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Chapter 13

Polymorphism and Adaptation of Primate Colour Vision

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Abstract Opsins provide an excellent model system for studying evolutionary interconnections at genetic, phenotypic and behavioural levels. Primates have evolved a unique ability for trichromatic colour vision from a dichromatic mammalian ancestor. This was accomplished via allelic differentiation (e.g. most New World monkeys) or gene duplication (e.g. Old World primates) of the middle to long-wavelength sensitive (M/LWS) opsin gene. However, questions remain

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regarding the behavioural adaptations of primate trichromacy. Allelic differentiation of the M/LWS opsins results in extensive colour vision variability in New World monkeys, where trichromats and dichromats are found in the same breeding population, enabling us to directly compare visual performances among different colour vision phenotypes. Thus, New World monkeys can serve as an excellent model to understand and evaluate the adaptive significance of primate trichromacy in a behavioural context. In this chapter, we summarise recent findings on colour vision evolution in vertebrates, with special emphasis on primates, and introduce our genetic and behavioural study on primate colour vision polymorphism and adaptation.

13.1 Introduction

Among mammals, primates are heralded for their specialised visual systems, including enhanced colour vision, acuity, stereopsis and cortical representation of the visual system. Of special interest to sensory ecologists is the unique evolution of trichromatic colour vision among primates, which arose from a dichromatic ancestor. Primate trichromacy is based on three cone opsins, which give rise to photopigments that are each sensitive to different wavelengths of light. In contrast, most mammals possess two cone opsins and, correspondingly, dichromatic colour vision. However, it is only in comparison with other eutherian mammals that primate colour vision can be regarded as specialised. The colour vision capabilities of many vertebrates exceed that of primates, due to the presence of cone oil droplets, as well as more extensive repertoires of cone opsins; zebrafish (*Danio rerio*), for example, have eight (Chinen et al. 2003) and many birds and reptiles possess four (Ebrey and Koutalos 2001). Therefore, to understand the adaptive significance of primate colour vision, it must be placed in the context of vertebrate colour vision evolution. To this end, we briefly trace the evolution of colour vision from early vertebrates through early mammals and up to extant primates. We then address the mechanisms, variation and hypotheses regarding the uses of colour vision among primates.

13.2 Evolutionary Background of Primate Colour Vision

13.2.1 Colour Vision in Early Vertebrates

Five families of visual opsins are known among vertebrates and have an early evolutionary origin. The rhodopsin (RH1) gene family generates the photopigment found in retinal rod cells which are responsible for highly sensitive vision in low light. The other four families, RH2 (rhodopsin-like, or green), SWS1 (short

wavelength sensitive 1, or ultraviolet), SWS2 (short wavelength sensitive 2, or blue) and M/LWS (middle to long wavelength-sensitive, or red-green) give rise to visual opsins found in cone cells, which are responsible for colour vision (Yokoyama 2000). Until recently, it was controversial whether the RH2 family appeared before or after the separation of *nathous* (jawed) from *anathous* (jawless) ancestors (Collin et al. 2003; Pisani et al. 2006) but recent studies support the occurrence of RH2 before the separation (Davies et al. 2009a, b). Therefore, all four extant lineages of cone opsins (as well as RH1) were likely present in the common ancestor of agnathous (jawless) and *nathous* (jawed) vertebrates, indicating a well-developed capacity for colour vision in the earliest vertebrates.

Cone oil droplets, which enhance colour vision by narrowing the spectral sensitivity of underlying photopigments and enabling more precise chromatic comparisons among cone cells, also have an early evolutionary origin. The presence of coloured oil droplets in lung fish indicates that they predate the ancestor of terrestrial vertebrates (Robinson 1994). Oil droplets also occur in many extant lineages of vertebrates; a coloured variety can be found among turtles, lizards and birds, while other vertebrate lineages, including sturgeon fish, coelacanths, frogs, monotremes and marsupials have colourless oil droplets (Bowmaker 2008). Neuronal adaptations in the retina for colour vision are also widespread among vertebrate lineages. These adaptations are less well known than receptor mechanisms, but at minimum they include spectrally opponent neurons, four types of horizontal cells, and both single and double cone photoreceptor cells. Given their wide distribution, these characteristics were also likely present in very early jawed vertebrates (Jacobs and Rowe 2004). From this early starting point the evolution of colour vision in different vertebrate lineages has been highly variable.

