INVITED REVIEW

Ecology and evolution of primate colour vision

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More than one hundred years ago, Grant Allen suggested that colour vision in primates, birds and insects evolved as an adaptation for foraging on colourful advertisements of plants—fruits and flowers. Recent studies have shown that well developed colour vision appeared long before fruits and flowers evolved. Thus, colour vision is generally beneficial for many animals, not only for those eating colourful food. Primates are the only placental mammals that have trichromatic colour vision. This may indicate either that trichromacy is particularly useful for primates or that primates are unique among placental mammals in their ability to utilise the signals of three spectrally distinct types of cones or both. Because fruits are an important component of the primate diet, primate trichromacy could have evolved as a specific adaptation for foraging on fruits. Alternatively, primate trichromacy could have evolved as an adaptation for many visual tasks. Comparative studies of mammalian eyes indicate that primates are the only placental mammals that have in their retina a pre-existing neural machinery capable of utilising the signals of an additional spectral type of cone. Thus, the failure of non-primate placental mammals to evolve trichromacy can be explained by constraints imposed on the wiring of retinal neurones.

Human beings and other Old World primates, such as great apes, baboons and the macaque monkey, are cone trichromats, having short- (S), middle- (M) and long- (L) wavelength cones peaking around 440, 530 and 560 nm, respectively (Figure 1)[1,2] but non-primate placental mammals are typically dichromats, having only S and L cones.[3] Old World primates evolved trichromacy from their dichromatic ancestors approximately 40 million years ago, by the duplication of a gene coding for the L cone visual pigment.[3-5] To understand the benefits of primate trichromacy,

we need to compare primate colour vision to that of other animals. While primates have a more sophisticated colour vision than non-primate mammals, colour vision in many non-mammalian vertebrates is likely to be better developed than ours. Fish, reptiles and birds often have four cone visual pigments.[6-10] Behavioural studies have shown that goldfish, turtle and birds use four cone types for colour vision and that signals of these cones are combined to produce tetrachromatic colour vision.[11-14] Many invertebrates have more than three spectral photoreceptor types.

It is probable that the most sophisticated colour vision has been developed by stomatopod crustaceans—mantis shrimps. These shrimps have 16 spectral types of photoreceptor cells, 12 of which are used for colour vision.[15,16]

## EVOLUTIONARY HISTORY OF VERTEBRATE COLOUR VISION

Modern vertebrates belong to two distinct lineages. Jawed vertebrates include fish, amphibians, reptiles, birds and mammals. Lampreys and hagfishes are the only liv-

ing jawless vertebrates.[17] The origin of lampreys dates back to early Cambrian, approximately 540 million years ago.[18] Molecular analyses have shown that cone visual pigments of jawed vertebrates belong to four distinct classes.[4,5] Recently, the same classes of cone visual pigments were found in a jawless vertebrate, lamprey *Geotria australis*.[19,20] This finding indicates that four visual pigments were present in the eyes of early vertebrates before the divergence of jawed and jawless forms. Therefore, early vertebrates could have had tetrachromatic colour vision more than 540 million years ago.

Terrestrial vertebrates improved their ancient tetrachromatic vision by evolving retinal coloured filters—oil droplets.[21] These retinal filters reduced the overlap in sensitivity between spectrally adjacent cones and hence, increased the number of discriminable colours.[22,23] Coloured oil droplets are present in eyes of diurnal birds, reptiles and in the closest living relative of first terrestrial vertebrates—the lungfish.[24,25] Thus, coloured oil droplets and four cone pigments were probably present in the retina of a common ancestor of all terrestrial vertebrates and lungfishes approximately 400 million years ago.[17] Coloured oil droplets and some visual pigments were later lost in many groups of fish and of terrestrial vertebrates.[21,26-28] Most placental mammals are dichromats, because our ancestors lost two spectral types of cones, when they became nocturnal.[21,26] Some nocturnal primates (owl monkeys and bushbabies) and marine mammals do not have functional gene coding S cone pigment and thus, are cone monochromats having only one type of L cone.[29,30]

