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New World Monkeys and Color

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Abstract The visual worlds of most primates are rich with potential color signals, and many representatives of the order have evolved the biological mechanisms that allow them to exploit these sources of information. Unlike the catarrhines, platyrrhines typically have sex-linked polymorphic color vision that provides individuals with any of several distinct types of color vision, including both trichromatic and dichromatic variants. In recent years, this polymorphism has been the target of an expanding range of research efforts. As a result, researchers now reasonably understand the proximate biology underlying the polymorphisms, and a number of ideas have emerged as to their evolution. Progress has also been made in illuminating how color vision capacities may be related to the particular visual tasks that New World monkeys face.

Keywords color vision · cone photopigments · ecology of color vision · opsin genes · platyrrhines

Introduction

The idea that color vision in platyrrhines is unusual first emerged nearly 70 yr ago from results of the pioneering studies of Walter F. Grether. From laboratory discrimination tests, he concluded that 3 male *Cebus* individuals probably had dichromatic color vision, while in the same tests a single female spider monkey (*Ateles*) performed much like a normal human trichromat. In considering the results, Grether (1939, p. 34) observed that 1) "the deficient color vision of cebus monkeys is not a general characteristic of South American primates" and 2) because defective color vision had long been known to be sex-linked among humans, the "generalization that two-color vision is characteristic of the genus *Cebus* is hardly justified by such a small sampling". Both observations turned out to be prophetic when, years later, it began

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to emerge that sex-linked polymorphic color vision is a hallmark feature of vision in platyrrhines (Jacobs 1984; Jacobs *et al.* 1987; Mollon *et al.* 1984; Tovee *et al.* 1992). The polymorphism is such that, among most New World monkey species, males are obligate dichromats while females may have either dichromatic or trichromatic color vision with, typically, 3 distinct phenotypes in each dimensional category. It seems entirely likely that the monkeys Grether tested were the earliest characterized exemplars of the polymorphism.

In the decade and a half following the discovery of color vision polymorphism in New World monkeys, researchers made steady progress in expanding the measurements to include additional species and in characterizing both the cone photopigments and the genes that specify the photopigment proteins. In 1998, I provided a summary of the research (Jacobs 1998). Since then there has been a dramatic increase in efforts to understand the color vision of New World monkeys, which often have involved conceptually new approaches. Here I update the story by summarizing what vision scientists now know about platyrrhine color vision, as to both its mechanics and utility.

M/L Photopigments in Platyrrhines

Polymorphic Species

The color vision polymorphism of the platyrrhines arises from variations in the retinal complement of cone photopigments absorbing maximally in the middle to long wavelengths (M/L pigments). Individual monkeys have either 1 or 2 of the cone types, and, in conjunction with a short-wavelength-sensitive (S) pigment common to all members of the species, it provides the photopigment basis for either dichromatic or trichromatic color vision. All primate M/L pigments have absorption peaks (λ_{max}) ranging from about 530 nm to 562 nm. Table I is a summary of a number of measurements made of the M/L pigments of New World monkeys. There is no evidence of any significant pigment variation at the specific level; accordingly, I collated results for monkeys from 11 platyrrhine genera. The M/L pigments probably occupy any of only 5 discrete spectral locations (Table I).

Several points emerge from the measurements in Table I. First, all of the polymorphic platyrrhines share the longest of the primate M/L pigments, one having a λ_{max} value of ~562 nm. The pigment is also common to all catarrhines. Beyond that, there is variation both in number of M/L pigments detected and in their spectral positions. With regard to the former, the most common arrangement features a total of 3 polymorphic photopigments. Although some studies have not detected all of them, probably because of sample limitations, it seems quite certain that all taxa of Cebidae have 3 polymorphic M/L pigments. The story for the Atelidae is less clear. Thus far researchers have directly measured only 2 pigments in 2 genera from the subfamily, but detected the 2 plus a third one in *Brachyteles*. Whether the difference between *Brachyteles* and the other 2 Atelinae is real or simply reflects the vagaries of sampling from polymorphic individuals remains to be established. Researchers have also inferred 3 pigments from genetic results obtained from *Pithecia*.

There is at least 1 clear general difference in the spectral positioning of the M/L pigments in the polymorphic platyrrhines. All of the Callitrichidae seem to share in common 3 pigment positions (λ_{max} of ~543, 556 and 562 nm) while Cebinae also share their 3 pigment positions (~530–535, 549, and 562 nm). For the remaining individuals, the generalities are less easy to come by. It appears that no monkey outside of the Callitrichidae has pigments with λ_{max} values of 543 and 556 nm and that all other species also share in common with the Cebinae a ~550 nm pigment.

There is variation in the locations of estimated spectral peaks for measurements of what are presumed to be the same photopigments. For instance, the 3 estimates for the peak of the shortest of the M/L pigments in *Cebus* cover a range of 6 nm with a nearly similar-sized variation for that same pigment as measured in *Saimiri*. Are the differences meaningful? Researchers have measured pigment spectra in the monkeys in 3 different ways: from the intact eye via an electrophysiological gross potential measurement; the electroretinogram (ERG), from individual cones via microspectrophotometry (MSP); and, by *in vitro* spectrophotometric measurements of photopigments reconstituted from opsin genes in an artificial expression system. Each technique brings with it a set of assumptions and some inherent measurement error, so it is difficult to draw precise comparisons. However, the *in vitro* measurements on reconstituted photopigment are almost inevitably slightly short-shifted relative to the *in vivo* measurements. Thus, of the 14 cases in Table I in which researchers measured an M/L pigment both *in vivo* and *in vitro*, the *in vitro* measurements yielded a shorter λ_{max} estimate on 13 occasions. One can also draw a similar conclusion from comparisons of measurements on other

Table I Wavelengths of peak sensitivity for M/L pigments of polymorphic platyrrhines[a]

Family	Genus	Peak wavelength				Reference
Atelidae	*Ateles*		550		561	1 (ERG)
			547		562	2 (E)
	Brachyteles	530	545		560	3 (I)
	Lagothrix		547		562	1 (ERG)
Pitheciidae	*Pithecia*				565	4 (ERG)
		535	550		562	5 (I)
Cebidae	*Cebus*	534				6 (MSP)
		536	549		561	4 (ERG)
		530	545			7 (E)
	Saimiri	537	550		565	8 (MSP)
		532	545		558	9 (E)
		536	548		561	4 (ERG)
Callitrichidae	*Saguinus*	545		557	563	4 (ERG)
	Leontopithecus	545		557		4 (ERG)
	Callimico	543			563	10 (I)
	Callithrix	543		556	563	11 (MSP)
		539		553	561	9 (E)
	Cebuella			556	563	12 (I)

[a] Peak values are in nm. The authors of various experiments obtained the values from *in vivo* measurements via electroretinogram (ERG) or microspectrophotometry (MSP), *in vitro* measurements from expressed cone pigment (E), or inferred (I) from analysis of gene structure. References: (1) Jacobs and Deegan II (2001); (2) Hiramatsu *et al.* (2005); (3) Talebi *et al.* (2006); (4) Jacobs and Deegan II (2003); (5) Boissinot *et al.* (1998); (6) Bowmaker *et al.* (1983); (7) Saito *et al.* (2005a); (8) Mollon *et al.* (1984); (9) Hiramatsu *et al.* (2004); (10) Surridge and Mundy (2002); (11) Travis *et al.* (1988); (12) Surridge and Mundy (2002).

mammalian cone pigments in which *in vitro* absorption measurements are nearly always shifted toward the shorter wavelengths relative to *in vivo* measurements on the same species (Yokoyama and Radlwimmer 1999). In general, the differences are not very large, and their interpretation is not obvious. There could be some mundane explanation for the difference traceable to the variant methodologies, but it is also possible that native pigment packaged in intact photoreceptors has slightly different spectral absorption properties than it does when measured *in vitro*. If so, while the latter then can give very accurate measurements of the spectral absorption properties of photopigment per se, the former may provide a better prediction of what is to be expected of photopigment behavior in the living eye. In any case, the small differences should not obscure the essential agreement on the spectral positioning of the polymorphic M/L pigments of platyrrhines.

Information about the M/L pigments for representatives of 5 genera of platyrrhines is missing from Table I. Of these, neither *Alouatta* nor *Aotus* are polymorphic. There are also recent measurements of the M/L pigments of *Callicebus*. Though they are also polymorphic, they seem to differ from the pattern illustrated in Table I. I have no datum on the M/L photopigments in *Chiropotes* and *Cacajao*.

Species Lacking Photopigment Polymorphisms

Two genera lack M/L photopigment polymorphisms. Night monkeys (*Aotus*) are nocturnal anthropoids whose retinas have a relatively modest population of cone receptors and lack a clear foveal specialization. Jacobs *et al.* (1993) employed both ERG and behavioral measurements and concluded that *Aotus* has only a single M/L pigment with no evidence of a polymorphism. Consistent with this result, behavioral tests also showed that *Aotus* lacks a color vision capacity. Further, in support of an earlier examination involving immunocytochemical labeling of photoreceptors (Wikler and Rakic 1990), we also failed to find evidence for the presence of S cones in *Aotus*. The conclusion was that *Aotus* has only single type of photopigment and thus technically must lack color vision entirely. As measured via ERG techniques, the M/L photopigment of *Aotus* has a λ_{max} of *ca.* 543 nm (Jacobs *et al.* 1993) while subsequent pigment measurements on expressed photopigment give a corresponding value of 539 nm (Hiramatsu *et al.* 2004).

The other exception to the polymorphic theme occurs in the howlers (*Alouatta*). A joint ERG and genetic investigation indicated that the retinas of howlers are unlike those of all other platyrrhines in that they routinely contain 2 spectrally discrete types of M/L pigments (Jacobs *et al.* 1996a). In this regard, they are very similar to all catarrhine monkeys, apes, and humans. Though researchers have not conducted the appropriate behavioral tests, the clear implication is that all howlers have trichromatic color vision. There is no accurate measurement of the 2 M/L pigments in *Alouatta*, but implications from the ERG results and from examinations of the structure of the opsin genes are consistent with the idea that the 2 pigments have respective peak values similar to those of catarrhines, i.e., with λ_{max} of *ca.* 530 nm and 560 nm (Jacobs *et al.* 1996a; Hunt *et al.* 1998; Saito *et al.* 2004).

Though researchers believe that *Aotus* and *Alouatta* lack M/L cone pigment polymorphisms, there is room for caution. Most other platyrrhines have high-frequency polymorphisms, so the likelihood of encountering the variant forms, even

in small samples, is relatively high. However, if either *Aotus* or *Alouatta* were to have a low-frequency polymorphism, it could well be that in each of the individuals only the most frequent pigments have so far been encountered because, in total, researchers have tested few monkeys of each genus. Because of the tight linkages between photopigment genes and the cone photopigments, it is now possible to use genetic techniques to infer pigment complements straightforwardly in large samples of subjects, which would be useful to do with *Aotus* and *Alouatta*.

Platyrrhine S-Cone Pigments

With the singular exception of *Aotus*, the retinas of all platyrrhines have a population of cones containing short-wavelength sensitive pigment. In platyrrhines, as in all other primates, S cones are the sparsest of the cone types, comprising only ca. 5–10% of the total cone complement (Calkins 2001). There are only a few measurements of the spectral properties of platyrrhine S cones. MSP measurements of S cones in marmosets and squirrel monkeys yielded mean λ_{max} values of *ca.* 424 nm and 431 nm, respectively (Mollon *et al.* 1984; Travis *et al.* 1988). Though the spectral difference is small, Bowmaker (1990) suggested it represents a real difference between the 2 genera. In any case, the peaks are reasonably similar to the λ_{max} values obtained from various catarrhine monkeys via the same measurement technique (Bowmaker *et al.* 1991). ERG measurements have verified the presence of S cones in many of the platyrrhines in Table I. However, because of complications introduced by the presence of spectrally selective preretinal filters in the eyes, e.g., lens, macular pigment, and because M/L pigments themselves have considerable sensitivity in the short wavelengths, and thus can contribute to recorded signals, measurements made from the intact eyes of primates cannot give very accurate measurements of the spectral sensitivity of S-cone pigments.

