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A perspective on color vision in platyrrhine monkeys

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Abstract

Studies carried out over the past two decades show that many platyrrhine (New World) monkeys have polymorphic color vision. This condition results from the sorting of allelic versions of X-chromosome cone opsin genes at a single gene site, yielding a mixture of dichromatic and trichromatic phenotypes in the population. Two genera of platyrrhine monkey are known to deviate significantly from this pattern. Examination of color vision, photopigments, and photopigment genes of all of these monkeys have stimulated a renewed interest in understanding the evolution of primate color vision. © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Although some subtle differences may exist, both the cone photopigments and color vision of the various species of catarrhine monkey so far studied seem similar to those of people with normal color vision [1–7]. A very different situation characterizes the platyrrhine (New World) monkeys. Studies carried out over the past two decades have demonstrated a striking array of cone photopigment and color vision adaptations in these animals. This paper provides a brief review of the current status of our understanding of color vision in platyrrhine monkeys.

2. Systematics and a brief history

There are 16 extant genera of New World monkeys comprising at least 70 species. Molecular and morphological data have been used to suggest several alternative phylogenetic arrangements [8–12]. A recent proposed classification based on an analysis of ϵ -globin gene sequences is given in Table 1. It will be used as the point of reference in this review. A useful synopsis of the New World monkeys can be found in a recent book [13].

Rudimentary measurements of color vision in platyrrhine monkeys date back to at least the beginning of the century [14], but the first discerning studies were those of Walter F. Grether [1]. In measurements of wavelength discrimination, color matches and spectral sensitivity, three male *Cebus* monkeys yielded discrimination data very different from that of comparably tested normal human trichromats and of several Old World monkeys. Grether concluded that *Cebus* had dichromatic color vision similar to that of human protanopes, and this suggested to him that these monkeys might be taken to represent one stage in the evolutionary development of human color vision. In the same study, however, Grether reported that a single female spider monkey (*Ateles*) had excellent wavelength discrimination, as good as that measured for trichromatic Old World monkeys. Thus it appeared that, at minimum, different platyrrhine species have different color vision capacities. Over the next 30 years only a small number of studies were done on color vision in New World monkeys. Although these studies reached a wide variety of different conclusions about the color vision of specific species, they supported the view that color vision among platyrrhine monkeys is much more variable than it is among catarrhine monkeys.

Around 1970 it began to become clear that the issue of color vision in platyrrhine monkeys was even more

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Table 1

Cladistic classification of the 16 genera of New World monkeys (after Ref. [12])

Platyrrhini

Family Atelidae

- Alouatta*: Howler monkey
- Ateles*: Spider monkey
- Lagothrix*: Woolly monkey
- Brachyteles*: Woolly spider monkey

Family Pitheciidae

- Callicebus*: Titi monkey
- Pithecia*: Saki monkey
- Chiropotes*: Bearded saki monkey
- Cacajao*: Uakari monkey

Family Cebidae

Subfamily Cebinae

- Cebus*: Capuchin monkey
- Saimiri*: Squirrel monkey

Subfamily Aotinae

- Aotus*: Owl monkey

Subfamily Callitrichinae

- Saguinus*: Tamarin
 - Leontopithecus*: Lion tamarin
 - Callimico*: Goeldi's monkey
 - Callithrix*: Marmoset
 - Cebuella*: Pygmy marmoset
-

complicated than was suggested by these early studies. Examination of the response patterns of spectrally-opponent cells in the lateral geniculate nucleus (LGN) of the squirrel monkey implied that although cells reflecting two spectrally-discrete M/L cone inputs were seen in some female monkeys, these same cells were, at best, only very sparsely represented in male monkeys [15]. This disparity suggested the likely presence of significant individual variations in cone-based vision. Such variations were eventually documented, both for spectral sensitivity and for several standard indices of color vision [16,17]. The pattern of individual variation suggested (a) an average difference between male and female monkeys, and (b) a significant range of variation within each of the sexes. Specifically, all male monkeys exhibited a spectral neutral point, and had poor wavelength discrimination in the middle-to-long wavelength part of the spectrum, whereas this was the case for only about one-third of the females. In addition, both male and female monkeys exhibited wide variations in their sensitivities to long wavelength lights. Microspectrophotometric (MSP) measurements of cone pigments were made in squirrel monkeys whose visual capacities had been previously measured and, from these, it became clear that the individual differences in vision directly reflected variations in the cone types present in the retinas of individual monkeys [18–21]. These results initiated a new series of examinations of color vision and its mechanisms in platyrrhine monkeys that has continued to the present day.

