Progress Toward Understanding the Evolution of Primate Color Vision

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Color vision requires the presence in the retina of multiple types of cone photopigment and appropriate nervous-system connections. In recent years, the structures of genes specifying photopigment opsins have come under increasing scrutiny. In many animal groups (e.g., fish, reptiles, and birds), representatives of four separate cone opsin gene families can be identified. In mammals, however, opsins derived from only two of these families are found, and this raises the possibility that two cone classes were lost during the early evolution of mammals. Accordingly, the dichromatic color vision that is characteristic of many modern mammals may be a direct reflection of this loss. On the other hand, keen trichromatic color vision is a feature of the perceptual world of many primates, so that capacity must have reemerged during primate evolution. Some ideas about the process can be drawn from an examination of the patterns of color vision detected in contemporary primates and of the pigments and opsin genes that make color vision possible.

COLOR VISION IN THE CATARRHINES

Old World monkeys, apes, and humans share common color-vision capacities. In these species, there are routinely three classes of cone photopigment with maximum sensitivity in short (S), middle (M), and long (L) wavelengths (respective peak values of about 430, 530, and 560 nm). In conjunction with spectrally opponent neural pathways that allow comparisons of signals initiated by cones containing these three pigment types, this arrangement supports trichromatic color vision. The gene specifying S cone opsin is on chromosome 7; the L and M cone opsin genes occupy neighboring locations on the X-chromosome, and these two are structurally very similar (about 98% identical at the DNA sequence level). At least among humans, there are frequently multiple copies of the M-cone opsin gene. Sequence comparisons have been interpreted as indicating that a second gene was added to the primate X-chromosome through a gene duplication that occurred shortly after the catarrhine/platyrrhine divergence. There has been an unresolved debate, as to which, if either, of the modern genes was the original single gene. It would be useful to settle this issue, as the result could be used to predict the nature of color vision in the ancestors of higher primates.

A striking feature of human color vision is the presence of polymorphic variations in the M and L genes, yielding color anomalies and color defects. Color defects affect as many as 8–9% of all males in some populations. These alterations in color vision result from the close physical proximity of the M and L opsin genes and their extensive sequence similarities. Polymorphic versions of the L and M gene array are produced by unequal meiotic recombinations, which delete either the M or the L gene type and so reduce color vision to a dichromacy. Alternatively, they produce unique versions of the opsin genes, resulting in shifts in the absorption spectra of the M and L pigments and anomalous trichromatic color vision. An interesting feature of catarrhine color vision is that polymorphic color vision...
defects are very infrequent in any genus other than Homo. For instance, a recent survey of Macaca detected aberrant opsin gene arrays that would predict dichromatic color vision in only 3 of more than 3,100 monkeys.9 The reason for the high frequency of color defects in people but not in other catarrhine species is unknown. Two possibilities are that the high frequency of defects in humans reflects a relaxation from selection against color defect, or that the gene arrays for the M and L opsins differ significantly enough between humans and Old World monkeys and apes that the latter species are much less prone to unequal recombination events.10 These two possibilities are not mutually exclusive.

**THE POLYMORPHIC PLATYRRHINES**

Over the past 20 years, much has been learned about color vision and its basis in platyrrhine monkeys, in turn advancing our understanding of the evolution of primate color vision. Almost without exception, platyrrhine species display striking color vision polymorphisms, individual animals having any of several types of dichromatic or trichromatic color vision.11 The result is that there may be six or more distinct color-vision phenotypes in a population. Measurements of photopigments and behavioral tests revealed early on that these different forms of color vision arise from individual variations in the complement of M and L photopigments.12,13 Some monkeys have only a single type of M/L photopigment and dichromatic color vision; others have two types of M/L pigment and are trichromatic. A defining feature of this platyrrhine polymorphism is that all male monkeys are dichromats, while females may be either dichromatic or trichromatic. Studies of cone pigment pedigrees and, subsequently, direct examination of the opsin genes provided an explanation for this fact.14,15 Platyrrhine monkeys have only a single X-chromosome opsin gene locus, but with several polymorphic versions of the gene. As males have only a single X-chromosome, the version of the gene a male receives determines the nature of his dichromacy. Homozygous females are also dichromatic, but heterozygous females produce two different M/L photopigments and are trichromats. The effective difference between the catarrhine and platyrrhine arrangements simply comes down to the number of X-chromosome opsin genes: one in platyrrhines, and two or more in catarrhines.