M/L Opsin Genes

Spectral Tuning

Visual pigments consist of a transmembrane protein called opsin that is covalently bound to a chromophore. The chromophore 11-*cis*-retinal is common to all primate photopigments, so the spectral positioning of the pigment is determined by the opsin structure. From examinations of pedigrees for human color vision defects, it has long been appreciated that the genes associated with the M and L pigments are located on the X-chromosome. In a signal achievement, Nathans *et al.* (1986) cloned and sequenced these genes. The investigation revealed that 1) the L and M opsin genes are positioned in a tandem array on the X-chromosome, 2) each of them has 6 exons and encodes a protein consisting of 364 amino acids, and 3) the 2 opsins are nearly identical in structure, differing by a total of only 18 amino acids (Neitz and Neitz 2003). The separate L and M opsin genes apparently emerged from duplication of an ancestral gene. Because the duplication occurred near the base of the catarrhine radiation, all contemporary catarrhines share in common their M and L cone

photopigments. Humans are nearly unique among catarrhines in that individual variations in the structure of M/L opsin genes are relatively common. The variations allow a wide range of well documented and much studied human color vision defects (Deeb 2005; Neitz and Neitz 2000;).

Male platyrrhines typically have only a single M/L cone pigment whereas females can have either 1 or 2. The observation, first made in squirrel monkeys, suggested that, unlike catarrhines, New World monkeys probably had only a single X-chromosome opsin gene, which limits males to a single M/L pigment, but also allows females heterozygous at the opsin gene site to have 2 different M/L pigments (Mollon *et al.* 1984). To sort the 2 pigments into separate photoreceptors then requires only the operation of the normal mammalian gene dosage mechanism: random X-chromosome inactivation. The inheritance of photopigments in squirrel monkeys was consistent with this idea (Jacobs and Neitz 1987), and, subsequently, direct evidence for an X-chromosome localization of the platyrrhine opsin genes has emerged (Kawamura *et al.* 2001).

Examination of the opsin genes from platyrrhines revealed that they are very similar in structure to the opsin genes of catarrhine primates. For instance, the M/L pigments of humans, squirrel monkeys, and marmosets share a sequence identity of ≥96% (Hunt *et al.* 1993; Neitz *et al.* 1991). The fact that the genes are so similar and yet encode photopigments with a variety of different spectral absorption properties suggested that it might be possible to learn what features of the opsin sequence correlate with the spectral positioning of the pigment. Pairwise comparisons of the amino acid sequences of 8 M/L pigments (2 from humans, 3 from squirrel monkeys, 3 from tamarins) indicated that substitutions of amino acids at only 3 sites (positions 180, 277, 285 in the opsin molecule) were compellingly associated with changes in the spectral tuning of these M/L pigments (Neitz *et al.* 1991). Specifically, at each of these locations (Fig. 1) replacement of a nonpolar with a hydroxyl-bearing amino acid was associated with a discrete shift in the spectral peak of the pigment toward longer wavelengths. Further, the peak-shifting effects of the substitutions at the 3 sites were additive. As summarized in Table II, researchers have found the same tuning sites to be operative in other platyrrhines (Shyue *et al.* 1998). The M/L opsins of callitrichids show no variation at position 277, and as a consequence the M/L pigments in the group do not extend over as wide a spectral range as they do in other platyrrhines. Remarkably, site-directed mutagenesis experiments on human opsin genes has verified that the same 3 amino acid locations also yield similar-sized spectral shifts in catarrhine M/L pigments (Asenjo *et al.* 1994; Merbs and Nathans 1992). Substitutions at 2 other amino acid positions (116, 230) produce very small spectral shifts in the catarrhine M/L pigments, but the same changes are not consistently associated with spectral shifts in platyrrhine M/L pigments. Moreover, the alanine/serine dimorphism at position 180 produces a small shift (~4–6 nm) in the position of the longest of the M/L pigment and that variation is a high-frequency polymorphism in human populations of European descent (Winderickx *et al.* 1992).

Howlers have 2 types of M/L pigment, and the spectral tuning of the pigments is consistent with the picture just sketched. For 1 of the M/L opsins of howlers the amino acids at the 3 tuning sites (Table II) are the same as the ones for all 4 of the genera that share in common a photopigment with λ_{max} of *ca.* 562 nm, while the other opsin has an amino acid composition at the 3 critical sites identical to the

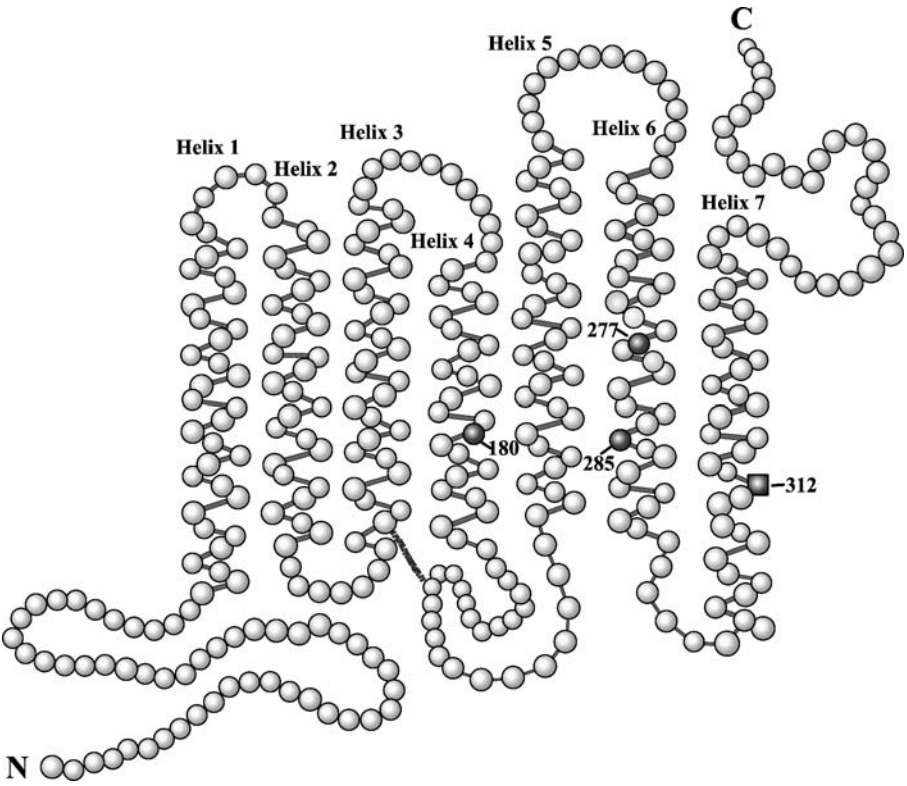

Fig. 1 Schematic diagram of the primate M/L cone opsin molecule. The 364 amino acids characteristic of the transmembrane protein are here indicated by the small circles. As described in the text, the 3 sites responsible for shifts in spectral tuning of the M/L pigments in platyrrhines are indicated by the 3 numbered locations. The amino acid combinations at the sites that are associated with the various pigment peak locations are indicated in Table 2. The chromophore attachment site is at position 312 (black square).

Table II Amino acids involved in spectral tuning of platyrrhine M/L pigments

Pigment peak	Genus	Position 180	Position 277	Position 285
562 nm	*Cebus* *Saimiri* *Callithrix* *Saguinus*	Serine	Tyrosine	Threonine
556 nm	*Callithrix* *Saguinus*	Alanine	Tyrosine	Threonine
550 nm	*Cebus* *Saimiri*	Alanine	Phenylalanine	Threonine
543 nm	*Callithrix* *Saguinus*	Alanine	Tyrosine	Alanine
535 nm	*Cebus* *Saimiri*	Alanine	Phenylalanine	Alanine

ones identified for 530–535 nm pigment of *Cebus* and *Saimiri* (Jacobs *et al.* 1996a). In *Aotus*, the other platyrrhine that has no M/L pigment polymorphism, the amino acid residues at the 3 tuning sites are the same as the ones in Table II for the tamarin and marmoset M/L photopigments having peak absorption at *ca*. 543 nm (Hiramatsu *et al.* 2004).

The very conservative mechanism for tuning the spectral positioning of the M/L pigments makes it possible to simply determine the amino acid composition at the 3 sites and thereby obtain a photopigment genotype. Because DNA can be obtained noninvasively, e.g., from samples extracted from primate feces (Surridge *et al.* 2002), one can now straightforwardly infer the photopigment phenotypes of platyrrhines. The approach can be of great value, e.g., in carrying out population surveys of opsin genes or in inferring the photopigment complement of individual subjects at a study site.

Evolution

There are tight linkages between opsin genes and photopigments. In turn, there are less compelling but nevertheless well understood relationships between photopigments and seeing. Consequently, examinations of collections of sequence data obtained for opsin genes of many different species have recently assumed critical importance for understanding the evolution of vision, especially for the issue of color vision. Several authors have reviewed the data for vertebrates in general (Jacobs and Rowe 2004; Neitz *et al.* 2001; Yokoyama and Radlwimmer 2001), as well as more specifically for mammals (Yokoyama and Radlwimmer 1999) and primates (Dulai *et al.* 1999; Jacobs 2004; Li *et al.* 2000; Vorobyev 2004). I focus on the platyrrhine results.

The X-chromosome opsin gene arrays differ fundamentally between catarrhines and platyrrhines. Hunt *et al.* (1998) argued that catarrhines routinely have 2 different X-chromosome opsin genes, 1 of which in humans is typically present in multiple copies. It appears that the 2 resulted from a gene duplication near the base of the catarrhine radiation. By contrast, platyrrhines predominantly have only a single X-chromosome opsin gene with multiple alleles coding for spectrally varied M/L cone pigments. An important early finding was that the amino acid substitutions used to tune the platyrrhine M/L cone pigments spectrally are, by and large, also utilized to tune catarrhine M/L cone pigments. A central question is where did the platyrrhine M/L polymorphism arise-before the catarrhine/platyrrhine divergence: once among the platyrrhines, or independently in each of the various platyrrhine lineages?

A comparison of the amino acid differences in the M/L opsins of representative platyrrhine and catarrhines primates speaks to the first of the possibilities (Hunt *et al.* 1998). It turns out that with the exception of the 3 tuning sites, i.e., positions 180, 277, and 285 in the opsin molecule; Fig. 1) there is essentially no similarity in amino acid substitutions between the M/L opsins of catarrhines and platyrrhines. One would not expect this if the catarrhine M and L genes arose from a polymorphism that predated the catarrhine/platyrrhine divergence, and so it seems likely that the 2 systems evolved separately. Researchers have argued that the use of the same amino acid spectral tuning sites in the 2 primate lines represents a case of convergent

evolution, perhaps attributable to the paucity of sites in the opsin molecules that can actually be used to alter the spectral absorption properties of photopigments (Hunt *et al.* 1998).

Boissinot *et al.* (1998) and Hunt *et al.* (1998) examined the specific issue of the origin of the M/L opsin gene polymorphisms in platyrrhines via phylogenetic analyses of nucleotide differences in exons 3, 4, and 5 of genes from 6 genera of New World monkeys, each of which has a triallelic arrangement (Fig. 2). Though the story is not unambiguous, it appears that the clustering of sequences is grouped mostly according to the spectral properties of the pigment rather than following a strict species pattern. For instance, the longest of the M/L pigments (λ_{max}=~562 nm) quite clearly seems to have a single origin for all of the monkeys. Note, however, there is some support for the possibility that the 543 nm and 556 nm pigments of the callitrichid species arose separately. In any case, the main conclusion drawn from the analyses is that the allelic forms of the M and L opsins in the polymorphic platyrrhines most likely had a single origin. An implication following from that conclusion is that the allelic system characteristic of the platyrrhines has been around for a long time, perhaps more than 20 million years, and its antiquity suggests in turn that it must have been maintained over this long span by natural selection (Boissinot *et al.* 1998; Hunt *et al.* 1998). Both conclusions are supported by results from a similar analysis that focused on allelic variations in a several species of Callitrichidae in which Surridge and Mundy (2002) inferred that the opsin gene polymorphism has persisted for 5–14 million years.