Cone Pigments

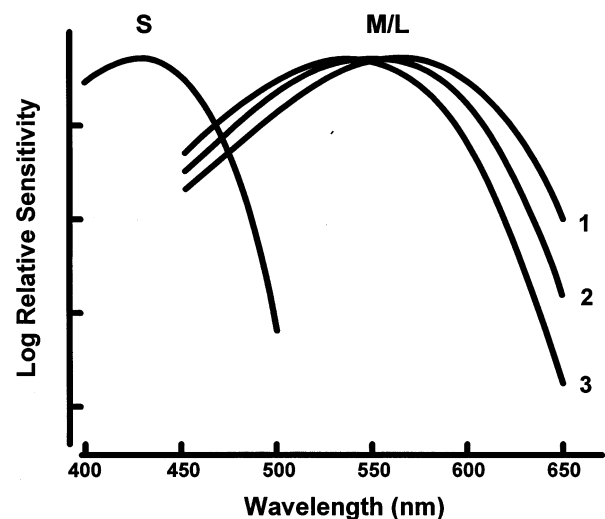


Fig. 1. Schematic representation of the photopigment basis for polymorphic color vision in platyrrhine monkeys. Shown at the top are spectral sensitivities of the four classes of cone found in squirrel monkeys. The box at the bottom shows the six combinations of these cone types, each of which is found in some individual animals.

3. The polymorphic themes

The picture that emerged from the combined behavioral and photopigment measurements made on squirrel monkeys is summarized in Fig. 1. The average cone spectral sensitivities are sketched at the top of Fig. 1. All animals were found to have an S cone with an absorption peak (λ_{\max}) of about 433 nm. In addition, three separate classes of M/L cones were identified. The absorption peaks of the three have varied slightly depending on the measurement procedure with average λ_{\max} values of about 535, 550 and 562 nm. The M/L pigments are distributed among individual monkeys in the manner illustrated at the bottom of Fig. 1, yielding a total of six different photopigment combinations. Three of these support dichromatic color vision; the other three yield trichromacy. The color vision and

spectral sensitivity variations seen in squirrel monkeys seem to be completely accounted for by variations in cone pigment complement. The discreteness of the pigments underlying the behavioral variations suggested that these individual variations were, in fact, polymorphisms.

In the original sample of squirrel monkeys tested all males were found to have dichromatic color vision whereas both trichromatic and dichromatic females could be identified. A simple genetic model was suggested to account for these facts [19,22]. The idea was that the M/L cone pigments are specified at a single X-chromosome gene locus by three allelic versions of the M/L cone opsin gene. In conjunction with an autosomal S-pigment gene, this would make all males and the homozygous females dichromatic. At the same time, females heterozygous at the gene site would produce two different types of M/L pigment and the two pigments would be sorted into individual photoreceptors through the mechanism of random X-chromosome inactivation. Such females would have trichromatic color vision. This model was evaluated by examining the photopigments present in a large sample of squirrel monkeys [23] and, eventually, through a direct examination of squirrel monkey photopigment genes [24]. All of these results suggest the model provides a correct account of the genetic basis of color vision variation in squirrel monkeys. An additional important observation is that the polymorphic photopigment genes seem to be of about equal frequency in the large sample of squirrel monkeys tested. This implies that there has been a selective advantage to the maintenance and maximization of the representation of heterozygous females in the population.

Although the evidence in each case is much less extensive, the polymorphic cone pigments and color vision first documented for squirrel monkeys appears to be an arrangement that is common among the platyrrhine monkeys. For instance, the genus first studied by Grether, *Cebus*, appears to have the same polymorphic sorting of cone photopigments as seen in the squirrel monkey [25,26]. And there is evidence that monkeys from two other genera—*Ateles* [27] and *Callicebus* [26]—may be similar. Whether the photopigments of all of these species are exactly the same, and whether the representation of the three cone types is equifrequent in the population as it appears to be for *Saimiri*, is presently less certain. What does presently seem quite clear is that in each of these cases there is only a single photopigment gene locus on the X-chromosome yielding routine male dichromacy and mixed female dichromacy/trichromacy.