The model just described accounts for color vision in many of the common platyrrhine monkeys. This list includes various cebid and callitrichid species, each of which has three possible M/L photopigments and a rich mixture of dichromatic and trichromatic individuals. So far, it seems that the genes specifying the three pigments are of near equal frequency in the population, allowing roughly two thirds of all females to become heterozygous and, thus, trichromatic. Although this is the common pattern, there are species in which the number of polymorphic genes differs from three.16 For example, from pigment measurement surveys, only two types of M/L photopigment were detected in both spider monkeys (Ateles) and woolly monkeys (Lagothrix), whereas titi monkeys (Callicebus) seem to have five different M/L photopigments. The principal practical consequence of this variation in the number of polymorphic M/L opsin genes is that it influences the incidence of female trichromacy: species with two opsin alternatives have proportionally fewer trichromats than do those species that maintain more types of opsin genes.

**PLATYRRHINE EXCEPTIONS**

Two significant exceptions to this picture of platyrrhine color vision have been discovered. The first is the owl monkey (Aotus), the only nocturnal simian. Aotus has only a single type of X-chromosome opsin gene, and so lacks any of the polymorphic character of other platyrrhines, resembling in this regard more the arrangement found in many nonprimate mammals. Surprisingly, however, the owl monkey retina also lacks any cones containing S pigment, and consequently these monkeys have no conventional color-vision capacity.17,18 Examination revealed that Aotus does have an S-opsin gene, but that gene contains mutations that obviate its expression.19 It seems reasonable to conclude that at some time during its evolution, Aotus abandoned dichromatic color vision. The photopigment/color vision arrangement of the owl monkey is not unique. Indeed, Aotus belongs to a rapidly expanding coterie of mammals, each of which was recently shown to have a single active M/L pigment gene and a nonfunctional S pigment gene. Included in this group are some prosimians (see below), rodents, and marine mammals. The evolutionary circumstances surrounding this apparently common loss of S-cone pigment remain mysterious and intriguing.

The second exception to the polymorphic rule are the howler monkeys (Alouatta). Howler monkeys have two separate X-chromosome gene sites supporting M and L cone opsin genes.20 This pattern yields two well-separated M and L cone pigments that should provide trichromacy for all howler monkeys, male and female alike. As far as is known, there are no polymorphic variations in these pigments, and thus no variation around the trichromatic norm. The pigment/color vision arrangement of the howler monkey is strikingly similar to that of catarrhine monkeys, and its emergence in the platyrrhines is provocative with regard to the evolution of primate color vision.

**THE PROSIMIAN PUZZLE**

Although there is still much to be learned about color vision and its antecedents in both catarrhine and platyrrhine primates, one can at least discern the themes. That is not the case for the prosimians. Although scattered species have been examined, the picture remains murky. Three different color-vision arrangements have been detected. The thick-tailed bushbaby (Otolemur crassicaudatus) is a nocturnal animal whose cone pigment complement resembles that of Aotus in that the retina contains only a single type of M/L pigment. Examination of the bushbaby opsin genes reveals that it, too, has an S-cone opsin gene harboring defects that block expression of a viable S-cone photopigment.19 Although direct behavioral measurements are lacking, it
seems quite certain that the bushbaby is monochromatic. Measurements of cone pigments were made on ringtail lemurs (Lemur catta) and brown lemurs (Eulemur fulvus), species described as having a diurnal or cathemeral lifestyle. Two classes of cone pigment (an S and an M/L type) were detected in each species. No polymorphism of M/L pigment was seen, and so the pigment arrays predict routine dichromacy. Finally, there was a recent survey of M/L opsin genes in 25 prosimian species. The striking finding is that at least three prosimian species (Coccoecel's sifaka, Propithecus verreauxi coquereli; red ruffed lemur, Varecia variegata; and greater dwarf lemur, Cheirogaleus minor) have an M/L opsin gene polymorphism. In each of these three cases, two allelic versions of the M/L gene were detected. Apparently, no assessment was made for the presence and viability of an S-opsin gene, but if it exists, then these gene complements would predict an arrangement similar to that described for platyrhine monkeys, in that males are confined to dichromatic color vision, while heterozygous females are potential trichromats. It is noteworthy that polymorphic M/L opsin genes were detected in both diurnal and nocturnal prosimians.