Howlers are unique among platyrrhines in having 2 X-chromosome opsin genes and thus they more closely approximate the way things are in the catarrhines. For the arrangement to support trichromatic color vision there must in addition be a means to ensure the selective expression of the 2 pigments into separate populations of cones. In catarrhines there is evidence that dynamic interactions between a single upstream locus control region (LCR) and the promoters of the M and L genes determine which gene gets expressed in a given cone (Smallwood *et al.* 2002). The

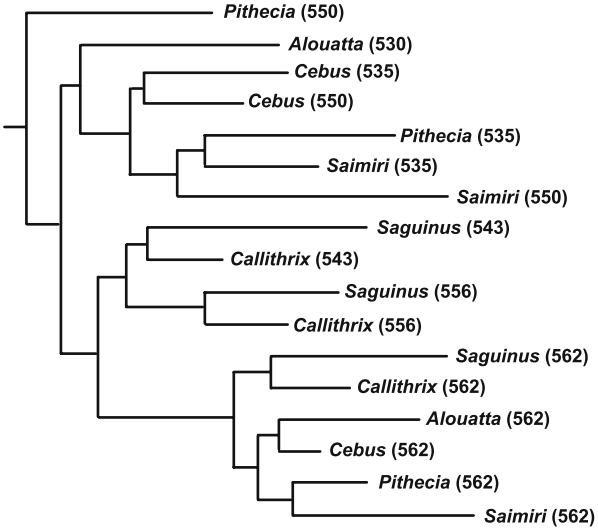

Fig. 2 Phylogeny of nucleotide differences in exons 3, 4, and 5 of the alleles of 6 platyrrhine genera. (Redrawn from Hunt *et al.* 2005).

opsin genes on the X-chromosome of howlers have a different arrangement in that there are 2 LCRs, 1 associated with each of the opsin genes (Dulai *et al.* 1999). Comparison of the upstream sequences of howlers and catarrhines suggests that the duplication event that led to the presence of separate M and L genes on the X-chromosome must have occurred much more recently in howlers than it did in the catarrhines (Kainz *et al.* 1998), thus reinforcing the general view that the evolution leading to trichromatic color vision of Old and New World primates occurred independently. Exactly how howlers use their 2 LCRs to achieve selective gene expression is a problem remaining to be solved.

M/L Opsin Genes on the Y Chromosome

In mammals, M/L opsin genes are located on the X-chromosome. *Aotus* has additional M/L opsin genes that have apparently translocated to the Y chromosome (Kawamura *et al.* 2002). Two different arrangements are present. In some males, a single intact copy of the M/L opsin gene occurs on the regular Y chromosome while in other individuals there were multiple copies of M/L opsin pseudogenes located on a Y/autosomal fusion chromosome. Subsequent investigation revealed that the 2 arrangements are characteristic of 2 species; respectively, *Aotus lemurinus griseimembra* and *A. azarae bolivensis* (Nagao *et al.* 2005). It is not obvious that the additional intact opsin gene has any implication for vision because it is not known if the gene is expressed in the retina and, even if it were to be expressed, the pigment product would be predicted to have spectral absorption properties identical to those of the photopigment produced by the X-chromosome M/L opsin gene. Thus it could not provide a basis for color vision and, unless there was also some concomitant change in the rod/cone mix, it would also seem unlikely to yield any other change in visual capacity. Even absent implications for visual function, the differences in the Y-chromosome opsin gene arrangements in the 2 species may provide a novel basis for elucidating the phylogenetic history of *Aotus* (Nagao *et al.* 2005).

Number of M/L Alleles and Allele Frequency

The clear theme among the polymorphic platyrrhines is 3 alleles (Table II), but there are some possible exceptions. First, as noted, among the Atelidae, Jacobs and Deegan II (2001) identified only 2 M/L polymorphic pigments in an ERG study of *Ateles* and *Lagothrix*. For the latter, they tested only a relatively small sample of individuals (n=9), so the absence of a third M/L pigment could quite conceivably represent nothing more than a sampling problem. However, they examined a reasonable number (n=47) of spider monkeys and suggested that the apparent absence of a third M/L pigment might be more meaningful. In fact, with a sample of 47 the hypothesis that *Ateles* has 3 M/L alleles present in equal frequency can be statistically rejected. Further, on statistical grounds one can also infer that if a third allele exists it would be expected to constitute ≤10% of the population total (Jacobs and Deegan II 2001). This result received support from a subsequent genetic examination that also failed to detect a third allele among a sample of 20 spider monkeys (Hiramatsu *et al.* 2005). However, although it is so far undocumented, Stoner *et al.* (2005) claim to

have detected a third allele in *Ateles*. Given these results, it is intriguing that the third allele in *Brachyteles* (the one absent in the *Ateles* and *Lagothrix* samples) is rare, with only 2 of the 29 genes (6.8%) characterized predicted to code for 530 nm pigment (Talebi *et al.* 2006). It may be that all the polymorphic atelid monkeys are, like most other platyrrhines, formally triallelic. Even if true, the 3 alleles seem likely to be unusually represented in the family. Because the platyrrhine M/L alleles are probably under active selection it is hard to imagine what advantage might accrue to having a 530 nm pigment in the population at very low frequency.

In a survey based on an analysis of opsin gene sequences (Table I), Surridge and Mundy (2002) also detected only 2 alleles in *Cebuella* and *Callimico*. Both cases may also reflect sampling problems. However, in the case of *Callimico*, Surridge and Mundy (2002) studied a total of 39 chromosomes and an effect of that magnitude begins to suggest that a third allele is at least infrequent.

The other potential exception to the 3-allele rule is titi monkeys (*Callicebus molloch*), in which, remarkably, the disparity seems in the opposite direction. A recent study involving ERG measurements of spectral sensitivity in a large sample of titi monkeys (Jacobs and Deegan II 2005) provides evidence for the presence of a total of 5 spectrally discrete pigments in the M/L range having mean λ_{max} values of ~530, 536, 542, 551, and 562 nm (Fig. 3). The argument that they actually represent different photopigment types is based on the following facts: 1) the variability in spectral positioning of individuals within each group is small; 2) the distributions of λ_{max} values of adjacent groups are statistically significantly different; and, 3) test/retest reliability in spectral sensitivity is very high. Because the categorizations are based on spectral sensitivity measurements, it is not absolutely necessary to infer from them that there are 5 allelic versions of M/L opsin genes, though it is not obvious how one could explained them in any other way. Assuming they represent alleles of M/L opsins, the result raises the possibility that early polymorphic platyrrhines in fact had 5 versions of the M/L opsin gene and that 2 of them were lost in the various lines to most contemporary platyrrhines while being retained in *Callicebus*. If nothing else, the several possible deviations from the 3-allele rule indicate that there is more to learn about the M/L opsin genes and photopigments in the polymorphic platyrrhines.

In nearly all platyrrhine taxa, females become trichromatic by being heterozygous. The likelihood of this happening depends both on the number of M/L opsin alleles and their relative frequency. If the polymorphic genes are of equal frequency in monkey populations with 2 alleles, half of the females are heterozygous and thus trichromatic; with 3 equally frequent alleles two-thirds of the females are heterozygous, and so on. Though it was clear even in early studies that the alleles are of high frequency, indeed it seems likely that the polymorphism might never have been discovered if it were not of high frequency. It has not been easy to get compelling indications of what the frequencies actually are. Most of the earlier studies of platyrrhines necessarily involved only small numbers of individuals that researchers usually drew from restricted breeding populations, either because they were captive in a single colony or from wild populations in single locales. These factors can serve to foster very biased estimates of allele frequency. In recent years, things have improved, thanks both to the expanded use of noninvasive opsin genotyping and to a general increase in interest in polymorphic primates.

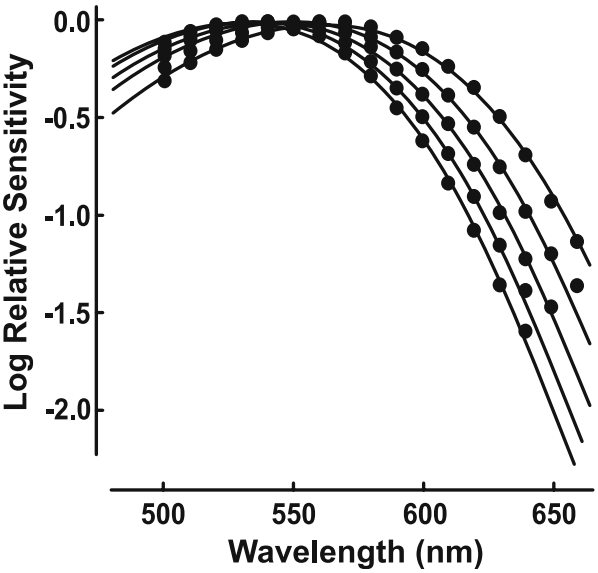

Fig. 3 Spectral sensitivity functions for the 5 types of M/L photopigment in *Callicebus moloch*. The spectra of the pigments came from electrophysiological measurements. They are presumed to represent the photopigment products of 5 M/L opsin gene alleles.

There are surveys of allele frequency in varied populations of 16 species of the Callitrichidae (Surridge and Mundy 2002) and of 3 of *Saimiri* spp. (Cropp *et al.* 2002). Each provided an account of >200 M/L opsin alleles. Rowe and Jacobs (2004) added the survey results to other accounts of allele frequencies in the monkeys to yield, in total, information about 362 squirrel monkey alleles and 406 alleles from a variety of callitrichids. For the compilations, the representation of the 3 opsin types in the squirrel monkeys did not differ from the expectation based on equal gene frequency while the callitrichid alleles deviated from this standard. In particular, the allele specifying the callitrichid 556 nm pigment (Table I) was significantly underrepresented, comprising <20% of the total. A subsequent analysis of opsin genes from additional wild populations of *Saguinus* supports the inequality of allelic representation (Surridge *et al.* 2005b). The samples are relatively large and are from many different sources. If they are taken as representative it would imply that for some triallelic species, like *Saimiri*, the number of heterozygous female monkeys probably reaches the maximum possible while at the same time various Callitrichidae seem not to achieve that standard.

Studies of opsin allele frequency in the monkeys stem in part from an interest in understanding what maintains these polymorphisms. Early on, Mollon *et al.* (1984) pointed out that there are several possible explanations. One is that it reflects an example of overdominant selection (heterozygous advantage) wherein heterozygous (and therefore trichromatic) females always have a visual advantage over all the dichromatic phenotypes. A second is frequency dependence according to which particular phenotypes are advantaged in the performance of particular visual tasks, which serves to maintain a variety of phenotypes. Finally, because most platyrrhines forage in groups, it is conceivable that the presence of a variety of visual phenotypes provides a net group benefit. The various explanations are obviously not mutually exclusive. However, overdominant selection implies a maximization of heterozygous

females and predicts that the opsin gene alleles will be of equal frequency while significant deviations from that standard suggest that other factors are involved in maintaining the polymorphism. If the surveys are representative, this may be the case for the callitrichid monkeys, in which the proportion of heterozygous females is not maximized and, perhaps more important, there is predicted to be an altered representation of the various retinal pigment complements. Examination of the distributions of opsin alleles among breeding groups of red-bellied tamarins (*Saguinus labiatus*) suggests that between males and females the opsin allele types are nonrandomly distributed (Surridge *et al*. 2005b), which may arise from an inbreeding avoidance mechanism and could serve to maintain opsin polymorphisms. All of the aforementioned facts raise questions about how well monkeys with different pigment complements are adapted to make particular kinds of visual discriminations.

Heterozygous platyrrhines have 3 classes of cones, 2 of which contain either one or the other of the allelic versions of the M/L pigments. The relative representation of the 2 in the retinal mosaic can potentially impact both visual sensitivity and color vision. For example, a relative paucity of the longer of the 2 pigments will reduce sensitivity to long-wavelength lights. As noted in the preceding text, the selective expression of the 2 genes is based on X-chromosome inactivation. If that is a random process, as it has been classically conceived, equal numbers of the 2 cone types should result. However, many studies of heterozygous human females have revealed a range of influences on relative gene representation, some taking place at the time of inactivation and some subsequently, that may produce significant biases toward over-representation of either maternal or paternal chromosomes (Migeon 1998). To estimate the M and L cone proportions in platyrrhines, Jacobs and Williams (2006) examined ERG-derived spectral sensitivity functions for heterozygous females drawn from a number of different polymorphic species. For a sample of 60 monkeys the average M:L ratio derived from fitting the spectral sensitivity functions with the appropriate cone fundamentals was very close to unity, implying that there is no systematic deviation from the expectation based on a random process.