Many vertebrate groups have maintained or enhanced their colour vision through retention of the four ancestral opsin gene types or by adding novel opsins through duplication and divergence of existing ones. In contrast, other groups have forgone chromatic discrimination in favour of heightened light sensitivity or as a result of overall degeneration of the visual system. For example, opsin functionality can be lost through the gradual accumulation of deleterious mutations in the upstream regions that regulate their expression when colour vision is not under purifying selection (Jacobs et al. 1993). The absence or deterioration of one or more colour vision mechanisms (and other visual features not discussed for brevity) in a vertebrate lineage is often correlated with the transition of that group from high-light (photopic) to low-light (scotopic) environments.

13.2.2 Colour Vision in Early Mammals

Mammals evolved as small, nocturnal creatures and persisted in this niche for millions of years, until new diurnal habitats became available following the fall of the dinosaurs (Hopson and Crompton 1969). Changes in the mammalian visual system reflect this long occupation of low-light habitats and include increased

retinal summation of the visual cells, loss of coloured cone oil droplets, and an increase in the ratio of rods to cones. The unifying result of these changes is increased sensitivity to facilitate scotopic vision, yet the loss or retention of colour vision mechanisms among three mammalian lineages is somewhat variable.

Although the majority of extant mammals have dichromatic vision, recent work demonstrates that the last common ancestor of mammals may not have been dichromatic. Davies et al. (2007) and Wakefield et al. (2008) have shown that monotremes (platypuses and echidnas) have a different set of cone opsin genes than marsupial or placental mammals. Monotremes possess the SWS2 and M/LWS opsin genes, whereas marsupials and placental mammals possess the SWS1 and M/LWS opsin genes. The remnant of the SWS1 is still detectable in the monotreme genome, suggesting that this opsin was retained until relatively recently. Unlike monotremes, marsupial and placental mammals lack the SWS2 type completely. Taken together, these results suggest that prior to the monotreme divergence, mammals possessed SWS1, SWS2 and M/LWS opsins and were correspondingly trichromatic. Also of much recent interest are the studies revealing trichromacy among Australian marsupials (Arrese et al. 2002, 2006; Ebeling et al. 2010). Marsupial trichromacy extends into the UV range and is independent from trichromacy in placental mammals. Arrese et al. (2002) suggest that it may be facilitated by retention of the RH2 opsin type, although more recently it has been suggested that the third opsin is an RH1 (rod) opsin modified to be expressed in a class of cone cells (Cowing et al. 2008). Yet, the presence of an RH2 gene has not been verified in marsupials and no evidence has been found in support of the cone expression of rhodopsin. In fact, all marsupials appear to be genetically dichromatic and the origins of the third photopigment type remain a mystery (Ebeling et al. 2010). Placental mammals have retained fewer of the ancestral visual features than have monotremes or marsupials. For example, cone oil droplets have been completely lost in the placental lineage. Two of the four types of retinal horizontal cells are also lost in placental mammals, although the evolutionary branch at which they disappeared remains unresolved (Jacobs and Rowe 2004).

