more equivocal with the branching order for the three alleles uncertain. A later investigation involving a more extensive nucleotide sequence comparison was taken as both suggesting a single origin of the three marmoset alleles and indicating that the three had existed for more than 20 million years (Boissinot et al., 1998). In sum, although the issue seems far from settled, there is no strong evidence to suggest that the 556-nm allele of the Callitrichids has emerged relatively recently.

An alternative possibility is that the unequal representation of the three M/L alleles in Callitrichid monkeys documented in Table 1 reflects adaptive pressures. Assuming the populations are

Table 1. *Allele frequencies of the M/L photopigment genes identified from animals of two subfamilies of platyrrhine monkeys*

	Cebid			
λ_{max} (nm)	535	550	562	All
Frequency (#/%)	106/29.3	124/34.3	132/36.5	362/100
	Callitrichid			
λ_{max} (nm)	543	556	562	All
Frequency (#/%)	149/36.6	80/19.7	177/43.6	406/100

at Hardy-Weinberg equilibrium, genotype (hence phenotype) frequencies are derived from gene frequencies *via* binomial expansion (for females; for males, genotype frequencies equal gene frequencies). Results of this expansion are illustrated in Table 2, where it can be seen that the unequal gene frequencies impact the incidence of the various pigment phenotypes in a number of ways. First, the overall representation of trichromacy among females will be reduced slightly, in this case from its theoretical maximum of 66.7% to 63.6%. Second, the distribution of the three dichromatic phenotypes will be altered yielding a decrease in the number of animals with the 556-nm pigment relative to the number having either the 543-nm pigment or the 562-nm pigment. Finally, the distribution of trichromatic phenotypes will be changed. The most dramatic change is that more than half of all female trichromacy will be based on the 543/562 M/L pigment pairing. Probably the most intriguing of all the changes is this alteration in the mixture of trichromatic phenotypes. In particular, the relative predominance of trichromacy based on the pigment combination that gives the largest spectral difference of the three possible pairings leads one to wonder if discriminations of natural objects may be more effectively accomplished with particular pigment pairings. That concern led to a behavioral experiment reported next.

Functional substitution of photopigment spectral sensitivities

Vorobyev et al. (1997, 2001) have described methods for displaying images depicting the information animals extract from biologically relevant visual stimuli. They began by computing the excitations of photoreceptors in animals viewing a scene. Images were then constructed by setting the intensities of the red, green, and blue guns of a computer monitor proportional to the computed photoreceptor excitations. An alternative, and perhaps better, method for studying the perceptual capabilities of other animals is to reproduce their neural activity in human nervous systems. For instance, rather than mapping photoreceptor excitations to the excitations of a monitor's phosphors, photoreceptor excitations should be mapped to photoreceptor excitations. With such functional substitutions, human observers can maximally utilize their own sensory systems to explore the perceptual worlds of other animals. In Fig. 2, we diagram our method both as a general concept and, more specifically, as applied to studies of color vision in cases where the primary information utilized is comparative photoreceptor spectral-sensitivity data. The stimulus transformation concept we employ is similar to that used by Pokorny and Smith (1977) to test a polymorphic photopigment explanation for human anomalous trichromacy. Brettel et al. (1997) and Carroll et al. (2001) have also used similar methods to portray the visual worlds of human dichromats and horses, respectively.

Table 2. *Predicted phenotype frequencies of Callitrichid monkeys based on the gene frequencies of Table 1 assuming Hardy-Weinberg equilibrium and that populations are 50% female*

	Dichromats				Trichromats			
λ_{max} (nm)	543	556	562	All	556/562	543/556	543/562	All
Frequency (%)	25.1	11.8	31.3	68.2	8.6	7.2	16.0	31.8

Through functional substitution, human subjects viewing calibrated computer monitors can act as surrogates for other animals. We do not, of course, propose such experiments as a replacement for behavioral research using animals. However, behavioral experiments with humans can usually be performed relatively quickly and inexpensively, so functional substitution may be used to refine experimental questions and/or to suggest reasonable answers in the absence of more direct examinations. In the present case, we would like to know if Callitrichids having particular M/L pigment combinations can perform some ecologically relevant tasks better than animals with other possible M/L pigment pairings. To answer that question, we asked human subjects to act as surrogates for all three types of trichromatic Callitrichid.