S Opsin Genes

The S-opsin gene is composed of 5 exons. In humans, as in Old and New World monkeys, the autosomal gene encodes a transmembrane protein made up of *ca.* 350 amino acids (Hunt *et al.* 1995; Nathans *et al.* 1986). The gene is a member of the *SWS1* gene family, which produces pigments that have maximal absorption extending over a broad range extending from the ultraviolet (~360 nm) to the short-wavelength portion of the visible spectrum (~435 nm) (Hunt *et al.* 2001). Researchers believe the ancestral *SWS1* gene of vertebrates encoded UV pigments and that a subsequent shift up into the visible range has been achieved on many occasions in different lineages. Molecular geneticists have examined the tuning of pigments produced by *SWS1* genes in a wide range of species and, as for the M/L opsin genes, have implicated amino acid substitutions at a few critical sites in spectral shifting (Hunt *et al.* 2004; Shi and Yokoyama 2003). There appears to be a small

spectral difference between the S-cone pigments of marmosets and squirrel monkeys, with that of the former shifted in peak toward the shorter wavelengths. The S-opsin genes of the 2 do not differ at the putative tuning sites, so the spectral difference of their pigments, if it is real, does not have a current genetic explanation (Hunt *et al.* 2004).

Aotus lacks functional S-cones, and examination of its S-cone opsin gene reveals several insertions and deletions in exon 1 that introduce a premature stop codon and thus presumably serve to obviate pigment expression (Jacobs *et al.* 1996b). Researchers have also identified fatal mutational changes in the S-cone opsin genes in other mammalian species, including some nocturnal strepsirrhines, some rodents, and a great many marine mammals (for a review, see Peichl 2005). The human color vision defect tritanopia also involves mutational changes in the S-cone opsin gene. However, the human condition is rare, affecting as it does <0.001% of the population, while the S-cone losses in species such as *Aotus* are ubiquitous because all members of the species have the defect, which could imply that there was an adaptive reason for the ancestral loss of S cones and concomitant loss of a dimension of color vision. Though vision scientists have offered suggestions on what these adaptive values might be, none seems able to explain why the loss occurred in different lineages that individually represent greatly variant photic environments and life histories.

Neuronal Organizations Subserving Color

Color vision requires both multiple classes of photopigments, each segregated in a separate class of cone, and a nervous system that is so organized that it provides a means of comparing signals that originate in the different classes. The early demonstrations that variations in platyrrhine color vision are predictable from variations in photopigment complements made it clear that the appropriate neural organizations must also be present in platyrrhines, but left open the question of whether the visual systems of conspecific monkeys having different types of color vision have fundamental differences that parallel their photopigment differences. For instance, a central question is whether the evolution of new opsins alone is sufficient to allow new color vision capacities to emerge.

Cone Photoreceptor Mosaics

Cones sample the retinal image and thus provide the signals that underlie photopic vision. Primate cone mosaics feature a density pattern that is typically characterized by very high spatial packing in the central fovea and by progressively significant declines in density toward the peripheral retina. To yield the signals needed to support color vision the various cone classes need to be distributed so as to allow for spatially local connections by downstream retinal cells.

Foveal cone densities are documented for some platyrrhine genera. The estimates are important since they can be used in conjunction with knowledge of the geometry of the eye to derive predictions of maximal visual acuity. Counts from marmoset

retinas yield estimates of *ca.* 200,000 cones/mm^2 (Trolio *et al.* 1993; Wilder *et al.* 1996); these values are quite similar to the ones that characterize human and macaque monkey foveas (Curcio and Hendrickson 1991). Cone density is higher in the retinal periphery in marmosets vs. catarrhines. Franco *et al.* (2000) and da Costa and Hokoc (2000) claimed somewhat lower peak densities for counts made in the foveas of *Cebus*, *Saguinus*, and *Saimiri.* Whether the differences are functionally significant or not is unclear, principally because the number of eyes sampled is necessarily small and because there are very large variations in cell numbers between individual retinas (often varying by a factor of ≥3). There are 2 genera whose peak cone densities seem to deviate significantly: *Aotus* and *Alouatta*. In the central retina of *Aotus* rods predominate and cone densities do not exceed 20,000/mm^2 (Silveira *et al.* 2001). The figure correlates rather closely with the lowered photopic visual acuity of the species (Jacobs 1977). In *Alouatta* the fovea features a very dense cone packing, averaging a striking 376,000/mm^2 for 2 eyes (Franco *et al.* 2000). We do not know why howlers have such seemingly unusual organization.

S-cones can be identified by opsin antibody labeling, thus it is possible to establish their retinal distributions. There is no difference in S-cone distributions in dichromatic and trichromatic marmosets, implying that S-based and M/L-based systems of color vision are independent in the polymorphic platyrrhines (Martin and Grunert 1999). In Old World primates, S cones are absent from a small region in the central fovea and beyond that they form a semi-regular triangular array across the retina. Neither of the features occurs in representative platyrrhines, which casts doubt on the idea that regularity in the S-cone mosaic necessarily improves the quality of spatial processing in S-cone pathways (Martin *et al.* 2000).

Currently there is no anatomical marker that one can use to identify M and L cones individually and thus examine the details of their retinal distribution. However, it is possible to use adaptive optics imaging to do it in the human retina (Roorda and Williams 1999). Researchers have not applied the technique to platyrrhines. On average the number of M and L cones in trichromatic platyrrhines is about equal (Jacobs and Williams 2006), but their spatial distributions remain to be studied.

Ganglion Cells and Color Coding

Because they are relatively accessible, there is a large literature on the form and function of mammalian ganglion cells, and there are several good general reviews of the issues that focus on primate retinas (Lee 2004; Martin 1998; Silveira *et al.* 2004). There is particularly good documentation of the morphology and physiology of ganglion cells for macaques. Briefly, the standard story is that signals originating in cones are effectively added or subtracted by ganglion cells to form channels that respectively transmit luminance and chromatic information up the optic nerve to brain targets. Parasol ganglion cells receive summed inputs from M and L cones—usually termed M or achromatic cells—project onward to the magnocellular layers of the lateral geniculate nucleus (LGN) of the thalamus and provide luminance information. Two chromatic channels emerge from ganglion cell operations: 1) small

bistratified ganglion cells compute differences between S-cone signals and summed signals from M and L cones: termed blue/yellow cells. They project to the koniocellular layers of the LGN and 2) midget ganglion cells difference M and L cone signals—red/green cells—and project to the parvocellular layers of the LGN. The first of the chromatic channels is apparently common to most, if not all, mammalian retinas while the second is unique to primates.

Much of the information about platyrrhine ganglion cells is from studies of *Callithrix* and *Cebus*. All 3 classes of ganglion cells can be readily identified by morphological criteria in *Callithrix* and *Cebus*. Indeed, their physiology seems formally very similar to that of catarrhines (Lee *et al.* 2000; Silveira *et al.* 1999). For the blue/yellow cells, there is no difference between dichromatic and trichromatic individuals, reinforcing the view that the chromatic channel differencing short and longer wavelength cone signals predates the divergence of catarrhines and platyrrhine lineages. Also, though there were some differences in their temporal response characteristics, capuchin M ganglion cells also have a physiology similar to those of macaque. Finally, though P cells recorded from dichromatic individuals lacked spectral opponency, they seem otherwise similar to catarrhine P cells. In short, though there are some differences in the details, the morphology and physiology of platyrrhine ganglion cells seems very similar to those of catarrhine primates, which strongly implies that after the appearance of a second M/L photopigment in early platyrrhines no additional modification of retinal organization was required to yield trichromacy in heterozygous females.

Central Visual System

There is a considerable body of descriptive work on the anatomical organization of the central visual systems of various platyrrhines, but results relevant to the issue of color coding are sparse. They echo the conclusion from studies of the retina in the sense that other than the expected presence or absence of a second channel for color coding there is no striking difference in organization between trichromatic and dichromatic conspecifics. Thus, recordings from the parvocellular layers of the LGN of *Callithrix* reveal a robust population of cells showing red/green opponency in trichromatic individuals that are absent in dichromats (Blessing *et al.* 2004; White *et al.* 1998; Yeh *et al.* 1995). Further, there seems to be no difference in the receptive field properties of parvocellular neurons in dichromats and trichromats, nor do cells carrying S-cone inputs differ for the 2 phenotypes. There are some differences that have potential implications for seeing. One is that a proportion of parvocellular neurons show strong rod inputs in dichromats, and the influence occurs even at quite high light levels (Yeh *et al.* 1995). Whether this translates into an expanded range for rod-based vision in platyrrhines—and thus perhaps an adaptation for a somewhat more crepuscular lifestyle—is unknown, though the recording results would suggest this is possible. A second interesting finding comes from a comparison of the responsiveness of cells to chromatically modulated test lights in trichromatic individuals. The sensitivity of such cells depends on the spectral separation of the M and L pigments, with more robust responses produced by cells with M and L

pigments that are separated by 20 nm than by similar cells with M and L pigments that are separated only by 7 nm (Blessing *et al.* 2004). This would predict that some color discriminations may be more readily made by the former trichromats than by the latter.

There seems to be only a single study directed at locations in the visual system beyond the LGN relevant to the issues I considered here. A detailed comparison of the anatomy of primary visual cortex (Area V-1) indicates that there is no significant difference in the organization of inputs to the cortex between trichromatic and dichromatic marmosets (Solomon 2002).

In sum, though there must be some difference in the neural organizations of the visual system of trichromatic and dichromatic platyrrhines reflecting their considerable color vision differences, none has yet been identified in early portions of the visual system. From the results thus far it seems entirely possible that the acquisition of a trichromatic capacity in heterozygous females is an example of neural learning being based on the plasticity of the central nervous system to adjust its operation in accord with the information provided to it. In this regard, one wonders if a heterozygous female monkey whose nervous system develops in an environment that is devoid of chromatic variation would develop trichromatic color vision.

Researchers have taken the fact that the visual systems of dichromatic and trichromatic platyrrhines show no obvious organizational difference to support the view that primate visual systems are so organized that the mere addition of a second M/L cone pigment is sufficient unto itself to allow a new dimension of color vision to emerge. Why that should be so has been the subject of much comment (Boycott and Wassle 1999; Kremers *et al.* 1999; Mollon 1995). The proposal typically offered is that the midget cell system of the primate retina provides an efficient physiological substrate for the establishment of opponent comparisons between signals generated by M/L cones, and thus the emergence of a second such cone type immediately leads to a novel source of spectral comparison and a new dimension of color vision. The presumption in this line of thinking is that the midget cell system evolved before the addition of a second M/L cone type. Evidence in support of the view comes from anatomical observations on nocturnal bush babies (*Otolemur garnettii*) indicating that their retinas have P and M pathways that share many similarities to those of anthropoids (Yamada *et al.* 1998). The role that the midget cell system might have subserved before the acquisition of trichromacy has in turn provoked considerable discussion (Lee 2004).

Ecology of Platyrrhine Color Vision

Among almost any group of foraging platyrrhines an enormous range of color vision capacities are represented. Accordingly, it is curious that the early reports of interindividual variations in color vision among the platyrrhines contain no comment on how the differences might be reflected in the visual lives of monkeys. Exploring the meaning of the variations became attractive once it was clear that they in fact

reflect maintained polymorphisms. In the past few years there has been an upsurge of studies directed toward understanding the natural implications of the color vision polymorphisms. Platyrrhines can be elusive, challenging to observe in their natural environments, and visually hyperactive. Thus the problem of understanding how they employ color vision in the course of their normal behavior is formidable indeed.

Further Demonstrations of Color Vision Polymorphisms

Studies conducted during the 1980s on squirrel monkeys, marmosets, and tamarins documented compelling linkages between direct laboratory measurements of color vision, cone photopigment measurements, and opsin gene complements. As a result of the associations, it became typical to assume that one could obtain inferences about all of the indices from studies of any one of them. Because it is relatively much more efficient to measure cone photopigments and examine opsin genes than to carry out behavioral tests of color vision, much of the subsequent documentation of platyrrhine color vision polymorphisms derives from the 2 strictly biological approaches. Despite the trend, it remains important to have behavioral tests of color vision in platyrrhines, both to bolster further the linkages among genes, pigments, and behavioral indices, and because many aspects of color vision can be assessed only with behavioral measurements. In the past few years several new laboratory tests of color vision in platyrrhines have appeared.