Despite losing many visual features and colour vision mechanisms, it is interesting that two functional cone photopigments, and thus dichromatic colour vision, were retained during mammalian evolution despite the extended period of nocturnality. Because colour vision does not function in the dark, monochromacy is the expected outcome of nocturnality. Several extant nocturnal primates (lorises and galagos, owl monkeys) and non-primate mammals (e.g. raccoons, kinkajous) are monochromatic via the additional loss of their SWS1 blue-sensitive photopigment (Hunt et al. 2007). These animals are truly colour-blind, except perhaps at mesopic light levels in which both rods and cones may contribute to colour perception (Kelber and Roth 2006; Pokorny et al. 2008). Conversely, some nocturnal primates (e.g. aye-ayes, tarsiers) and many additional nocturnal mammals still retain the two functional cone opsin genes and photopigment types (Hendrickson et al. 2000; Hunt et al. 2007). One explanation for this puzzle is that extant, nocturnal, dichromatic animals have not occupied this night-active niche as long as monochromatic animals (Tan et al. 2005). Alternatively, dichromatic colour vision could be adaptive for some nocturnal animals (Perry et al. 2007). Dichromatic colour vision may

function at twilight and under bright moonlight, for example (Melin et al. 2012). It has also been suggested that visual opsin genes may have a non-visual purpose such as regulation of circadian rhythms (Nei et al. 1997). Undoubtedly, this interesting problem is far from resolved and future research into when and how nocturnal animals exploit their environments may provide interesting insights.

13.3 Trichromatic Vision in Primates

Primates are the only placental mammal known to have trichromatic colour vision. They share the SWS1 opsin common to other mammals and have acquired trichromacy via the allelic differentiation or the duplication and divergence of the M/LWS opsin, causing “L”, “M” and their intermediate opsins (Jacobs and Nathans 2009). The resultant red–green chromatic channel adds a new dimension of colour vision to the pre-existing blue–yellow channel. However, primate trichromacy is variable among lineages (Fig. 13.1). In catarrhine primates (humans, apes and Old World monkeys), and independently in howler monkeys (*Alouatta*), a genus of platyrrhine primates (New World monkeys), the L and M opsins occupy loci on the X-chromosome enabling routine trichromacy for all males and females (Jacobs 2008). In contrast, a polymorphic M/LWS opsin gene occupies a single locus on the X-chromosome in the majority of New World monkeys (Jacobs 2007) and in some lemurs (Tan and Li 1999; Jacobs et al. 2002; Tan et al. 2005; Veilleux and Bolnick 2009), although it is debated whether this represents shared heritage or independent evolutionary events (Tan and Li 1999; Heesy and Ross 2004). Among polymorphic species, heterozygous females are trichromatic, having two different M/LWS opsin alleles, while males and homozygous females have dichromatic colour vision.

Among the routinely trichromatic catarrhines, humans uniquely possess a high occurrence of opsin gene polymorphisms (Deeb 2006) and in this way more closely resemble the platyrrhine colour vision system. Approximately 3–8 % of males have deficient colour vision (dichromacy or anomalous trichromacy) due to deletion of the L or M opsin gene and/or hybridization of the two genes. Even people with normal colour vision often carry hybrid opsin genes (Deeb et al. 1992). Congenital colour vision defects are typically found in men because women have two X chromosomes and thus are more likely to have a “normal” gene in either one.

Compared to humans, the incidence of colour vision defects in other catarrhines is low (Onishi et al. 1999; Jacobs and Williams 2001; Terao et al. 2005). Our recent study on gibbons detected no incidence of deletion or hybridization of the L and M opsin genes among ~150 individuals representing three genera and suggested that spectral difference between these opsins is maintained by purifying selection opposing gene conversions homogenising the two genes (Hiwatashi et al. 2011). A lower incidence of multiple M/LWS gene copies may in part explain the low incidence of colour vision defects in some species (Onishi et al. 1999, 2002; Terao et al. 2005; Verrelli et al. 2008). However, other studies report that multiple