There have also been recent studies of genes, photopigments and color vision in several species from the subfamily *Callitrichinae* (Table 1). Among these are representatives from *Callithrix* [28–30], *Saguinus*

[31,32], and *Leontopithecus* (Jacobs and Deegan II, unpublished observations). With one important difference, the arrangement of photopigment genes, photopigments and color vision is quite parallel to that described above for the squirrel monkey. The difference is in the spectral absorption curves of the M/L cone pigments. The *Callitrichinae* and *Cebinae* (and others) all appear to share in common the longest M/L pigment (λ_{\max} = ca. 562 nm), but they differ in the spectral positioning of the remaining two M/L pigments. For the *Callitrichinae*, the latter pigments have peak values of about 543 and 556 nm. These variations in M/L pigment identities between these two groups of platyrrhine monkeys have made them a valuable resource for studies directed at determining the genetic mechanisms underlying the spectral tuning of primate cone pigments [30,33].

4. Variations on the polymorphic theme

The presence of multiple M/L cone pigments produced by the allelic sorting of three cone opsin genes is clearly a predominant arrangement among platyrrhine monkeys. But it is not universal. In addition to the very important fact that we remain ignorant of the photopigment/color vision arrangements for a considerable number of platyrrhine species, two striking variations on this theme have been identified. Both of these are of considerable interest from the perspective of the adaptive value of cone-based vision.

One of the important variants involves monkeys from the subfamily *Aotinae* (Table 1). *Aotus*, the owl monkey, is the only nocturnal simian [34]. These monkeys are believed to have become nocturnal as a secondary adaptation, and their unique status has long made them a target for studies of vision. In accord with its nocturnality, *Aotus* has a rod-rich retina. Curiously, the presence of a fovea can be detected in an occasional individual [35]. Two recent studies indicate the uniqueness of cone vision in *Aotus*. First, an opsin-antibody-staining experiment revealed the presence of a population of M/L cones in the owl monkey retina, but failed to detect any S cones [36]. Second, a series of psychophysical and electrophysiological experiments identified a single type of M/L cone (with λ_{\max} of ca. 543 nm), but also failed to find any evidence for the presence of an S-cone class [37]. Taken together, these studies make it apparent that *Aotus* is a cone monochromat.

The puzzle of cone vision in *Aotus* was lessened somewhat by the discovery that this monkey has an S-cone opsin gene that is highly homologous to the human S-cone gene. Examination of the sequence of this gene revealed deleterious mutational changes in exon one that result in the presence of a stop codon,

thus apparently obviating the production of any viable S-cone pigment [38]. The arrangement is superficially similar to the genetic changes underlying human tritanopia in which point mutations in S-cone genes appear to impact the function or number of S cones [39], but whereas the loss of a viable S-cone is a rare condition in people it appears that the analogous loss is a species characteristic in the owl monkey. These findings raise an interesting question about the role of S-cones in strongly nocturnal species like the owl monkey: could the operation of such cones be detrimental to efficient rod-based vision? At any rate, the fact that *Aotus* seems to have abandoned a potential dichromacy reminds us that the evolution of color vision need not be a one-way street. It has been suggested that the loss of S-cone function in this platyrrhine monkey is an arrangement that may characterize some other strongly nocturnal mammals [38,40].

A second exception to the polymorphic theme of color vision in platyrrhine monkeys has been recently discovered among howler monkeys (*Alouatta* sp.). Electrophysiological measurements of M/L photopigments revealed that both male and female howler monkeys have separate classes of M and L cones [38]. In short, unlike all other platyrrhine monkeys examined to date, howler monkeys should have uniform trichromatic color vision. That conclusion was supported by a molecular genetic examination of X-chromosome pigment genes in two different species (*A. caraya*-the black howler monkey; *A. seniculus*-the red howler monkey). All of these animals, both male and female, showed the specific nucleotide variations in exon five that are associated with the presence of two spectrally well-separated M and L cone pigments [38,40]. Somehow these species have escaped the color vision confines defined by a single X-chromosome pigment gene and acquired a genotype/phenotype arrangement that is very similar to that documented for catarrhine monkeys.