Unlike the earlier examinations of color vision in platyrrhines that used calibrated lights as test stimuli via adaptations of standard laboratory tests of human color vision, more recent investigators have employed various versions of colored papers as stimuli to evaluate color vision, either drawn from the standard series of Munsell test papers or colored papers that were designed and calibrated for use in a particular experiment. It is well documented that a major issue in any test of animal color vision is to ensure that discrimination is based solely on chromatic cues (Jacobs 1981, 1993; Kelber *et al.* 2003). This can pose a particular problem with primates because they are expert at exploiting any brightness or lightness differences between chromatically variant stimuli and can thus readily mislead investigators as to the presence and nature of their color vision (Jacobs 1999). To ease the problem, investigators typically strive to make brightness or lightness irrelevant as cues by randomly varying brightness/lightness differences among the stimuli to be discriminated. A second useful strategy is to test in parallel humans with well established normal and defective color vision. In this way, one can gain confidence that primates with known phenotypes behave in a fashion that is at least predictable from their photopigment arrays. Researchers have employed both strategies in the newer experiments.

Several research teams have demonstrated the presence of color vision polymorphisms for *Cebus apella* (Gomes *et al.* 2002; Saito *et al.* 2005a), black-handed tamarins (*Saguinus midas niger*; Pessoa *et al.* 2003), golden-headed lion tamarins (*Leontopithecus chrysomelas*; Pessoa *et al.* 2005b), and black-tufted ear marmosets (*Callitrhix penicillate*; Pessoa *et al.* 2005a). Gomes *et al.* (2005) also established that dichromatic *Cebus* are not able to make trichromatic discrimination when viewing large-field stimuli, as some dichromatic humans allegedly are able to. Careful experiments that use colored papers as test stimuli seem capable of distinguishing between dichromatic and trichromatic animals, but it is not yet obvious that they are

sufficiently discerning that they can be used to categorize independently the subtypes of color vision in each of the dimensional categories. In any case, the recent examinations usefully extend the evidence that links genes, pigments, and color vision in platyrrhines.

Modeling Approaches

The transition from laboratory studies of color vision to understanding how color vision is used in natural environments is neither easy nor straightforward. Probably the most obvious approach is simply to watch monkeys in natural environments and from the observations infer how the subjects use color information to guide behavior. Though compelling in concept, in practice the approach is very challenging, not least because it is problematic for a distant observer to know exactly what aspects of the visual environment the darting eyes of a monkey are sampling at any moment in time. Accordingly, some investigators have taken an alternative approach to understand the ecology of vision that starts with physical measurements of the visual information offered by objects of potential importance to a species, e.g., foods, predators, conspecifics. To understand color vision this would include minimally measurements of the reflectance properties of objects and the backgrounds against which they may be displayed, as well as the irradiance spectra of a range of illuminants appropriate for the natural environments under which the objects are typically viewed. With that information and a computational model of how color information is extracted by visual systems, one can examine how efficiently any given color vision system deals with the spectral information provided to it and, from that, attempt to predict how various color vision phenotypes may be matched to visual performance.

In recent years, the modeling approaches have become quite popular. One result is the accumulation of a number of reflectance spectra of potential foods, backgrounds, and irradiance spectra appropriate for various platyrrhine habitats. Some investigators have made their measurements available for the use of others (one can access results from Regan *et al.* 2001 at http://vision.psychol.cam.ac.uk/spectra/; Endler 1993; Smith *et al.* 2003b), and one can expect more compilations to become available in the near future.

Researchers have developed 2 basic types of model to examine the utility of primate color vision. One assumes that discriminability between objects is determined by differences in the outputs of red/green and yellow/blue chromatic channels defined, respectively, as L/(L + M) and S/(M +L), in which S, M, and L are the quantal capture rates of the S, M, and L receptors (Dominy and Lucas 2001; Regan *et al.* 1998, 2001). The other model also starts from the quantal capture rate of the receptors, but is then based on an alternative possibility that proposes discriminability to be set by noise in the photoreceptors without any further limitations imposed by subsequent opponent mechanisms (Osorio and Vorobyev 1996; Vorobyev and Osorio 1998). In still other cases, both models are used, the second to assess discrminability of chromatic signals and the other to derive a prediction of perceived color, i.e., identification (Riba-Hernandez *et al.* 2004). Both computational models are physiologically realistic, and indeed predictions from them also agree on several features having to do with the effects of the spectral positioning of cone pigments on color thresholds (Osorio *et al.* 2005). However, they also have limitations. For example, in the former

model (Regan *et al.* 1998) the capacities of the 2 chromatic channels are treated separately, assuming that either one or the other but not both will be appropriate for any behavioral task. Conversely, the application of the noise model as designed is apparently limited to viewing situations that involve large static stimuli presented against achromatic backgrounds (Vorobyev and Osorio 1998). Finally, neither model meaningfully includes some variables that may be important for chromatic discrimination, e.g., viewing time (Rowe and Jacobs 2007).

Rowe and Jacobs (2004) proposed an alternative approach that effectively attempts to mate color vision modeling with behavioral measurements. The idea behind the approach is to alter the spectral stimuli presented to a human subject in a fashion that effectively mimics a change in the retinal photopigments of that subject. The goal of the technique, termed functional substitution, is to convert a human subject into a human/monkey chimera such that any set of photopigments can be simulated; e.g., using different combinations of M and L cone photopigments one can compare the ability to discriminate between fully ripened and partially ripened fruit. It can be argued that a hybrid approach like this could be used to evaluate the importance of various viewing parameters, e.g., time, light level, for individuals equipped with various combinations of cone photopigments, perhaps thereby serving as a guide to the development of computational models and to those who pursue experiments with monkeys.

The Utility of Color

In his classic book, Walls (1942, p. 463) suggested that color vision is useful because it "promotes the perception of contrasts and hence, visibility." Others followed the theme, in the course adding a list of other potential advantages of color vision that might support its evolution (Jacobs 1993; Kelber *et al.* 2003; Mollon 1989; Vorobyev 2004).

As Walls (1942) implied, color vision can serve as a direct aid in the detection of objects, which is obviously true in scenes where there is no luminance variation and only chromaticity related cues are available. In such cases, a color-blind individual would also be blind to spatial structure. Such circumstances are undoubtedly quite rare in natural environments and later writers emphasized that color vision may be particularly useful for detection in circumstances where luminance-related cues are incomplete and inconsistent, e.g., where shadows produce a patchy environment or where an object is viewed through a screen of foliage. Indeed, color vision may have first evolved as a means to defeat the cue ambiguity inherent in the uneven illuminations characteristic of shallow aquatic environments (Maximov 2000). A second powerful advantage of color vision is as an aid to perceptual segregation. Accordingly, the shared color property of spatially discrete elements can aid identification of an object. The classic example of color segregation occurs in the standard plate tests for color vision wherein the shared color of spatially discrete elements allows the observer to perceive a complete figure. Finally, color vision can support the identification of object properties. This may be particularly the case when object form is by itself insufficient for such an evaluation, e.g., in determining

whether a fruit is ripe or not, whether skin color signifies fever or anoxia, whether meat is properly cooked, etc.

Relative Advantages of the Color Vision Phenotypes

It is a long held view that the evolution of primate color vision is linked to the evolution of fruit coloration. In his seminal book on the vertebrate visual system, Polyak (1957, p. 973) made the idea explicit: "In most instances fruit would not be easily noticed by animals if it were not for its color" and, so, "we are therefore entitled to hypothesize that fruit coloring, whenever present, was evolved for the direct purpose of attracting by its specific hues, the attention of the animals, including Primates, which feed upon it." Though he gives no evidence that he was specifically aware of any predecessor opinion, Polyak (1957) was effectively reiterating a view expressed much earlier by the naturalist Grant Allen (1879), who had proposed that coloration of fruits occurred in parallel to the evolution of animal color vision.

Claims for trichromatic superiority Though there are some earlier computational attempts at a general evaluation (Lythgoe and Partridge 1989), the beginnings of actual tests of a potential linkage between the chromatic signals offered by fruits and primate color vision appeared in an article that introduced a computational model designed to predict how well individuals having various combinations of primate photopigments would fare in the task of discriminating spectra appropriate for a sample of edible fruits from spectra measured for leaves (Osorio and Vorobyev 1996). They found that a trichromat with pigments similar to the ones in catarrhine eyes is predicted to be much superior to a dichromat at detecting fruit among a background of leaves. From computations they further concluded that the trichromatic eye would be even better at the task if the catarrhine M pigment were to be shifted from its normal position (~530 nm) to a slightly shorter location, and that discrimination then becomes worse if the M pigment position is alternatively shifted closer to the spectral location of the L pigment. Researchers generally interpreted the results from the investigation to be in accord with the idea that primate color vision may serve as an adaptation to a frugivorous lifestyle.

A more direct approach, followed first by Regan *et al.* (1998, 2001), starts with light measurements —of fruits, foliage, and illuminants— made at primate natural study sites and then uses them in a computational model designed to evaluate how well animals with various photopigment arrays might perform in discrimination tasks relevant to finding and evaluating foods. Specifically, they made light measurements in French Guiana inhabited by 2 polymorphic platyrrhines (*Cebus* and *Ateles*) and by the routinely trichromatic *Alouatta*. Regan *et al.* (2001) subsequently evaluated the predicted capacities subserved by various pigment combinations in the 3 species for a large number of combinations of fruits, foliage, and ambient illuminants. The general outcome of the investigation echoes that of the aforementioned study in affirming that the color vision of trichromatic platyrrhines is well matched to the task of detecting fruits against a background of leaves. Their calculations also suggest, as did the previous study, that a trichromacy based on M and L pigments that are even more separated might be superior to those nature offers. Similar calculations

performed on fruits that *Ateles geoffroyi* consume also predict an advantage of trichromatic over dichromatic monkeys (Riba-Hernandez *et al.* 2004).

All the modeling studies seem to agree that primate trichromacy is well suited for supporting the detection of red, yellow, and green targets against foliage backgrounds (Parraga *et al.* 2002). Because primates often harvest ripened fruits displaying these hues, it is reasonable to assume that primate trichromacy may be an adaptation allowing the exploitation of the conspicuous coloration characteristic of many ripened fruits. Nonetheless, primate diets can be highly varied across species and dependent on resource availability, among other things, so that while many primates eat a variety of fruits, many other items, e.g., foliage, gums, and insects, are included in primate diets. For example, many of the routinely trichromatic catarrhines enjoy young leaves as an important part of their diet. In tropical climates young leaves have a reddish flush and model calculations show that, like ripe fruits, the young leaves are better discriminated by the trichromatic than by the dichromatic viewer; therefore, they might have been the food items of greatest importance in the evolution of routine trichromacy (Dominy and Lucas 2001; Lucas *et al.* 1998). Other modeling studies support the conclusion about the discriminabilty to the trichromatic eye of young leaves (Sumner and Mollon 2000), but there is continuing debate as to whether primate trichromacy, either routine or polymorphic, evolved in support of frugivorous or folivorous lifestyles (Dominy 2004; Sumner and Mollon 2003) or indeed whether still other explanations may be appropriate; e.g., skin color variations (Changizi *et al.* 2006). It seems unlikely that spectroradiometric measurements and computational modeling by themselves are sufficient to yield definitive insights into the question. At this stage, it may be more useful to examine directly how conspecific monkeys of the polymorphic genera differ behaviorally in ways that may be linked to their variations in color vision.

Some advances in that direction have been made in investigations of the relative food foraging efficiencies of marmosets and tamarins in seminatural circumstances. Several experiments have compared the abilities of captive marmosets to search out corn cereal that had been dyed green or orange with food coloring. When the food was spread across a natural substrate consisting of grass and dirt, trichromatic individuals found significantly more orange targets than dichromatic individuals did, whereas both types of monkey harvested green targets equally efficiently (Caine and Mundy 2000). This suggests an advantage for trichromats that is based on the color of the food, but in a second test in which the food was presented at closer range, the difference between individuals with differing color vision disappeared. If color was the relevant cue for food selection, one would not automatically expect the difference in outcome between the 2 tests. A follow-up experiment used the same paradigm to determine if camouflaging the foods by interspersing them amongst similar or mixed colored substrates differentially influenced foraging efficiency (Caine *et al.* 2003). Trichromatic marmosets were impaired under the color camouflaged condition whereas dichromats performed similarly irrespective of whether the targets were color camouflaged or not. The authors suggest the results from trichromatic marmosets are in line with laboratory demonstrations that have shown a significant deleterious effect on the ability of human trichromats to detect color targets in color camouflage circumstances (Morgan *et al.* 1992). One might have expected to see differences between the dichromatic and trichromatic

individuals in foraging under the 2 test conditions. There were none, though large individual variations may have masked any effect. In support of the possibility, a laboratory investigation provided evidence that dichromatic *Cebus* are in fact superior to trichromatic monkeys in detecting geometric patterns in color camouflaged test papers (Saito *et al.* 2005b).