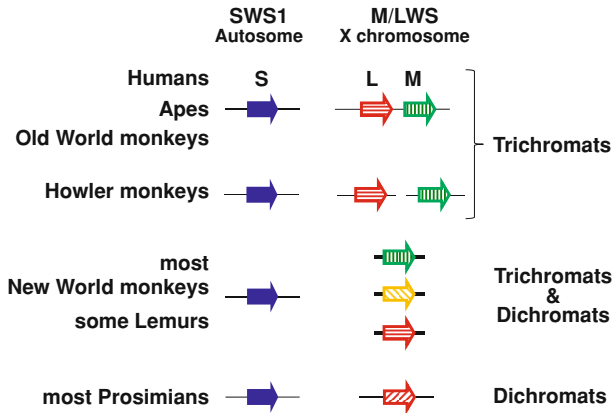


Fig. 13.1 Gene organisations of primate visual opsins. Humans, apes and Old World monkeys have the L and M opsin genes on the X chromosome and the S opsin gene on an autosome. Howler monkeys are considered to have a similar M/LWS opsin gene organisation as them, but the order of the L and M opsin genes remains unknown. Most New World monkeys and some lemurs have two or more M/LWS opsin alleles of a single locus. Three alleles are shown here. Many prosimians have a single M/LWS opsin locus with no allelic variation

opsin copies are common among Old World monkeys and apes (Ibbotson et al. 1992; Dulai et al. 1994; Hiwatashi et al. 2011).

The uniquely high prevalence of colour vision deficiencies expressed in humans may therefore indicate the relaxation of selection pressure during human evolution against the gene deletion and conversions in the coding region that affect “normal” trichromatic vision (Hiwatashi et al. 2011). This may be due, for example, to a shift from forest to savannah dwelling or increased food sharing and cooperative foraging. Alternatively, red–green colour vision deficiencies may have had fitness benefits (see Sect. 13.3.3).

The selective pressures leading to primate trichromacy are under considerable debate and may differ between routine and polymorphic systems. In the following sections we describe hypotheses of balancing selection maintaining polymorphic trichromacy, review the debate on the uses of primate colour vision, and offer suggestions for future research.

13.3.1 Balancing Selection Models for Colour Vision Polymorphisms in New World Monkeys

We recently investigated the pattern of nucleotide variation of the M/LWS opsin gene in wild populations of New World (capuchin and spider) monkeys in Costa Rica (Santa Rosa Sector of the Área de Conservación Guanacaste) and found that the M/LWS opsin gene was significantly more polymorphic than the neutral references in the same samples. Our population-genetic analysis, including

a coalescence simulation and evaluation of Tajima's D statistic, provided the first explicit evidence for balancing selection maintaining the polymorphism of the M/LWS opsin gene in New World monkeys (Hiwatashi et al. 2010). However, the mechanism(s) maintaining opsin gene polymorphisms remains unclear. Four hypotheses have been proposed to explain the persistence of allelic trichromacy (Mollon et al. 1984). Evaluating among these hypotheses is difficult, in part because measuring the pertinent behavioural and fitness consequences among wild primates is time consuming and challenging, and also because the predictions generated by these hypotheses are not mutually exclusive. We briefly review these four hypotheses below and comment on the research that has been done to date to evaluate them.

The heterozygote advantage hypothesis predicts that the fitness of heterozygous females (trichromats) will exceed the fitness of all dichromats and is the hypothesis most commonly proffered to explain primate colour vision polymorphism (e.g. Caine and Mundy 2000; Surridge and Mundy 2002). Also known as heterosis or overdominance selection, this mechanism maintains a stable polymorphism if trichromatic females have a consistent advantage for activities affecting their reproductive success. For example, trichromats are predicted to have foraging advantages (see Sect. 13.3.2), which could lead to better health and shorter inter-birth intervals. This hypothesis has received considerable support from experiments on captive monkeys (e.g. Smith et al. (2003)) and theoretical models (Osorio and Vorobyev 1996; Sumner and Mollon 2000a; Regan et al. 2001).