5. Evolution of primate color vision

The wealth of new information on monkey color vision, photopigments and photopigment genes has stimulated a range of comment on the evolution of primate color vision. The discussion principally centers on two issues: primate color vision as an adaptive capacity and the mechanics of its evolution. Color vision has often been considered a specialization for finding food [41,61]. In the context of primate color vision, the idea is that most primates include some fruits in their diets and that trichromatic animals may be particularly advantaged in the detection of yellow and orange fruits embedded in a sea of green foliage [42,43]. Measurements of the reflectance spectra of fruits and foliage have been used in computational

schemes to illustrate the fact that, indeed, trichromatic primate visual systems may offer considerable advantage over dichromatic ones in fruit/foliage discriminations [44,45]. One implication is that the polymorphic color vision of most platyrrhine species is a less than optimal arrangement for a frugivorous life style. According to this idea trichromatic females would be well adapted for fruit detection, but the remainder of the animals (up to two-thirds of all monkeys and every male) would be relatively poorer at distinguishing fruit from foliage on the basis of chromaticity cues alone. If this is a correct conclusion, one might expect to see some consistent individual variations in diet choice or harvesting style in these polymorphic species that reflect these variations in color vision capacity. So far none have been noted.

Comparative analysis of opsin gene sequences is currently a growth industry that promises to lead to a much better understanding of the evolution of the photopigment components of color vision. Examination of the homologies among opsins support the idea that the genes for S, M/L, and rod opsins emerged from a common ancestor long ago (perhaps 500–800 million years ago) and that the emergence of separate M and L pigment genes is a much more recent event-estimated at 30–50 million years ago [46,47]. Since the presence of two separate cone opsins appears to substantially predate the appearance of the earliest mammals, this suggests that separate classes of S and M/L pigments and the dichromacy it can offer represent a baseline arrangement for the mammals. That speculation is buttressed by the apparent widespread occurrence of dichromacy among a greatly varied array of contemporary mammals [48]. Given that, the earliest anthropoid would have likely been (at least) a dichromat. The divergence of separate M and L pigment genes is estimated to have occurred at around the time of the split between New (NW) and Old World (OW) primates.

Presently there is no single accepted scenario for the evolution of trichromacy. A number of plausible pathways to the color vision of contemporary OW and NW monkeys do exist. Some of these possibilities are: (1) M/L gene polymorphism may have evolved prior to the split between OW and NW monkeys and, following that, an unequal crossover and gene conversion led to two X-chromosome sites and routine trichromacy in OW monkeys while leaving most NW monkeys with polymorphic color vision [21,49,50]; (2) the NW/OW monkey separation pre-dated any change from the basic mammalian plan, so that the subsequent steps to NW and OW monkey color vision are completely independent, in which case the evolution of OW color vision may or may not have included a polymorphic stage; (3) two X-chromosome gene sites and trichromacy might have been acquired prior to OW/NW

separation and the second site was subsequently lost (along with routine trichromacy) in the evolution of NW monkeys [51]. Although there is very little to provide strong guidance among these possibilities at present, these scenarios have to accommodate the fact that the molecular machinery for the spectral tuning of photopigments is common to OW and NW primates. Since the same tuning sites are also seen in a wide variety of other species [52], this coincidence likely reflects the conservative nature of photopigment molecules and is, thus, probably an example of convergent evolution [53]. The schemes also have to contend with exceptions to the predominant polymorphism of NW monkeys noted above—in particular, the routine trichromacy of *Alouatta*. Comparative examination of the M/L opsin gene sequences suggests that howler monkeys acquired their trichromacy subsequent to the platyrrhine radiation [38,40] and that conclusion is reinforced by an examination of the structure of the promoter regions of M/L pigment genes in NW monkeys and people [54]. These observations would seem to lessen the likelihood that the ancestral platyrrhines were in fact trichromatic. If they were not, then how and why have howler monkeys been the only platyrrhines to acquire routine trichromacy? The answers to the ‘how’ question may well come from more detailed examination of the howler monkey pigment genes and their flanking regions. In the meantime, those who admire the elegance of primate trichromacy may also appreciate the irony in the fact that howler monkeys have a lower encephalization index (a characterization of the brain-weight to body-weight ratio) than any of the other platyrrhines whose color vision and photopigments have been considered here [55].