Smith and colleagues have also examined the foraging efficiency of captive *Saguinus* in a seminatural setting (Smith *et al.* 2003b). In this case, they identified the objects to be harvested —small boxes containing varying amounts of fudge— with colored papers designed to mimic the reflectance properties of unripe, partially ripe, and fully ripe fruits that form a natural part of the diet of the species in the wild. Smith *et al.* (2003b) attached 21 of the boxes equally divided among the fruit colors to a wire screen either with or without a leafy background. Trichromatic individuals were quicker to learn to associate fruit color with the baited boxes and faster to acquire the fully ripe faux fruits, which contained the largest amount of reward. The experiment clearly suggests a foraging advantage for trichromats wherein more realistic color cues are associated with reward. Interestingly, though trichromats were more efficient at the color-cued task, the total number of ripe fruits acquired during a test period of 15 min did not depend on color vision status, suggesting that with color as the relevant cue a persistent dichromat may in the end acquire the same total harvest as a trichromat.

In one of the early discussions of the utility of color vision polymorphism in the platyrrhines, Travis *et al.* (1988, p. 490) speculated that the trichromatic female monkey might "use chromatic differences to lead her troop toward fruit that is concealed amongst foliage." In a field study Dominy *et al.* (2003) tested that possibility by asking whether, in foraging groups of tamarins, males or females were more likely to lead successful searches to baited food stations. In such groups all males are obligate dichromats while some fraction of the females is expected to be trichromatic. Despite the average difference in color vision capacity, males and females were equally adept at first locating food, i.e., ripe (yellow) bananas displayed in natural foliage. Assuming the investigators were just not unlucky in having only dichromatic females in their experimental groups, the results suggest that trichromacy does not automatically confer an advantage in fruit exploitation. Results from a similar examination of groups of naturally foraging tamarins support the conclusion. That study also rejects the idea that color vision status is compellingly linked to leadership in foraging (Smith *et al.* 2003a).

Quite apart from the use to which it may be put, one characteristic feature of color is its distinctiveness; i.e., humans automatically distinguish the presence or absence of color in a scene irrespective of the details of the scene. Derrington *et al.* (2002) asked if such capacity is a general emergent property of primate visual systems. They show that dichromatic marmosets rapidly learn to discriminate images containing color from grayscale images and that the capacity then readily transfers to new images and new colors. Though not directly relevant to the relative capacities of the various color vision phenotypes, their study makes the important point that color per se is as distinctive to New World monkeys as it is to humans.

Potential advantages for individual phenotypes Clearly, significant questions about platyrrhine color vision polymorphisms remain unanswered. Two of them are: 1) If

the polymorphisms are maintained by pure heterozygous advantage, are all of the trichromatic variants equally good? 2) If other forces are at play, might some forms of dichromacy be especially suited to the performance of particular visual tasks?

One can only offer tentative answers to either question. With regard to the trichromatic phenotypes, Osorio *et al.* (2004) conducted a computational study that predicted the ability of tamarins and squirrel monkeys to discriminate spectra measured for >100 species of plants that tamarins consumed from spectra characteristic of leaves. In comparing the 3 trichromatic phenotypes present in both monkeys, the trichromatic subgroups featuring the largest spectral separation of their M and L pigments are better overall at predicted discrimination than are the other 2 forms of trichromacy. In general, the differences between the other 2 phenotypes for both squirrel monkeys and tamarins were rather modest, though mostly the subtype with the largest M/L spectral separation was predicted to have better discrimination. Interestingly, the difference among the subgroups is enhanced when the computations are made for conditions modeled as representing lower overall illumination levels. From their computational studies, Regan *et al.* (2001) made a somewhat similar suggestion, that the variant forms of trichromacy in *Cebus* and *Ateles* might each prove to be individually superior in different microhabitats; e.g., one type of trichromat might be advantaged under the illumination characteristic of the canopy, another at forest floor locations, etc. Finally, a field study correlating light levels and foraging behavior provides some mixed support for the view that primates with different color vision phenotypes preferentially forage under different illumination conditions (Yamashita *et al.* 2005). All of the studies imply that ferreting out the relative merits of the trichromatic polymorphs in natural environments will require close attention to details of the photic environment.

So far, there is no behavioral study using naturalistic stimuli that have compared the discrimination behavior of different types of trichromatic platyrrhines. In an earlier laboratory study that compared squirrel monkeys of different phenotypes, trichromats with larger and smaller M/L pigment separations showed fairly similar wavelength discrimination abilities (Jacobs 1984). However, the tests involved bright monochromatic stimuli and may not provide a very good predictor of how discrimination capacities will be revealed under more challenging viewing conditions. That the details of viewing conditions may be important is suggested in a recent study involving the use of functional substitution. In that experiment, Rowe and Jacobs (2007) studied the abilities of trichromatic human subjects viewing naturalistic stimuli through the 3 combinations of M/L pigments of *Saguinus* under varying luminance levels and viewing time. All 3 trichromatic phenotypes showed similar discrimination for relatively bright stimulus conditions and for targets presented at relatively longer times. However, at lower luminance levels and shorter viewing times the phenotype designed to mimic the smallest M/L pigment separation in the callitrichids, i.e., 556/562 nm, performed significantly poorer than for the other trichromats. The study reinforces the conclusion from the computational studies that to achieve an understanding of the relative advantages and disadvantages of the various trichromatic phenotypes it will be necessary to pay careful attention to the operative viewing conditions.

In considering the linkage between color vision capacity and behavior, it is important to note that human color defectives acquire a variety of coping skills to compensate for the loss of sensory capacity. It would be surprising indeed if fellow primates do not do the same. For example, the studies just described would predict that individuals with some cone combinations could enhance their discrimination abilities by foraging at higher light levels or perhaps by altering their search strategy to incorporate longer viewing times.

There is a significant body of research on human color defectives directed toward asking whether human dichromats show better performance in some visual tasks than normal trichromats do (Sharpe *et al.* 2005). The general expectation has been that though such individuals will suffer color vision loss, they may enjoy some relative advantage in discriminating stimuli with high temporal and spatial variations based on the fact that they presumably have higher densities of cones containing only a single pigment type and that their L/M opponent pathways have been usurped to serve as luminance channels. Relatively little is known about whether there may be some compensating advantages for the dichromats among the polymorphic New World monkeys. In laboratory tests involving detection of flickering lights, no differences occurred between dichromatic and trichromatic squirrel monkeys and tamarins, though there were some clear specific differences (Jacobs 1990). There is evidence that in circumstances involving color camouflaged stimuli, dichromatic monkeys outperform trichromats. Whether the results have much relevance for natural environments is unclear. Computational studies predict that in fruit discrimination tasks dichromatic monkeys will not do as well, but the differences are not large (Osorio *et al.* 2004; Stoner *et al.* 2005). The same studies compared the predicted performances of the various dichromatic subtypes, finding only relatively small differences among them. Perhaps the most intriguing possibility from the computational studies is the prediction that the advantage of trichromatic over dichromatic conspecifics is greatly increased in dimmer illuminations (Osorio *et al.* 2004).

Although color specialists have made some starts, understanding the relative merits of the polymorphic subvarieties remains largely a task for the future. In pursuing that goal, it will be important to begin to pay attention to the likely demands of real-world visual tasks. Clearly, the problems for foraging monkeys are much more complex than have been effectively studied. One direction for further exploration may come from studies of visual search in humans: tasks that would seem more akin to what a monkey must accomplish. For instance, in humans, when color is used to identify a target in a complex visual field, differences emerge among individuals with different types of color vision with color defectives being generally less efficient at visual search (Cole *et al.* 2004). It would be interesting to know if analogous differences may be present among the platyrrhine polymorphisms.

Coda

Primates have demonstrably superb vision, and I here focused on one important aspect of that capacity, color. But much as it may grieve vision scientists to admit it,

primates have many sensory avenues for gaining useful information about the environment, not only vision but also an array of external senses including hearing, smell, and touch. All of them can be brought to bear on the problems of foraging as well as finding critical use in the informed analysis of location, friends, and foes. In addition, as Dominy *et al.* (2001) emphasized, an array of more proximate sensory capacities, such as taste and texture in the mouth, can be central to feeding decisions. Clearly, as our understanding of how New World monkeys use color to guide behavior expands it will be necessary to keep in mind that it forms but one feature in the full picture of primate sensory capacities.

In summary, as clearly illustrated here, in the past few years there has been significant progress in our understanding of the processes that underlie color vision in New World monkeys. To a good first approximation, the distribution of color vision among platyrrhines is known. Moreover, researchers are also rapidly cataloging the opsin genes and cone photopigments that underlie this ability and directing some attention toward understanding the organization of the afferent visual systems of these primates. Less is currently understood about the behavioral details of platyrrhine color vision and, in particular, how they can use the capacity to understand the environment. Nevertheless, a good start has been made toward developing a realistic ecology of color vision for New World monkeys. With a combination of laboratory, field, and computational approaches that topic is sure to receive much attention in the years ahead.

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References

Allen, G. (1879). *The colour-sense: Its origin and development*. Boston: Houghton, Osgood, & Company.

Asenjo, A. B., Rim, J., & Oprian, D. D. (1994). Molecular determinants of human red/green color discrimination. *Neuron, 12*, 1131–1138.

Blessing, E. M., Solomon, S. G., Hashemi-Nezhad, M., Morris, B. J., & Martin, P. R. (2004). Chromatic and spatial properties of parvocellular cells in the lateral geniculate nucleus of the marmoset (*Callithrix jacchus*). *Journal of Physiology, 557*, 229–245.

Boissinot, S., Tan, Y., Shyue, S.-K., Schneider, H., Sampaio, I., Neiswanger, K., *et al*. (1998). Origins and antiquity of X-linked triallelic color vision systems in New World monkeys. *Proceedings of the National Academy of Sciences USA, 95*, 13749–13754.

Bowmaker, J. K. (1990). Cone visual pigments in monkeys and humans. In Committee on Vision (Ed.), *Advances in Photoreception* (pp. 19–30). Washington, D.C.: National Academy Press.

Bowmaker, J. K., Astell, S., Hurst, D. M., & Mollon, J. D. (1991). Photosensitive and photostable pigments in the retinae of Old World monkeys. *Journal of Experimental Biology, 156*, 1–19.

Bowmaker, J. K., Mollon, J. D., & Jacobs, G. H. (1983). Microspectrophotometric measurements of Old and New world species of monkeys. In J. D. Mollon & L. T. Sharpe (Eds.), *Colour Vision-Physiology and Psychophysics* (pp. 56–68). London: Academic Press.

Boycott, B., & Wassle, H. (1999). Parallel processing in the mammalian retina. *Investigative Ophthalmology and Visual Science, 40*, 1313–1327.

Caine, N. G., & Mundy, N. I. (2000). Demonstration of a foraging advantage for trichromatic marmosets (*Callthrix geoffroyi*) dependent on food colour. *Proceedings of the Royal Society of London B, 267*, 439–444.

Caine, N. G., Surridge, A. K., & Mundy, N. I. (2003). Dichromatic and trichromatic *Callithrix geoffroyi* differ in relative foraging ability to red-green color-camouflaged and non-camouflaged food. *International Journal of Primatology, 24*, 1163–1175.

Calkins, D. J. (2001). Seeing with S cones. *Progress in Retinal and Eye Research, 20*, 255–287.

Changizi, M. A., Zhang, Q., & Shimojo, S. (2006). Bare skin, blood and the evolution of primate colour vision. *Biology Letters, 2*, 217–221.

Cole, B. L., Maddocks, J. D., & Sharpe, K. (2004). Visual search and the conspicuity of coloured targets for colour vision normal and colour vision deficient observers. *Clinical and Experimental Optometry, 87*, 294–304.

Cropp, S., Boinski, S., & Li, W.-H. (2002). Allelic variation in the squirrel monkey X-linked color vision gene: Biogeographical and behavioral correlates. *Journal of Molecular Evolution, 54*, 734–745.

Curcio, C. A., & Hendrickson, A. (1991). Organization and development of the primate photoreceptor mosaic. *Progress in Retinal Research, 10*, 89–120.

da Costa, B. L. S. A., & Hokoc, J. N. (2000). Photoreceptor topography of the retina in the New World monkey *Cebus apella*. *Vision Research, 40*, 2395–2409.