The other three mechanisms of balancing selection each predict that multiple alleles are maintained via selection favouring the persistence of multiple phenotypes in the population. Negative frequency-dependent selection (NFDS) predicts the fitness of any given phenotype to be reciprocal to the frequency of that phenotype in the population. In such cases, individuals with uncommon phenotypes would have higher fitness. For example, NFDS is generally invoked for predator–prey interactions, where less common phenotypes experience reduced predation pressure (Punzalan et al. 2005; Olendorf et al. 2006), or in a disassortative mating system, where mating with a different type from oneself in terms of the genetic trait in question has fitness gains (Conner and Hartl 2004). This hypothesis is often confounded with the niche-divergence hypothesis. However, under the niche-divergence scenario the population size of each phenotype can fluctuate independently of each other and irrespectively of its frequency. This is because individuals with different phenotypes exploit different resources or niches and population size of the phenotype changes as the carrying capacity of their niche changes and not as population size of another phenotype changes.

The niche-divergence hypothesis predicts that individuals of each phenotype will specialise in a distinct visual niche, such as foraging in open versus closed canopy conditions, or ecological niche, such as foraging for different types of food (Mollon et al. 1984). Few studies have yet evaluated the niche divergence hypothesis, although several have found differences in foraging strategies between individuals with different colour vision phenotypes (Regan et al. 2001; Yamashita et al. 2005; Leonhardt et al. 2009), which would be a natural precursor to niche

separation. However, our study on the foraging behaviour of the free-ranging capuchin monkeys did not find niche divergence among different colour vision phenotypes although the scale evaluated was rather coarse and differences on a finer scale may be present (Melin et al. 2008).

An extension of the niche-divergence hypothesis is to predict varying benefit to individuals possessing different M/LWS allelic composition. For trichromats, red–green colour discrimination would be greatest in individuals having the longest and the shortest wave-sensitive M/LWS alleles than in individuals having an intermediate wave-sensitive allele. On the other hand, for dichromats, the blue–yellow colour resolution would be worst in individuals having the shortest wave-sensitive M/LWS allele and be best having the longest wave-sensitive allele. Thus, the longest wave-sensitive allele would be favoured by both trichromats and dichromats, whereas the shortest one would be at a balance between the benefit for the trichromats and the cost for the dichromats (Osorio et al. 2004). Hence, different alleles could be maintained by different demands for them among vision types. Indeed, our study on the wild populations of capuchin and spider monkeys (Hiramatsu et al. 2005) and others on spider and woolly monkeys (Jacobs and Deegan II 2001) and muriquis (Talebi et al. 2006) have found the longest wave allele most frequent. We also found that foraging accuracy for figs in free-ranging capuchin monkeys was highest in trichromats with the widest spectral separation between M/LWS alleles (Melin et al. 2009). However, in squirrel monkeys and callitrichines (tamarins and marmosets), the prevalence of the longest wave-sensitive allele is not obvious (Cropp et al. 2002; Surridge et al. 2005).

The final hypothesis proposed is mutual benefit of association, which predicts that individuals benefit from being associated with individuals of other phenotypes in a polymorphic group. In other words, the fitness of individuals living in a polymorphic group would be greater than that of individuals living in homogeneous groups where all individuals had the same phenotype. This has been hypothesised to explain human colour vision polymorphism (Morgan et al. 1992). Given that early humans lived in small groups and engaged in hunting and gathering lifestyles, if dichromatic humans could break the camouflage of prey or predators, they would have been valuable group members, which may have affected their fitness. Trichromatic group members would benefit from living with dichromats and likewise, dichromatic humans would also have benefited from the presence of trichromats in the group, if the latter could extend the types of resources or threats that could be discriminated. However, no studies directly testing the mutual benefit hypothesis have been conducted on human or non-human primates to date.