Color vision requires both multiple photopigments and an appropriate nervous system organization. Examination of both anatomy and physiology indicates there are many similarities between the organization of platyrrhine and catarrhine visual systems [56–58]. In particular, the portion of the primary visual system believed to support color vision, the P-cell system, is very similar in trichromatic OW and NW monkeys and the only apparent difference between dichromatic and trichromatic platyrrhines is the presence or absence of M/L opponency. This suggests a single origin for the P-cell system, but unless trichromacy was a characteristic of the ancestor common to platyrrhine and catarrhine monkeys the original purpose for this system was probably not color vision. A frequently suggested alternative is that the P-cell system is an adaptation for high spatial acuity [59]. If that is the case, the addition of a second M/L cone type could exploit a neural pathway already elaborated for other purposes [60]. This would explain why trichromacy emerges immediately in heterozygous female NW monkeys. Unfortunately, there are also some difficulties in accepting the

idea that the P-cell pathway is well suited for supporting precise spatial vision (e.g. its low responsivity [56]), so for the present the origin of the commonalities in the organization of NW and OW monkey visual systems remain speculative.

6. Prospect

Studies of platyrrhine color vision and its biological basis have helped to solidify our understanding of the relationships between genes, photopigments and color vision and they have been instrumental in re-awakening interest in the evolution of primate color vision. Future expansion of these studies promises a deep understanding of the evolution of primate cone pigments, as well as further insights into relationships between the receptor mechanisms for color vision and the nervous system organization required to realize the capacity. The color vision polymorphisms of these species continue to provide an unparalleled opportunity to examine and understand the ecology of primate color vision.

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References

- [1] Grether WF. Color vision and color blindness in monkeys. *Comp Psychol Monogr* 1939;29:1–38.
- [2] De Valois RL, Morgan HC, Polson MC, Mead WR, Hull EM. Psychophysical studies of monkey vision I. Macaque luminosity and color vision tests. *Vis Res* 1974;14:53–67.
- [3] Harwerth RS, Smith III EL. The rhesus monkey as a model for normal vision of humans. *Am J Optom Physiol Opt* 1985;62:633–41.
- [4] Baylor DA, Nunn BJ, Schnapf JL. Spectral sensitivity of cones of the monkey *Macaca fascicularis*. *J Physiol* 1987;357:145–60.
- [5] Bowmaker JK, Astell S, Hunt DM, Mollon JD. Photosensitive and photostable pigments in the retinas of Old World monkeys. *J Exp Biol* 1991;156:1–19.
- [6] Jacobs GH, Deegan II JF. Spectral sensitivity of macaque monkeys measured with ERG flicker photometry. *Vis Neurosci* 1997;14:921–8.
- [7] Deegan II JF, Jacobs GH. Photopigment basis for trichromatic color vision in colobine monkeys. *Am J Primatol* 1997;42:104.
- [8] Mittermeier RA, Coimbra-Filho AF. Systematics: species and subspecies. In: Coimbra-Filho AF, Mittermeier RA, editors. *Ecology and Behaviour of Neotropical Primates*. Rio de Janeiro: Academia Brasileira de Ciencias, 1981:29–109.
- [9] Ford SM. Systematics of the New World monkeys. In: Swindler DR, Erwin J, editors. *Comparative Primate Biology: Systematics, Evolution and Anatomy*. New York: Alan R Liss, 1986:73–135.