Deeb, S. S. (2005). The molecular basis of variation in human color vision. *Clinical Genetics, 67*, 369–377.

Derrington, A. M., Parker, A. R., Barraclough, N. E., Easton, A., Goodson, G. R., Parker, K. S., *et al*. (2002). The uses of colour vision: Behavioural and physiological distinctiveness of colour stimuli. *Philosophical Transactions of the Royal Society of London B, 357*, 975–985.

Dominy, N. J. (2004). Color as an indicator of food quality to anthropoid primates: Ecological evidence and an evolutionary scenario. In C. F. Ross & R. F. Kay (Eds.), *Anthropoid Origins: New Visions* (pp. 615–644). New York: Kluwer Academic/Plenum Publishers.

Dominy, N. J., Garber, P. A., Bicca-Marques, J. C., & Azevedo-Lopes, M. A. D. (2003). Do female tamarins use visual cues to detect fruit rewards more successfully than do males? *Animal Behaviour, 66*, 829–837.

Dominy, N. J., & Lucas, P. W. (2001). Ecological importance of trichromatic colour vision to primates. *Nature, 410*, 363–365.

Dominy, N. J., Lucas, P. W., Osorio, D., & Yamashita, N. (2001). The sensory ecology of primate food perception. *Evolutionary Anthropology, 10*, 171–186.

Dulai, K. S., von Dornum, M., Mollon, J. D., & Hunt, D. M. (1999). The evolution of trichromatic color vision by opsin gene duplication in New World and Old World primates. *Genome Research, 9*, 629–638.

Endler, J. A. (1993). The color of light in forests and its implications. *Ecological Monographs, 63*, 1–27.

Franco, E. C. S., Finlay, B. L., Silveira, L. C. L., Yamada, E. S., & Crowley, J. C. (2000). Conservation of absolute foveal area in New World monkeys. *Brain, Behavior and Evolution, 56*, 276–286.

Gomes, U. R., Pessoa, D. M. A., Suganuma, E., Tomaz, C., & Pessoa, V. F. (2005). Influence of stimulus size on color discrimination in Capuchin monkeys. *American Journal of Primatology, 67*, 437–446.

Gomes, U., Pessoa, D. M. A., Tomaz, C., & Pessoa, V. F. (2002). Color vision perception in the capuchin monkey (*Cebus apella*): A re-evaluation of procedures using Munsell papers. *Behavioural Brain Research, 129*, 153–157.

Grether, W. F. (1939). Color vision and color blindness in monkeys. *Comparative Psychology Monographs, 29*, 1–38.

Hiramatsu, C., Radlwimmer, F. B., Yokoyama, S., & Kawamura, S. (2004). Mutagenesis and reconstitution of middle-to-long-wave-sensitive visual pigments of New World monkeys for testing the tuning effects of residues at sites 229 and 233. *Vision Research, 44*, 225–2231.

Hiramatsu, C., Tsutsui, T., Matsumoto, Y., Aurrell, F., Fedigan, L. M., & Kawamura, S. (2005). Color vision polymorphism in wild capuchins (*Cebus capuchinus*) and spider monkeys (*Ateles geoffroyi*) in Costa Rica. *American Journal of Primatology, 67*, 447–462.

Hunt, D. M., Cowing, J. A., Patel, R., Appukuttan, B., Bowmaker, J. K., & Mollon, J. D. (1995). Sequence and evolution of the blue cone pigment gene in Old and New World primates. *Genomics, 27*, 535–538.

Hunt, D. M., Cowing, J. A., Wilkie, S. E., Parry, J. W. L., Poopalasundaram, S., & Bowmaker, J. K. (2004). Divergent mechanisms for the tuning of shortwave sensitive visual pigments in vertebrates. *Photochemical and Photobiological Sciences, 3*, 713–720.

Hunt, D. M., Dulai, K. S., Cowing, J. A., Juillot, C., Mollon, J. D., Bowmaker, J. K., *et al*. (1998). Molecular evolution of trichromacy in primates. *Vision Research, 38*, 3299–3306.

Hunt, D. M., Jacobs, G. H., & Bowmaker, J. K. (2005). The genetics and evolution of primate visual pigments. In J. Kremers (Ed.), *The Primate Visual System: A Comparative Approach* (pp. 73–126). Chichester: John Wiley & Sons.

Hunt, D. M., Wilkie, S. E., Bowmaker, J. K., & Poopalasundaram, S. (2001). Vision in the ultraviolet. *Cellular and Molecular Life Sciences, 58*, 1583–1598.

Hunt, D. M., Williams, A. J., Bowmaker, J. K., & Mollon, J. D. (1993). Structure and evolution of polymorphic photopigment gene of the marmoset. *Vision Research, 33*, 147–154.

Jacobs, G. H. (1977). Visual capacities of the owl monkey (*Aotus trivirgatus*): II. Spatial contrast sensitivity. *Vision Research, 17*, 821–825.

Jacobs, G. H. (1981). *Comparative color vision.* New York: Academic Press.

Jacobs, G. H. (1984). Within-species variations in visual capacity among squirrel monkeys (*Saimiri sciureus*): Color vision. *Vision Research, 24*, 1267–1277.

Jacobs, G. H. (1990). Discrimination of luminance and chromaticity differences by dichromatic and trichromatic monkeys. *Vision Research, 30*, 387–397.

Jacobs, G. H. (1993). The distribution and nature of colour vision among the mammals. *Biological Reviews, 68*, 413–471.

Jacobs, G. H. (1998). A perspective on color vision in platyrrhine monkeys. *Vision Research, 38*, 3307–3313.

Jacobs, G. H. (1999). Prospects for trichromatic color vision in male *Cebus* monkeys. *Behavioural Brain Research, 101*, 109–112.

Jacobs, G. H. (2004). Photopigment variations and the evolution of anthropoid vision. In C. F. Ross & R. F. Kay (Eds.), *Anthropoid origins: New visions* (pp. 645–664). New York: Kluwer Academic/ Plenum Publishers.

Jacobs, G. H., & Deegan II, J. F. (2001). Photopigments and colour vision in New World monkeys from the family Atelidae. *Proceedings of the Royal Society of London B, 268*, 695–702.

Jacobs, G. H., & Deegan II, J. F. (2003). Cone pigment variations in four genera of New World monkeys. *Vision Research, 43*, 227–236.

Jacobs, G. H., & Deegan II, J. F. (2005). Polymorphic monkeys with more than three M/L cone types. *Journal of the Optical Society of America A, 22*, 2072–2080.

Jacobs, G. H., Deegan II, J. F., Neitz, J. A., Crognale, M. A., & Neitz, M. (1993). Photopigments and color vision in the nocturnal monkey, *Aotus*. *Vision Research, 33*, 1773–1783.

Jacobs, G. H., & Neitz, J. (1987). Inheritance of color vision in a New World monkey (*Saimiri sciureus*). *Proceedings of the National Academy of Sciences USA, 84*, 2545–2549.

Jacobs, G. H., Neitz, J., & Crognale, M. (1987). Color vision polymorphism and its photopigment basis in a callitrichid monkey (*Saguinus fuscicollis*). *Vision Research, 27*, 2089–2100.

Jacobs, G. H., Neitz, M., Deegan, J. F., & Neitz, J. (1996a). Trichromatic colour vision in New World monkeys. *Nature, 382*, 156–158.

Jacobs, G. H., Neitz, M., & Neitz, J. (1996b). Mutations in S-cone pigment genes and the absence of colour vision in two species of nocturnal primate. *Proceedings of the Royal Society of London B, 263*, 705–710.

Jacobs, G. H., & Rowe, M. P. (2004). Evolution of vertebrate colour vision. *Clinical and Experimental Optometry, 87*, 206–216.

Jacobs, G. H., & Williams, G. A. (2006). L and M cone proportions in polymorphic New World monkeys. *Visual Neuroscience, 23*, 365–370.

Kainz, P. M., Neitz, J., & Neitz, M. (1998). Recent evolution of uniform trichromacy in a New World monkey. *Vision Research, 38*, 3315–3320.

Kawamura, S., Hirai, M., Takenaka, O., Radlwimmer, F. B., & Yokoyama, S. (2001). Genomic and spectral analyses of long to middle wavelength-sensitive visual pigments of common marmoset (*Callithrix jacchus*). *Gene, 269*, 45–51.

Kawamura, S., Takenaka, N., Hiramatsu, C., Hirai, M., & Takenaka, O. (2002). Y-chromosomal red-green opsin genes of nocturnal New World monkey. *FEBS Letters, 530*, 70–72.

Kelber, A., Vorobyev, M., & Osorio, D. (2003). Animal colour vision-behavioural tests and physiological concepts. *Biological Reviews, 78*, 81–118.

Kremers, J., Silveira, L. C., Yamada, E. S., & Lee, B. B. (1999). The ecology and evolution of primate color vision. In K. R. Gegenfurtner & L. T. Sharpe (Eds.), *Color vision: From genes to perception* (pp. 123–142). Cambridge: Cambridge University Press.

Lee, B. B. (2004). Paths to colour in the retina. *Clinical and Experimental Optometry, 87*, 239–248.

Lee, B. B., Silveira, L. C. L., Yamada, E. S., Hunt, D. M., Kremers, J., Martin, P. R., *et al*. (2000). Visual responses of ganglion cells of a New-World primate, the capuchin monkey, *Cebus apella*. *Journal of Physiology, 528*, 573–590.

Li, W.-H., Boissinot, S., Tan, Y., Shyue, S.-K., & Hewitt-Emmett, D. (2000). Evolutionary genetics of primate color vision: Recent progress and potential limits to knowledge. In M. T. Clegg (Ed.), *Evolutionary biology* (pp. 151–178). New York: Plenum Press.

Lucas, P. W., Darvell, B. W., Lee, P. K. D., Yuen, T. D. B., & Choong, M. F. (1998). Colour cues for leaf food selection by long-tailed macaques (*Macaca fascicularis*) with a new suggestion for the evolution of trichromatic colour vision. *Folia Primatologica, 69*, 139–152.

Lythgoe, J. N., & Partridge, J. C. (1989). Visual pigments and the acquisition of visual information. *Journal of Experimental Biology, 146*, 1–20.

Martin, P. R. (1998). Colour processing in the retina: Recent progress. *Journal of Physiology, 513*, 631–638.

Martin, P. R., & Grunert, U. (1999). Analysis of the short-wavelength sensitive ("blue") cone mosaic in the primate retina: A comparison of New World and Old World monkeys. *Journal of Comparative Neurology, 406*, 1–14.

Martin, P. R., Grunert, U., Chan, T. L., & Bumsted, K. (2000). Spatial order in short-wavelength-sensitive cone photoreceptors: A comparative study of the primate retina. *Journal of the Optical Society of America A, 17*, 557–567.

Maximov, V. V. (2000). Environmental factors which may have led to the appearance of colour vision. *Philosophical Transactions of the Royal Society of London B, 355*, 1239–1242.

Merbs, S. L., & Nathans, J. (1992). Absorption spectra of human cone pigments. *Nature, 356*, 433–435.

Migeon, B. R. (1998). Non-random X chromosome inactivation in mammalian cells. *Cytogenetic and Genome Research, 80*, 142–148.

Mollon, J. D. (1989). Tho she kneel'd in that place where they grew. The uses and origins of primate colour vision. *Journal of Experimental Biology, 146*, 21–38.

Mollon, J. D. (1995). Seeing colour. In Lamb, T., and Bourriau, J. (eds.), *Colour: Art and Science*. Cambridge University Press, Cambridge, pp. 127–150.

Mollon, J. D., Bowmaker, J. K., & Jacobs, G. H. (1984). Variations of colour vision in a New World primate can be explained by polymorphism of retinal photopigments. *Proceedings of the Royal Society of London B, 222*, 373–399.

Morgan, M. J., Adam, A., & Mollon, J. D. (1992). Dichromats detect colour-camouflaged objects that are not detected by trichromats. *Proceedings of the Royal Society of London B, 248*, 291–295.

Nagao, K., Takenaka, N., Hirai, M., & Kawamura, S. (2005). Coupling and decoupling of evolutionary mode between X- and Y-chromosomal red-green opsin genes in owl monkeys. *Gene, 352*, 82–91.

Nathans, J., Thomas, D., & Hogness, D. S. (1986). Molecular genetics of human color vision: The genes encoding blue, green and red pigments. *Science, 232*, 193–202.