13.3.2 Hypotheses on Advantages on Trichromatic Vision

13.3.2.1 Recognition of Social Signals

While our understanding of primate colour vision has grown in recent years, hypotheses regarding the selective pressures remain a subject to debate. The social signalling hypothesis posits that trichromacy is advantageous for discriminating emotional states, health, sexual signals or threat displays of conspecific animals via fluctuations in skin or pelage colour. In support of this hypothesis, Changizi et al. (2006) found that trichromats were more sensitive to spectral modulation of the skin of conspecific animals. These authors also suggest that primates with trichromatic vision tend to have more bare skin and less hair to facilitate signalling in accordance with their increased sensitivity. Thus, they argue that social signalling may be an important selective pressure influencing the expression of colour vision. However, social signals may not have been the source of initial selective pressure. A recent study places the evolution of reddish social signals through pelage or skin *after* the evolution of primate trichromacy (Fernandez and Morris 2007). Fernandez and Morris suggest that the pre-existing capacity for trichromacy helped to drive the evolution of reddish signals via gregarious mating systems and sexual selection.

13.3.2.2 Detection of Predators

Trichromats may alternatively have an advantage for detecting predators in the forest (Caine 2002; Miller 2002). For example, most species of large felids that prey on wild primates and have yellowish pelage that would be more conspicuous to a trichromatic than to a dichromatic viewer against green foliage. In a study of wild mixed-species troops of saddleback (*Saguinus fuscicollis*) and moustached (*S. mystax*) tamarins, trichromats space themselves further from their neighbours than their dichromatic conspecifics do during vigilance, which is suggested to be indicative of better perception of predation risk by trichromats (Smith et al. 2005). However, given the elusive behaviours of wild felids and the rarity of attacks on primates, this hypothesis is generally difficult to test and there have been no studies published to date that directly measure whether trichromats are less susceptible to predation.

13.3.2.3 Foraging on Foods

Fruit hypothesis. The remaining hypothesis predicts that the utility of colour vision lies in detection and selection of food items in natural scenes. This has received by far the most attention in the colour vision literature. The hypothesis that primate trichromacy is adaptive for finding ripe fruit against a mature leaf background was

founded over 130 years ago (Allen 1879). Fruit colour is often correlated with other characteristics of the fruit such as size, number of seeds, type of flesh, hardness and amount of edible tissue (Gautier-Hion et al. 1985; Willson and Whelan 1990; Leighton 1993; Tamboia et al. 1996; McConkey et al. 2002). Such characteristics may differentially attract the animals that most effectively disperse the seeds for given plant species. Primates are often effective seed dispersers (Chapman and Russo 2007; Valenta and Fedigan 2009) and many studies on primate fruit selection list colour as an important characteristic of fruit selectivity by primates (Sourd and Gautier-hion 1986; Julliot 1996; McConkey et al. 2002, 2003; Urbani 2002). Colour may also signal nutritional quality (concentrations of sugars), not only intraspecifically among fruits of varying ripeness (Sumner and Mollon 2000b), but also interspecifically (Riba-Hernández et al. 2005). If the colours of desirable fruits are more conspicuous to trichromats than to dichromats (e.g. red, orange or yellow), then trichromats should have an advantage for frugivory. In favour of this hypothesis, an analysis of the spectra of a wide variety of human-consumed fruits showed that the spectral separation of catarrhine L and M cones is near optimal for discriminating fruits from mature leaves (Osorio and Vorobyev 1996). This result was later supported by similar analyses of tropical fruits eaten by free-ranging monkeys and apes (Sumner and Mollon 2000a; Regan et al. 2001).