Materials and methods

Smith et al. (2003) measured spectral reflectances of leaves and fruit at various stages of ripeness. The fruits were *Abuta fluminum*, a species normally eaten by tamarins (*Saguinus* spp.), common Callitrichids. From the measured reflectances, Smith et al. (2003) computed the quantal catch rates of all four types of Callitrichid cone (one S and three M/L). We recreated the same relative quantal catch rates three at a time (one S and two M/L) in humans observing simulated fruit against a simulated leaf background.

Stimuli were generated with the aid of MATLAB® (the MathWorks, Inc., Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) running on a Power Macintosh G3 (Apple Computer, Inc., Cupertino, CA) and presented on a Diamond Pro 710 monitor (Mitsubishi Electronics America, Inc., Cypress, CA) driven by a 10-bit video card (Radius, Inc., Sunnyvale, CA). The monitor was calibrated with a SpectraScan® PR-650 spectroradiometer (Photo Research, Inc., Chatsworth, CA). Quantal catch rates for human cones were calculated using the spectra of the monitor's phosphors and the Smith-Pokorny cone fundamentals (Smith & Pokorny, 1975, tabulated in the Color and Vision Database, http://www.cvrl.org).

Subjects were given a "same/different" task to determine how well they could discriminate the colors of fully versus partially ripe fruit. Fruit colors were displayed as squares with their centers on the border of an imaginary circle with a radius of 2 deg of visual angle. The squares subtended 1 deg of visual angle on a side and were briefly presented (2 or 4 frames at 85 Hz; approximately 23 or 46 ms) as subjects fixated a small spot in the center of the imaginary circle. During a trial, subjects were shown squares simulating the colors of two ripe fruit, two partially ripe ("mid-ripe" in the parlance of Smith et al., 2003) fruit, or one of each and had to indicate with key presses whether or not the squares appeared the same. An audible tone after each trial indicated whether or not the choice was correct. Stimuli were presented against a variegated pattern derived from leaf-reflectance measurements. This leaf pattern consisted of a random assortment of overlapping rectangles that all produced the same relative cone excitations but differed in absolute intensity. The relative cone excitations for human observers viewing the rectangles were computed to be the same as the relative cone excitations of a tamarin observing an average leaf.

Selection acting upon different color-vision phenotypes will assess fitness, in part, according to how well animals discriminate food items in the field. These items and the objects surrounding them will be illuminated to various extents depending upon how well they are shaded from sources. Variations in illumination confound variations in reflectance, and one presumptive benefit of