Neitz, J., Carroll, J., & Neitz, M. (2001). Color vision: Almost reason enough for having eyes. *Optics and Photonics News, 12*, 26–33.

Neitz, M., & Neitz, J. (2000). Molecular genetics of color vision and color vision defects. *Archives of Ophthalmology, 118*, 691–700.

Neitz, M., & Neitz, J. (2003). Molecular genetics of human color vision and color vision defects. In L. M. Chalupa & J. S. Werner (Eds.), *The visual neurosciences* (pp. 974–988). Cambridge: MIT Press.

Neitz, M., Neitz, J., & Jacobs, G. H. (1991). Spectral tuning of pigments underlying red-green color vision. *Science, 252*, 971–974.

Osorio, D., Smith, A. C., Vorobyev, M., & Buchanan-Smith, H. M. (2004). Detection of fruit and the selection of primate visual pigments for color vision. *American Naturalist, 164*, 696–708.

Osorio, D., & Vorobyev, M. (1996). Colour vision as an adaptation to frugivory in primates. *Proceedings of the Royal Society of London B, 263*, 593–599.

Osorio, D., Vorobyev, M., & Jacobs, G. H. (2005). The ecology of the primate eye: Retinal sampling and color vision. In J. Kremers (Ed.), *The primate visual system: A comparative approach* (pp. 99–126). Chichester: John Wiley & Sons.

Parraga, C. A., Troscianko, T., & Tolhurst, D. J. (2002). Spatiochromatic properties of natural images and human vision. *Current Biology, 12*, 483–487.

Peichl, L. (2005). Diversity of mammalian photoreceptor properties: Adaptations to habitat and lifestyle? *Anatomical Record A, 287A*, 1001–1012.

Pessoa, D. M. A., Araujo, M. F. P., Tomaz, C., & Pessoa, V. F. (2003). Colour discrimination learning in black-handed tamarin (*Saguinus midas niger*). *Primates, 44*, 413–418.

Pessoa, D. M., Cunha, J. F., Tomaz, C., & Pessoa, V. F. (2005a). Colour discrimination in the black-tufted-ear marmoset (*Callitrhix penicillata*): Ecological implications. *Folia Primatologica, 76*, 125–134.

Pessoa, D. M. A., Perini, E. S., Carvalho, L. S., Tomaz, C., & Pessoa, V. F. (2005b). Color vision in *Leontopithecus chrysomelass*: A behavioral study. *International Journal of Primatology, 26*, 147–158.

Polyak, S. (1957). *The vertebrate visual system*. Chicago: University of Chicago Press.

Regan, B. C., Julliot, C., Simmen, B., Vienot, F., Charles-Dominique, P., & Mollon, J. D. (1998). Frugivory and colour vision in *Alouatta seniculus*, a trichromatic platyrrhine monkey. *Vision Research, 38*, 3321–3327.

Regan, B. C., Julliot, C., Simmen, B., Vienot, F., Charles-Dominique, P., & Mollon, J. D. (2001). Fruits, foliage and the evolution of primate colour vision. *Philosophical Transactions of the Royal Society of London B, 356*, 229–283.

Riba-Hernandez, P., Stoner, K. E., & Osorio, D. (2004). Effect of polymorphic colour vision for fruit detection in the spider monkey *Ateles geoffroyi*, and its implications for the maintenance of polymorphic colour vision in platyrrhine monkeys. *Journal of Experimental Biology, 207*, 2465–2470.

Roorda, A., & Williams, D. R. (1999). The arrangement of the three cone classes in the living human eye. *Nature, 397*, 520–522.

Rowe, M. P., & Jacobs, G. H. (2004). Cone pigment polymorphisms in New World monkeys: Are all pigments created equal? *Visual Neuroscience, 21*, 217–222.

Rowe, M. P., & Jacobs, G. H. (2007). Naturalistic color discrimination in polymorphic platyrrhine monkeys: Effects of stimulus luminance and duration examined with functional substitution. *Visual Neuroscience, 24*, 17–23.

Saito, C. A., da Silva-Filho, M., Lee, B. B., Bowmaker, J. K., Kremers, J., & Silveira, L. C. L. (2004). *Alouatta* trichromatic color vision-single-unit recording from retinal ganglion cells and micro-spectrophotometry. *Investigative Ophthalmology and Visual Science, 45*, E-abstract 4276.

Saito, A., Kawamura, S., Mikami, A., Ueno, Y., Hiramatsu, C., Koida, K., *et al*. (2005a). Demonstration of genotype-phenotype correlation in polymorphic color vision of a non-callitrichine New World monkey, capuchin *Cebus apella*. *American Journal of Primatology, 67*, 471–485.

Saito, A., Mikami, A., Kawamura, S., Ueno, Y., Hiramatsu, C., Wildayati, K. A., *et al*. (2005b). Advantage of dichromats over trichromats in discrimination of color-camouflaged stimuli in non-human primates. *American Journal of Primatology, 67*, 425–436.

Sharpe, L. T., de Luca, E., Hansen, T., Jagle, H., & Gegenfurtner, K. R. (2005). Advantages and disadvantages of human dichromacy. *Journal of Vision, 6*, 213–223.

Shi, Y., & Yokoyama, S. (2003). Molecular analysis of the evolutionary significance of ultraviolet vision in vertebrates. *Proceedings of the National Academy of Sciences USA, 100*, 8308–8333.

Shyue, S.-K., Boissinot, S., Schneider, H., Sampaio, I., Schneider, M. P., Abee, C. R., *et al*. (1998). Molecular genetics of spectral tuning in New World monkey color vision. *Journal of Molecular Evolution, 46*, 697–702.

Silveira, L. L., Lee, B. B., Yamada, E. S., Kremers, J., Hunt, D. M., Martin, P. R., *et al*. (1999). Ganglion cells of a short-wavelength-sensitive cone pathway in New World monkeys: Morphology and physiology. *Visual Neuroscience, 16*, 333–343.

Silveira, L. C. L., Saito, C. A., Lee, B. B., Kremers, J., Filho, M. S., Kilavik, B. E., *et al*. (2004). Morphology and physiology of primate M- and P-cells. In C. A. Heywood, A. D. Milner, & C. Blakemore (Eds.), *The roots of visual awareness* (pp. 21–46). Amsterdam: Elsevier.

Silveira, L. C., Yamada, E. S., Franco, E. C. S., & Finlay, B. L. (2001). The specialization of the owl monkey retina for night vision. *Color Research and Application, 26*, S118–S122.

Smallwood, P. M., Wang, Y., & Nathans, J. (2002). Role of a locus control region in the mutually exclusive expression of human red and green cone pigment genes. *Proceedings of the National Academy of Sciences USA, 99*, 1008–1011.

Smith, A. C., Buchanan-Smith, H. M., Surridge, A. K., & Mundy, N. I. (2003a). Leaders of progressions in wild mixed-species (*Saguinus fuscicollis*) and mustached tmarains (*S. mystax*), with emphasis on color vision and sex. *American Journal of Primatology, 61*, 145–157.

Smith, A. C., Buchanan-Smith, H. M., Surridge, A. K., Osorio, D., & Mundy, N. I. (2003b). The effect of colour vision status on the detection and selection of fruits by tamarins (*Saguinus* spp.). *Journal of Experimental Biology, 206*, 3159–3165.

Solomon, S. G. (2002). Striate cortex in dichromatic and trichromatic marmosets: Neurochemical compartmentalization and geniculate input. *Journal of Comparative Neurology, 450*, 366–381.

Stoner, K. E., Riba-Hernandez, P., & Lucas, P. W. (2005). Comparative use of color vision for frugivory by sympatric species of platyrrhines. *American Journal of Primatology, 67*, 399–409.

Sumner, P., & Mollon, J. D. (2000). Catarrhine photopigments are optimized for detecting targets against a foliage background. *Journal of Experimental Biology, 203*, 1963–1986.

Sumner, P., & Mollon, J. D. (2003). Did primate trichromacy evolve for frugivory or folivory? In J. D. Mollon, J. Pokorny, & K. Knoblauch (Eds.), *Normal and defective colour vision* (pp. 21–30). Oxford: Oxford University Press.

Surridge, A. K., & Mundy, N. I. (2002). Trans-specific evolution of opsin alleles and the maintenance of trichromatic colour vision in Callitrichine primates. *Molecular Ecology, 11*, 2157–2169.

Surridge, A. K., Smith, A. C., Buchanan-Smith, H. M., & Mundy, N. I. (2002). Single-copy nuclear DNA sequences obtained from noninvasively collected primate feces. *American Journal of Primatology, 56*, 185–190.

Surridge, A. K., Suarez, S. S., Buchanan-Smith, H., & Mundy, N. I. (2005a). Non-random association of opsin alleles in wild groups of red-bellied tamarins (*Saguinus labiatus*) and maintenance of colour vision polymorphism. *Biology Letters, 1*, 465–468.

Surridge, A. K., Suarez, S. S., Buchanan-Smith, H. M., Smith, A. C., & Mundy, N. I. (2005b). Color vision pigment frequencies in wild tamarins (*Saguinus spp*.). *American Journal of Primatology, 67*, 463–470.

Talebi, M. G., Pope, T. R., Vogel, E. R., Neitz, M., & Dominy, N. J. (2006). Polymorphism of visual pigments in the muriqui (*Primates, Atelidae*). *Molecular Ecology, 15*, 551–558.

Tovee, M. J., Bowmaker, J. K., & Mollon, J. D. (1992). The relationship between cone pigments and behavioural sensitivity in a New World monkey (*Callithrix jacchus jacchus*). *Vision Research, 32*, 867–878.

Travis, D. S., Bowmaker, J. K., & Mollon, J. D. (1988). Polymorphism of visual pigments in a callitrichid monkey (*Callithrix jacchus jacchus)*. *Vision Research, 28*, 481–490.

Trolio, D., Howland, H. C., & Judge, S. J. (1993). Visual optics and retinal cone topography in the common marmoset (*Callitrhix jacchus*). *Vision Research, 33*, 1301–1310.

Vorobyev, M. (2004). Ecology and evolution of primate colour vision. *Clinical and Experimental Optometry, 87*, 230–238.

Vorobyev, M., & Osorio, D. (1998). Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society of London B, 265*, 351–358.

Walls, G. L. (1942). *The vertebrate eye and its adaptive radiation.* Bloomfield Hills, MI: Cranbrook Institute of Science.

White, A. J. R., Wilder, H. D., Goodchild, A. K., Sefton, J., & Martin, P. R. (1998). Segregation of receptive field properties in the lateral geniculate nucleus of a New-World monkey, the marmoset *Callithrix jacchus*. *Journal of Neurophysiology, 80*, 2063–2076.

Wikler, K. C., & Rakic, P. (1990). Distribution of photoreceptor subtypes in the retina of diurnal and nocturnal primates. *The Journal of Neuroscience, 10*, 3390–3401.

Wilder, H. D., Grunert, U., Lee, B. B., & Martin, P. R. (1996). Topography of ganglion cells and photoreceptors in the retina of a New World monkey: The marmoset, *Callithrix jacchus*. *Visual Neuroscience, 13*, 335–352.

Winderickx, J., Lindsey, D. T., Sanocki, E., Teller, D. Y., Motulsky, A. G., & Deeb, S. S. (1992). Polymorphism in red photopigment underlies variation in colour matching. *Nature, 356*, 431–433.

Yamada, E. S., Marshak, D. W., Silveira, L. C. L., & Casagrande, V. A. (1998). Morphology of P and M retinal ganglion cells of the bush baby. *Vision Research, 38*, 3345–3352.

Yamashita, N., Stoner, K. E., Riba-Hernandez, P., Dominy, N. J., & Lucas, P. W. (2005). Light levels used during feeding by primate species with different color vision phenotypes. *Behavioral Ecology and Sociobiology, 58*, 618–639.

Yeh, T., Lee, B. B., Kremers, J., Cowing, J. A., Hunt, D. M., Martin, P. R., *et al*. (1995). Visual responses in the lateral geniculate nucleus of dichromatic and trichromatic marmosets (*Callithrix jacchus*). *Journal of Neuroscience, 15*, 7892–7904.

Yokoyama, S., & Radlwimmer, F. B. (1999). The molecular genetics of red and green color vision in mammals. *Genetics, 153*, 919–932.

Yokoyama, S., & Radlwimmer, F. B. (2001). The molecular genetics and evolution of red and green color vision in vertebrates. *Genetics, 158*, 1697–1710.