- [10] Kay RF. The phyletic relationships of extant and fossil Platyrrhini (Platyrrhini, Anthropoidea). *J Hum Evol* 1990;19:175–208.
- [11] Schneider H, Schneider MPC, Sampaio I, Harada ML, Stanhope M, Czelusniak J, Goodman M. Molecular phylogeny of the New World monkeys (Platyrrhini, primates). *Mol Phylogenetics Evol* 1993;2:225–42.
- [12] Harada ML, Schneider H, Cruz-Schneider MP, Sampaio I, Czelusniak J, Goodman M. DNA evidence on the phylogenetic systematics of New World monkeys: support for sister-grouping of *Cebus* and *Saimiri* from two unlinked nuclear genes. *Mol Phylogenetics Evol* 1995;4:331–49.
- [13] Kinzey WG. *New World Primates: Ecology, Evolution and Behavior*. New York: Aldine de Gruyter, 1997.
- [14] Watson JB. Some experiments bearing on color vision in monkeys. *J Comp Neurol Psychol* 1909;19:1–28.
- [15] Jacobs GH. Vision in squirrel monkeys: physiological and psychophysical evidence of sex-related differences. *Physiologist* 1974;17:254.
- [16] Jacobs GH. Visual sensitivity: significant within-species variations in a nonhuman primate. *Science* 1977;197:499–500.
- [17] Jacobs GH. Within-species variations in visual capacity among squirrel monkeys (*Saimiri sciureus*): color vision. *Vis Res* 1984;24:1267–77.
- [18] Jacobs GH, Bowmaker JK, Mollon JD. Behavioural and microspectrophotometric measurements of colour vision in monkeys. *Nature* 1981;292:541–3.
- [19] Mollon JD, Bowmaker JK, Jacobs GH. Variations of colour vision in a New World primate can be explained by polymorphism of retinal photopigments. *Proc R Soc Lond* 1984;B222:373–99.
- [20] Bowmaker JK, Jacobs GH, Spiegelhalter DJ, Mollon JD. Two types of trichromatic squirrel monkey share a pigment in the red-green spectral region. *Vis Res* 1985;25:1937–46.
- [21] Bowmaker JK, Jacobs GH, Mollon JD. Polymorphism of photopigments in the squirrel monkey: a sixth phenotype. *Proc R Soc Lond* 1987;B231:383–90.
- [22] Jacobs GH, Neitz J. Color vision in squirrel monkeys: sex-related differences suggest the mode of inheritance. *Vis Res* 1985;25:141–4.
- [23] Jacobs GH, Neitz J. Inheritance of color vision in a New World monkey (*Saimiri sciureus*). *Proc Natl Acad Sci USA* 1987;84:2545–9.
- [24] Jacobs GH, Neitz J, Neitz M. Genetic basis of polymorphism in the color vision of platyrrhine monkeys. *Vis Res* 1993;33:269–74.
- [25] Bowmaker JK, Mollon JD. Primate microspectrophotometry and its implications for colour deficiency. In: Verriest G, editor. *Colour Deficiencies V*. Bristol: Hilger, 1980:61–4.
- [26] Jacobs GH, Neitz J. Polymorphism of the middle wavelength cone in two species of South American monkey: *Cebus apella* and *Callicebus molloch*. *Vis Res* 1987;27:1263–8.
- [27] Jacobs GH, Deegan II JF. Polymorphism of cone photopigments in New World monkeys: is the spider monkey unique? *Invest Ophthalmol Vis Sci* 1993;34:749.
- [28] Travis DS, Bowmaker JK, Mollon JD. Polymorphism of visual pigments in a callitrichid monkey (*Callithrix jacchus jacchus*). *Vis Res* 1988;28:481–90.
- [29] Tovée MJ, Bowmaker JK, Mollon JD. The relationship between cone pigments and behavioural sensitivity in a New World monkey (*Callithrix jacchus jacchus*). *Vis Res* 1992;32:867–78.
- [30] Williams AJ, Hunt DM, Bowmaker JK, Mollon JD. The polymorphic photopigments of the marmoset: spectral tuning and genetic basis. *EMBO J* 1992;11:2039–45.
- [31] Jacobs GH, Neitz J, Crognale M. Color vision polymorphism and its photopigment basis in a callitrichid monkey (*Saguinus fuscicollis*). *Vis Res* 1987;27:2089–100.
- [32] Jacobs GH, Deegan II JF. Photopigment polymorphism in cottontop tamarins (*Saguinus oedipus*). *Am J Primatol* 1994;33:217.
- [33] Neitz M, Neitz J, Jacobs GH. Spectral tuning of pigments underlying red-green color vision. *Science* 1991;252:971–4.
- [34] Martin RD. *Primate Origins and Evolution*. Princeton: Princeton University Press, 1990.
- [35] Ogden TE. Nerve fiber layer of the owl monkey retina: retinotopic organization. *Invest Ophthalmol Vis Sci* 1982;24:265–9.
- [36] Wikler KC, Rakic P. Distribution of photoreceptor subtypes in the retina of diurnal and nocturnal primates. *J Neurosci* 1990;10:3390–401.
- [37] Jacobs GH, Deegan II JF, Neitz JA, Crognale MA, Neitz M. Photopigments and color vision in the nocturnal monkey, *Aotus*. *Vis Res* 1993;33:1773–83.
- [38] Jacobs GH, Neitz M, Neitz J. Mutations in S-cone pigment genes and the absence of colour vision in two species of nocturnal primate. *Proc R Soc Lond* 1996;B263:705–10.
- [39] Weitz CJ, Miyake Y, Shinzato K, Montag E, Zrenner E, Went LN, Nathans J. Human tritanopia associated with two amino acid substitutions in the blue sensitive opsin. *Am J Hum Genet* 1992;50:498–507.
- [40] Jacobs GH, Neitz M, Deegan JF, Neitz J. Trichromatic colour vision in New World monkeys. *Nature* 1996;382:156–8.
- [41] Polyak S. *The Vertebrate Visual System*. Chicago: University Chicago Press, 1957.
- [42] Snodderly DM. Visual discriminations encountered in food foraging by a neotropical primate. In: Burt EH, editor. *The Behavioral Significance of Color*. New York: Garland STPM Press, 1979.
- [43] Mollon JD. “Tho she kneel’d in that place where they grew.” The uses and origins of primate colour vision. *J Exp Biol* 1989;146:21–38.
- [44] Osorio D, Vorobyev M. Colour vision as an adaptation to frugivory in primates. *Proc R Soc Lond* 1996;B263:593–9.
- [45] Regan BC, Vienot F, Charles-Dominique PC, Pefferkorn S, Simmen B, Julliot C, Mollon JD. The colour signals that fruits present to primates. *Invest Ophthalmol Vis Sci* 1996;37:648.
- [46] Nathans J, Thomas D, Hogness DS. Molecular genetics of human color vision: the genes encoding blue, green and red pigments. *Science* 1986;232:193–202.
- [47] Yokoyama S, Yokoyama R. Molecular evolution of human visual pigment genes. *Mol Biol Evol* 1989;6:186–97.
- [48] Jacobs GH. The distribution and nature of colour vision among the mammals. *Biol Rev* 1993;68:413–71.
- [49] Hunt DM, Williams AJ, Bowmaker JK, Mollon JD. Structure and evolution of the polymorphic photopigment gene of the marmoset. *Vis Res* 1993;33:147–54.
- [50] Dulai KS, Bowmaker JK, Mollon JD, Hunt DM. Sequence divergence, polymorphism and evolution of middle-wave and long-wave visual pigment genes of great apes and old world monkeys. *Vis Res* 1994;34:2483–91.
- [51] Mollon JD. Uses and evolutionary origins of primate colour vision. In: Cronly-Dillon JR, Gregory RL, editors. *Evolution of the Eye and Visual System*. Boca Raton: CRC Press, 1991:306–19.
- [52] Yokoyama S, Yokoyama R. Adaptive evolution of photoreceptors and visual pigments in vertebrates. *Annu Rev Ecol Syst* 1996;27:543–67.
- [53] Shyue SK, Hewett-Emmett D, Sperling HG, Hunt DM, Bowmaker JK, Mollon JD, Li WH. Adaptive evolution of color vision genes in higher primates. *Science* 1995;269:1265–7.
- [54] Kainz PM, Neitz J, Neitz M. Recent evolution of uniform trichromacy in New World monkeys. *Vis Res* 1998;38:3315–20.
- [55] Stephan H, Baron G, Frahm HD. Comparative sizes of brains and brain components. In: Steklis HD, Erwin J, editors. *Com-*