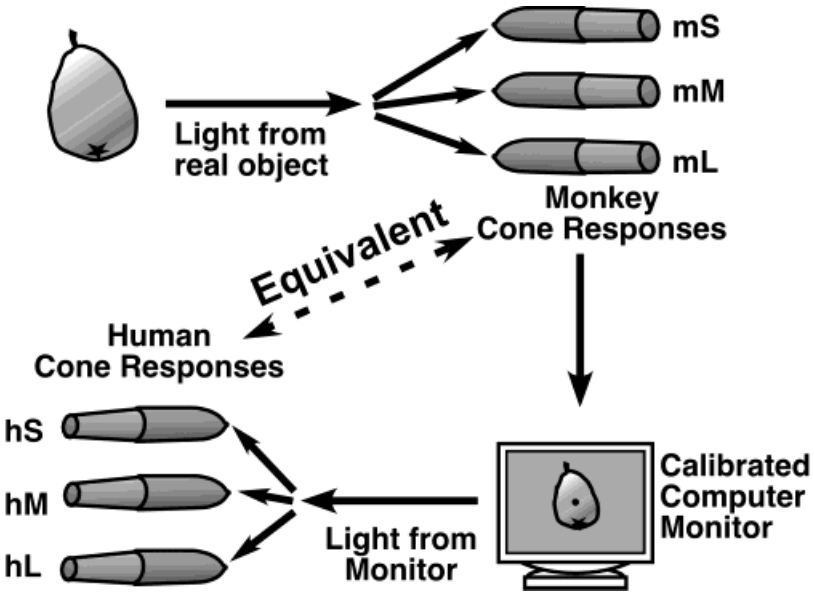

Fig. 2. Functional substitution of cone fundamentals. This diagram outlines basic steps in using the human visual system as a substitute for the visual system of a monkey. Light reflected from an object will excite monkey cones (mS, mM, mL) to various extents depending, in part, upon the photopigment each photoreceptor contains. With light from a computer monitor, equivalent excitations can be generated in human cones (hS, hM, hL). In principle, the human observer's nervous system now has the equivalent information from the monitor that the monkey's nervous system has from the object.

color vision is the ability it confers to extract information about reflectance independent of illumination. The relative cone excitations caused by light coming from a particular object will depend upon the spectrum of the light illuminating that object. However, we assume that for monkeys feeding high in the daytime canopy, variations in overall intensity of illumination are more important than variations in relative spectral content. Thus in designing tasks, a primary concern was testing subject's abilities to make discriminations between simulated fruit without the aid of differences in brightness. Nevertheless, because there are significant differences in the spectral content of the illumination within natural forested environments (Endler, 1993; Regan et al., 2001) we also attempted to address the question of how spectral content of illumination might influence the relative performances of the three trichromatic phenotypes.

The experiment was performed three different ways. Absolute reflectances of *A. fluminum* fruit are considerably higher than those of leaves, and consequently fruit colors are brighter than leaf colors. In one condition, "isoluminant fruit," we mimicked this brightness difference by making the squares considerably brighter (50–75 cd/m^2) than the leaf background (13 cd/m^2). In a second condition, "isoluminant fruit and leaves," we increased the brightness of the background to assess the extent to which this brightness difference affected performance. In this condition, we equated the luminance of the brightest leaves with the luminance of the fruit. We set this luminance as high as possible (73 cd/m^2) given monitor limitations. We maintained the pattern of the leaves, however, so the average luminance of the background was lower (62 cd/m^2). The third condition, "isoluminant fruit and leaves, shade spectrum," was similar to the second except that relative quantal catch rates for each color were modified to approximate the relative quantal catch rates of tamarin cones viewing the objects under the indirect sunlight of forest shade. This transformation was accomplished using irradiance data reported by Regan et al. (2001). For all conditions reported here, the squares presented on any given trial had the same luminance as each other so that subjects could not use relative brightness as a cue. Three adult humans with normal color vision were tested under all three viewing conditions. Subjects completed ten blocks (50 trials/block) for each pigment set substitution within each condition. All blocks for a given condition were run in a single session with the order of pigment set substitution randomized across the session.

Results

In preliminary measurements, we found considerable variation in the ability of individual subjects to perform this task. Accordingly, it was necessary to manipulate presentation times to avoid floor and ceiling effects, that is, presentation times so short that a subject could not perform above chance, and presentation times so long that subjects could achieve perfect scores. For the best subject, 23 ms was an adequate presentation time for all conditions, whereas the other two subjects required 46 ms for the second and third conditions.