There have been, however, arguments against the frugivory hypothesis. Dominy et al. (2001) argue that many fruits can be distinguished from background leaves via the blue–yellow chromatic dimension or luminance dimension that is available to both di- and trichromatic primates. In support of this, our research on spider monkeys has revealed that achromatic contrast was an important determinant of foraging efficiency for both dichromatic and trichromatic phenotypes (Hiramatsu et al. 2008). Additionally, some fruits are not conspicuously coloured (e.g. green or brown), yet constitute a significant portion of primate diets, and fruit colour did not correlate consistently with nutritional reward in a study of the frugivorous diets of the primates of Kibale Forest, Uganda (Dominy 2004). These less conspicuously coloured fruits are also usually more odiferous, and we have found that both capuchins and spider monkeys rely more heavily on their sense of smell when foraging for greenish coloured fruits (Hiramatsu et al. 2009; Melin et al. 2009). The extent to which (1) “conspicuous” versus “non-conspicuous” fruits are important in primate diets; and (2) olfaction and luminance contrast are useful, or can compensate for chromatic deficiencies, during fruit foraging remain to be determined and future research in these areas will facilitate ongoing evaluation of the fruit hypothesis.

Young leaf hypothesis. A variation on the foraging hypothesis is that trichromacy is an adaptation for feeding on young leaves. According to this hypothesis, young leaves provide a critical fallback resource during periods of fruit shortage (Lucas et al. 1998). Regardless of tree species, young leaves are preferable to mature ones as they are tender and rich in proteins as well as free amino acids (Dominy and Lucas 2001). Young leaves are more red in hue than greenish mature leaves and distinguishable via the red–green colour channel available to trichromats. Therefore, the ability to discern between young and mature leaves may have been a major selective force for primate trichromacy (Lucas et al. 2003). The young leaf hypothesis is

strengthened in the context of the historical biogeography of figs and palms. Cryptic figs and palms are an important resource for many neotropical primates. They are non-seasonal and thus provide food during periods of low overall fruit availability. Furthermore, given their green/brown colouration they are not likely to present a disadvantage to dichromatic primates. Alternatively, figs and palms are relatively scarce in Africa, where catarrhine evolution occurred (Fleagle 1999). During times of fruit scarcity, routine trichromatic vision may have evolved to facilitate exploitation of reddish proteinaceous young leaves as a replacement. However, the young leaf hypothesis does not provide an explanation for the evolution and maintenance of trichromacy outside Africa. In fact, many of the small-bodied neotropical monkeys rarely, if ever, consume leaves.

Protein-limitation hypothesis. Recently, Valenta and Melin ([in press](#)) have suggested that efficient detection of proteinaceous foods—either leaves or fruit—has favoured the evolution of trichromacy among primates. These authors suggest that primates are often protein-limited and emphasise the importance of efficiently detecting reddish protein-rich vegetative foods. They identify the importance of reddish figs (neotropics) and young red leaves (paleotropics), which provide a key source of protein to primates year-round. This hypothesis serves to unify the fruit and folivory hypotheses, but has yet to be systematically evaluated.

13.3.2.4 Vision in the Greenish Forest

Colourimetric measurements of natural forest scenes reveal that the chromaticity of mature leaves falls in a very narrow range along the red–green chromatic axis but spreads widely along the blue–yellow axis and also varies strongly in luminance. Thus, chromaticity of fruits, young leaves (or biologically relevant non-food items, such as pelage and skin) often deviate from mature leaves principally along the red–green axis. This leads to the prediction that trichromat advantage is manifested for detecting *anything* differing from the background foliage in red–green contrast (Sumner and Mollon 2000a, 2003; Regan et al. 2001).

In this hypothesis, viewing distance may be important because at long viewing distances in a forest the scene contains greater blue–yellow and luminance variation than would a closer, more homogeneous view. In addition, during close viewing, other sensory cues, such as odours, are available and visual cues may be relied on less (Regan et al. 2001). However, psychophysical studies suggest that the human visual system is more sensitive to low spatial frequencies of chromatic spatial modulation than to luminance spatial modulation (Mullen 1985) and the spatiochromatic properties of human red–green colour vision may be optimised for the encoding of any reddish or yellowish objects from mature leaves at relatively small viewing distances, commensurate with a typical grasping distance (Parraga et al. 2002). Field studies that aim to test the effect of viewing distance on trichromatic advantage would help to identify the interplay between viewing distance and colour vision, and will hopefully be forthcoming in future research efforts.