- parative Primate Biology: Neurosciences. New York: Alan R Liss, 1989:1–38.
- [56] Yeh T, Lee BB, Kremers J, Cowing JA, Hunt DM, Martin PR, Troy JB. Visual responses in the lateral geniculate nucleus of dichromatic and trichromatic marmosets (*Callithrix jacchus*). J Neurosci 1995;15:7892–904.
- [57] Wilder HD, Grunert U, Lee B B, Martin PR. Topography of ganglion cells and photoreceptors in the retina of a New World monkey: the marmoset *Callithrix jacchus*. Vis Neurosci 1996;13:335–52.
- [58] Silveira LCL, Lee BB, Yamada ES, Kremers J, Hunt DM. Post-receptoral mechanisms of colour vision in new world primates. Vis Res 1998;38:3329–37.
- [59] Wassle H, Boycott BB. Functional architecture of the mammalian retina. Physiol Rev 1991;71:447–80.
- [60] Mollon JD, Jordan G. Eine evolutionaire Interpretation des menschlichen Farbensehens. Farbe 1988;35:139–70.
- [61] Jacobs GH. Color-vision polymorphisms in New World monkeys: implications for the evolution of primate trichromacy. In: Kinzey WG, editor. New World Primates: Ecology, Evolution and Behavior. New York: Aldine de Gruyter, 1997:45–74.