Although there was significant variability in accuracy both within and across subjects, differences in performance always depended on the pigment set employed. As illustrated in Fig. 3, under all three simulated illuminant conditions, subjects were significantly less accurate at discriminating ripe from semiripe fruit when viewing them through the pairing of the 556-nm and 562-nm pigments than when viewing them through the combinations that included the 543-nm pigment. In the isoluminant fruit condition, pigment set substitution accounted for 30% of the variance in our data (two-way analysis of variance: $F(2,81) = 35.6$, $P \ll 0.001$). Under the other two conditions, pigment set substitution accounted for a smaller but still significant amount of the variance, 10% for isoluminant fruit and leaves (two-way analysis of variance: $F(2,81) = 5.07$, $P < 0.01$) and 23% for the shade spectrum (two-way analysis of variance: $F(2,81) = 19.5$, $P \ll 0.01$).

Post hoc analyses of the data examined with pairwise comparisons of pigment set substitutions indicated that subjects were always significantly more accurate with the 543/562 pigment pairing than they were with the 556/562 pigment pairing. Accuracy with the 543/562 pairing was never significantly different from accuracy with the 543/556 pairing, but it was close in the isoluminant fruit condition (two-way analysis of variance: $F(1,54) = 6.46$, $P = 0.014$). Substitution with the 543/556 pairing provided

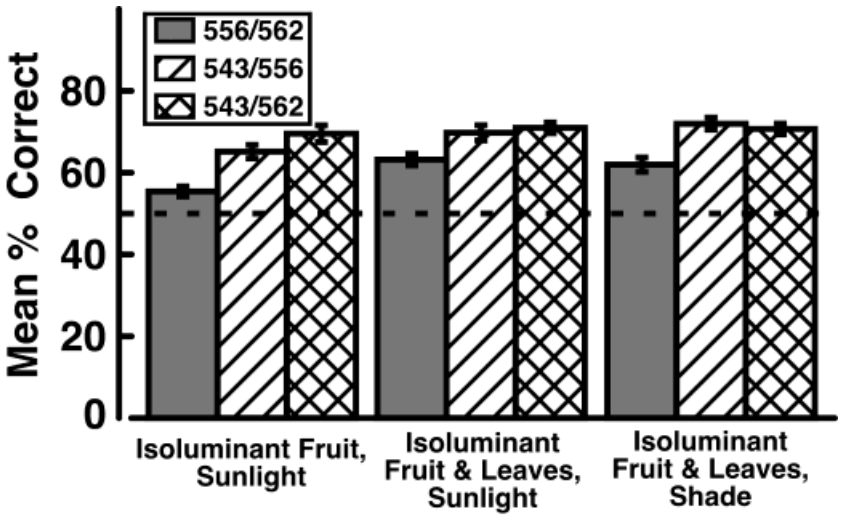

Fig. 3. Psychophysical results. Bar heights depict the mean accuracy for each substitution; data from the three subjects were pooled. Error bars = ±1 SEM.

significantly more accurate performance than substitution with the 556/562 pairing in two of the three conditions. Under the isoluminant fruit and leaves condition, we failed to distinguish accuracy mediated by these two pairings (two-way analysis of variance: $F(1,54) = 3.97$, $P > 0.05$).

General discussion

Our survey of M/L opsin gene frequency in two groups of triallelic platyrrhine monkeys suggests that among several Callitrichid species the three genes do not occur with equal frequency. If real, this inequality will alter the relative frequency of the cone pigment and color-vision phenotypes in these populations, and this in turn suggests there may be adaptive explanations for the gene frequency distribution. To examine the potential visual impact of varying M/L gene complement, we conducted psychophysical experiments with human observers using a technique involving functional substitutions of photopigments. Results from three different simulated viewing conditions—isoluminant fruits viewed in direct sunlight, isoluminant fruit and leaves viewed in direct sunlight, and isoluminant fruits and leaves viewed in forest shade—yielded differences in performance that varied with the simulated M/L pigment complement. For all three of the viewing conditions, performance was poorest for the M/L pigment combination having the smallest spectral separation (556/562) while differences between the other two phenotypes were statistically indistinguishable. Clearly, all forms of trichromatic color vision are not equally good at these tasks. The fact that the relative advantages of the different pigment sets did not vary across viewing conditions is in contrast to the modeling results of Regan et al. (2001) which predict that some monkeys should be able to discriminate fruit better in the shade than in direct sunlight, and monkeys with other phenotypes should find their advantage in sunlight rather than shade. However, Regan and colleagues examined the pigments of Cebid monkeys rather than that of Callitrichids and used a larger variety of fruit in their studies. These differences as well as differences in the assumptions underlying the respective models could explain the apparent discrepancy. Direct observation under natural circumstances of the feeding strategies of monkeys with known pigment complements would seem an obvious and useful step toward better understanding of these issues.