13.3.3 Advantages of Dichromatic Vision

Uniform dichromacy is the norm in many lemurs, including many diurnal species that possess a single, monomorphic M/LWS opsin gene (Tan et al. 2005), as is the case with most placental mammals. Even in primate species with polymorphic trichromacy, the majority of the individuals are dichromats due to the high proportion of males and homozygous females in polymorphic populations. Colour vision deficiencies are also common in humans. There are at least two possible explanations for the high occurrence of dichromacy among primates. The first explanation is that routine trichromacy *would be* advantageous in polymorphic non-human primates but a gene duplication event has not occurred. In the case of humans, the decrease in trichromacy could indicate that the selective pressures maintaining trichromacy in humans were relaxed (SurrIDGE et al. 2003). The alternative hypothesis is that natural selection has favoured the persistence of dichromats. The later possibility implies that dichromacy may confer an advantage over trichromacy, at least occasionally, in humans and non-human primates.

Psychophysical studies conducted on human observers have revealed a potential advantage of dichromatic vision over trichromatic. Morgan et al. (1992) tested for differences among human observers after reviewing anecdotal reports, first appearing during the Second World War and continuing thereafter, suggesting that colour-deficient men were more able to penetrate military and natural-world camouflage. The work of Morgan et al. supports the hypothesis that dichromats can break camouflage. They found that dichromatic humans had a superior ability to detect boundaries between textured regions in the presence of random colour variegation. The visual system can only perceptually segment an image by one type of information at a time and chromatic information cues are generally important for pre-attentive segmenting of scenes. Therefore, the disadvantage of trichromacy arises because an enhanced ability to detect colours may inhibit the ability to differentiate between targets and backgrounds that differed in texture or luminance. Because dichromats make fewer chromatic distinctions, they may be less susceptible to chromatic interference and would be able to use achromatic cues more effectively.

Penetrating camouflage may be an important real-world challenge that non-human primates must frequently overcome. For example, some primate predators, such as snakes, use crypsis to help avoid detection by their prey (Isbell 2009). In foraging situations, camouflage-breaking ability would be useful for detecting prey, specifically palatable, exposed invertebrates, which are often camouflaged (Lev-Yadun et al. 2004; Gullan and Cranston 2005; Endler 2006). Our experimental study on captive, non-human primates found that dichromats have an enhanced ability to break camouflage (Saito et al. 2005). Our studies on free-ranging capuchins and other studies on tamarins found that dichromatic monkeys ate more camouflaged invertebrates than their trichromatic counterparts and that dichromatic monkeys outperform trichromats when foraging for insects in shaded conditions (Buchanan-Smith et al. 2005; Melin et al. 2007, 2010; Caine et al. 2010). Dichromatic marmosets are also predicted to outperform trichromats under low light conditions when foraging for some fruits (Perini et al. 2009)

13.4 Conclusion

Primate colour vision is unique among vertebrates in its evolutionary history. The form of trichromacy found uniquely in primates was generated from ancestral dichromacy via allelic differentiation or gene duplication of the M/LWS type opsin gene. Polymorphic colour vision is maintained by balancing selection in New World monkeys and uniform trichromacy is maintained by purifying selection in most Old World primates, with the possible exception of humans. But there is still controversy concerning the advantages of trichromatic colour vision and of polymorphic colour vision. Additionally, a deeper knowledge of the functional significance of colour vision in non-human primates will help us to understand the selective pressures acting on colour vision in our own species. Studies of New World monkeys are particularly important to this goal due to their extensive colour vision polymorphisms. We anticipate that further interdisciplinary studies on genes, physiology and behaviour will provide a wealth of data for increasing our understanding of the evolution of colour vision and will generate important advances in the near future.

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