Tarsiers, of course, have a unique taxonomic status and so deserve special mention in any discussion of primate color vision. Although these animals are rigorously nocturnal, their eyes show some classical diurnal manifestations including, importantly, the presence of a retinal fovea. Recent immunocytochemical staining experiments revealed that both S and M/L cone types are present in the tarsier retina, predicting a possible dichromatic color vision capacity. Interestingly, the tarsier places its iconic stamp even on this common arrangement, as the S cones of the tarsier are atypically concentrated in the periphery of the retina. Even more intriguing, the sequences of opsin genes in two tarsier species (Tarsius bancanus and T. syrichta) are reported to differ in a way which predicts that the spectra of their M/L pigments should also differ. This could suggest that the ancestors of these contemporary tarsiers may themselves have had an M/L opsin gene polymorphism.

Clearly, we stand at the beginning of an understanding of opsin genes, cone pigments, and their visual consequences in prosimians. As new results emerge, it will be important to remember a fundamental fact: studies of opsin genes and photopigments yield predictions (and only that) about the dimensional limits of color vision (i.e., whether the animal could have monochromatic, dichromatic, or trichromatic color vision), but they cannot reveal much about the potential quality and utility of color vision. To cite one cogent example, many nocturnal primates have only a small population of cones that are widely scattered around the retina. The neural signals derived from this array that can be used to support color vision will inevitably prove to be very feeble relative to those available in a species with the same types of cone pigment but a larger cone population. Although both types of species may prove to be dichromatic, the keenness of their color capacities will be enormously different.

**THE EVOLUTIONARY PICTURE**

The results summarized above have all been accumulated over the past two decades, so we have come far in the quest for a better understanding of primate color vision. At the same time, the evolutionary picture of primate color vision remains incomplete. The variations in color vision, photopigments, and opsin genes among primates can be taken to suggest various scenarios as to the evolution of primate color vision, but mostly they remain just that—alternative possibilities. The reader should keep that firmly in mind.

It seems reasonable to suppose that color vision in mammals emerged from a primordial pattern involving the presence of two classes of cone, S cones and some single version of M/L cones. Primates appear to share a neural pathway through the retina (and perhaps centrally), where signals from S cones are contrasted to L/M cone signals. There is reason to believe that other mammals have similar organizational features and, in that sense, a basic dichromy is the mammalian ground plan. How this plan began to be altered in early primates is unclear. Comparison of catarrhine M and L opsin genes indicates that the two separate genes emerged about 30–40 million years ago. Two possible ways in which this occurred have been suggested: 1) There could have been a gene duplication followed by an accumulation of sequence changes sufficient to yield two spectrally discrete photopigments. 2) A polymorphism of genes at a single site (much like that of most platyrhines) could have been followed by an unequal crossover that placed two alleles on a single X-chromosome. In either case, the gene duplication in catarrhines is believed to have occurred after the catarrhine/platyrhine divergence. What is left unclear in this scenario is whether the early migrant platyrhines were polymorphic, or whether they had only a single X-chromosome opsin gene and it was left for subsequent evolution in the New World to produce all of the contemporary variations.

When polymorphism was first discovered in platyrhine monkeys, with its unique mixture of dichromatic and trichromatic individuals, it was suggested that these animals might provide an example of a (if not the) normal path to becoming routinely trichromatic. That certainly remains a possibility, and the howler monkey perhaps shows us its contemporary realization. Although the trichromacy of howler monkeys is formally similar to that of catarrhine species, DNA sequence comparisons indicate that the gene duplication adding a second X-chromosome site and clearing the way for routine trichromacy specifically occurred in that lineage (and, importantly, not in closely related atelid species) by a mechanism different from that of the analogous catarrhine gene duplication.

Until recently, it seemed likely that contemporary prosimians were either monochromatic or dichromatic, and it was reasonable to suggest that their color vision was probably much like that of other nonanthropoid mammals. The recent discovery indicating the presence of pigment polymorphism in some prosimian species de-
molishes that idea. It also leaves open the provocative possibility that photopigment polymorphism might have been present in very early primates. Further work on prosimian color vision and its mechanisms seems likely to be challenging but rewarding.

REFERENCES