The viewing conditions in these laboratory experiments of course represent only a highly stylized version of what monkeys face while foraging in natural environments. They also greatly simplify the actual behaviors of these monkeys. For example, many Callitrichids are opportunistic feeders with diets that include not only fruits like those simulated in these experiments, but also insects, small vertebrates, and plant exudates; as well, there are also significant variations in preferred foraging locations—canopy, midlevel, forest edge, etc. (for a summary of these issues see Kinzey, 1997). Nevertheless, despite their artificiality, these experiments do lend some empirical support to the idea that the M/L pigment complements of the polymorphic platyrrhines can provide differential advantages in discriminating among important objects. The general finding that animals having only small separation of their M/L pigments do not do as well in these tasks as those with greater M/L pigment separation is not surprising. In a general sense, one expects that the strength of neural signals extracted by opponent comparison will vary with the spectral separation of the originating pigments. Perhaps more to the point, the 6-nm peak separation of the pigments of one of the Callitrichid phenotypes is similar to that characteristic of human anomalous trichromats, who on average have relatively poorer color-discrimination capacities than normal trichromats whose M/L pigments have greater spectral separation (Pokorny et al., 1979).

The disparity in opsin gene frequency among the Callitrichids favors trichromats with the largest M/L pigment separation and such an arrangement can provide superior discrimination of ecologically relevant targets. That correspondence suggests that the deviation from equal gene frequencies may well reflect adaptive pressure. With larger pigment separations, such as those found in Cebid monkeys, the discrimination advantage seems likely to be smaller, or absent entirely, perhaps accounting for the differences in relative gene frequencies between these two groups of platyrrhines. Underscoring this point, we note our inability to statistically discriminate performance between 543/556 substitutions and 543/562 substitutions. The smallest separation between Cebid pigments is 12 nm, almost the same as the difference for the Callitrichid 543/556 pairing. Since our experiments did not distinguish between 13-nm and 19-nm separations, it could be that selection similarly cannot distinguish between 12-, 15-, and 27-nm separations. Of course, it is also likely that differences in the

ecology of the two groups (what they eat, what eats them, and how they interact with each other) dictates different selective pressures irrespective of the alleles upon which those pressures operate.

Although the focus here has been on the relative merits of various platyrrhine trichromacies, it is well to remember that all of these trichromatic phenotypes should perform better in these particular tasks than any of their dichromatic conspecifics, and that difference may well provide a countervailing pressure influencing the ultimate distribution of M/L opsin genes. The M/L gene frequencies of these Callitrichid monkeys show (Table 2) that a relatively modest deviation from equal allele frequency can significantly alter the distribution of trichromatic phenotypes while at the same time causing only a relatively small decrease in the overall incidence of trichromacy.

Finally, quite beyond the merits of the arguments about platyrrhine M/L opsin gene frequencies and their interpretations, we suggest that the experimental approach of functional substitution may have some general utility. Here we have substituted relative photoreceptor quantal catch rates, but the basic goal is to replicate in human nervous systems the activity believed to occur in populations of neurons in other animals. As in the present case, such substitution can provide a rapid means of testing hypotheses about nonhuman perception that may be difficult to achieve with nonhuman subjects.

Acknowledgments

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