While the loss of visual pigments occurred many times, the duplication of cone visual pigment occurred only a few times during the past 540 million years of the evolution of vertebrate colour vision.[4,5] Among terrestrial vertebrates duplication of genes coding cone visual pigments has been described only in primates and recently in a megabat, *Haplonycteris fischery*.[31] Duplication of a gene coding L cone visual pigment leading to uniform trichromacy of Old World primates probably occurred after the separation of New and Old World
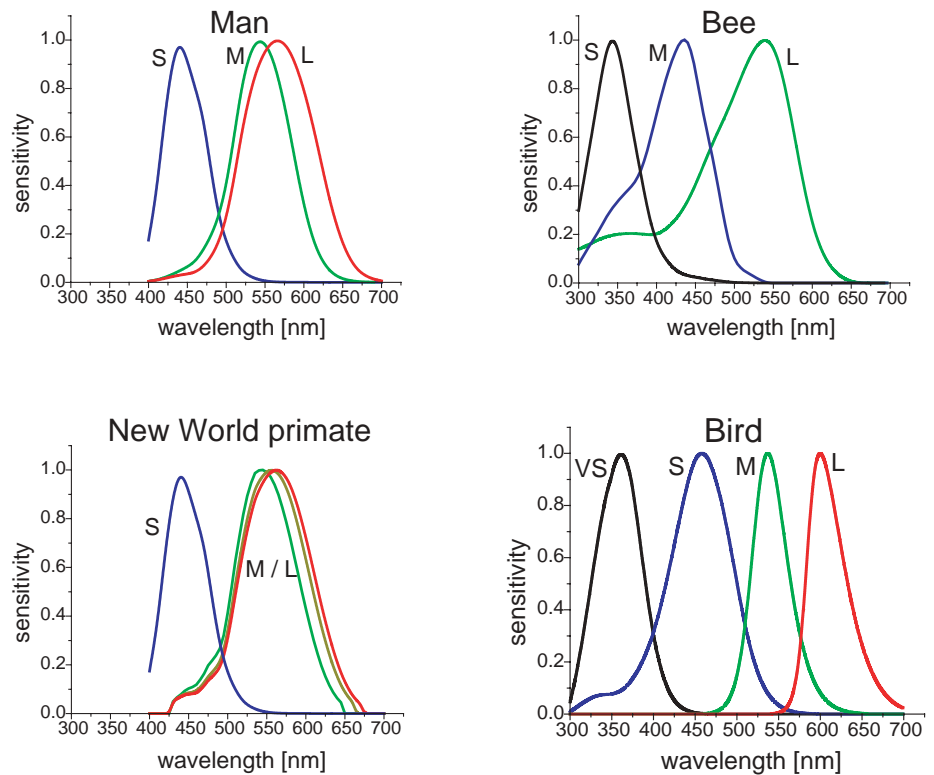
Figure 1. Photoreceptor spectral sensitivities of a human,[92] New World monkey (the common marmoset *Callithrix jacchus*),[87] the honeybee (*Apis melifera*)[51] and a bird (blue tit, *Parus caeruleus*).[93] The New World monkey has three L/M visual pigments. Note that the spectral sensitivities of L and M pigments in primates strongly overlap but both bees and birds have largely non-overlapping spectral sensitivities. In diurnal birds and reptiles, cone sensitivities are narrowed due to light filtering in coloured oil droplets.

primates, approximately 40 million years ago.[4,5,32,33] Uniform trichromacy evolved independently in one species of New World primates—the howler monkey.[34,35] Other New World primates do not have uniform trichromacy but have polymorphic genes coding for M and L cone pigments.[4,5,33,35-37] Also, some lower primates (prosimians), such as lemurs, have polymorphic L cone genes.[38] Several hypotheses have been proposed to explain the reasons leading to the origins of primate trichromacy and of colour vision in general.[33,39-45] Probably, the most popular hypothesis is that colour vision evolved as an adaptation for foraging on colourful objects, such as fruits and flowers.[33,39,40,44-48]

COLOUR VISION AS AN ADAPTATION FOR FORAGING ON COLOURFUL OBJECTS

A hypothesis that colour vision in insects, birds and mammals co-evolved with flowers and fruits was first formulated in the late 19th Century by a prominent Canadian writer, Grant Allen.[39] He stated this hypothesis in the following condensed formula: 'Insects produce flowers. Flowers produce the colour-sense in insects. The colour-sense produces a taste for colour. The taste for colour produces butterflies and brilliant beetles. Birds and mammals produce fruits. Fruits produce a taste for colour in birds and mammals. The taste for colour produces the

external hues of humming-birds, parrots and monkeys. Man's frugivorous ancestry produces in him a similar taste and that taste produces the final result of human chromatic arts.' From the supposition that colour vision co-evolved with flowers and fruits, it follows that animals foraging on colourful fruits or flowers must have well-developed colour vision, while animals dependent on other food sources must have less developed or no colour vision.

When Allen proposed the explanation of the origin of colour vision and colours of plants and animals, the knowledge about colour vision of animals was based predominantly on the observations of animals' habits and colouration. For example, brightly coloured feathers of birds indicated that they have developed colour vision.[39] During the past three decades, a large body of data on visual pigments and photoreceptor spectral sensitivities in a variety of animals has been accumulated.[4,5,10,20,49,50]

The analysis of these data does not support the hypothesis of co-evolution of colour vision in insects and birds with colours of flowers and fruits. Frugivorous birds have cone sensitivities that are similar to those of a turtle foraging on green and brown objects,[8-10] and photoreceptors in flower-foraging bees are practically identical to those in predatory wasps.[51] A discovery of multiple cone pigments in lamprey[19] and of coloured oil droplets in lungfish[24,25] indicates that well-developed colour vision in vertebrates appeared long before fruits and flowers.

However, primates evolved trichromacy from their dichromatic ancestors after fruits advertised to the eyes of birds appeared,[52] so primate trichromacy could have emerged as a specific adaptation for finding fruits. Later, fruits could have adapted their colour to the vision of primates, leading to co-evolution of primate colour vision and colours of fruit.[33] Analyses of reflectance spectra of fruits and leaves seem to provide evidence in favour of this hypothesis.[44,46-48] Alternatively, primate colour vision could have evolved as an adaptation for many visual tasks, rather than solely for looking at fruits.

BENEFITS OF COLOUR VISION

Humans and animals often need to detect and recognise objects in conditions of patchy and changing illumination. This problem can be solved by comparing the signals of receptors tuned to different parts of the spectrum, that is, by using chromatic vision.[42,43] Shadows generally yield strong variations in the intensity of illumination and hence, change signals of different spectral types of cones by nearly the same factor. Thus, division of cone signals (or subtraction of their logarithms) gives the value that remains invariant when the intensity of illumination varies.[53] Real colour vision systems probably use chromatic signals that approximate such a 'cone ratio model'.[53] Patchy illumination is common in forests and in shallow water, where refraction of light on the surface of water yields strong variations in the illumination.[33,43] Colour vision in the first vertebrates could have appeared as an adaptation to patchy light in their shallow aquatic habitat.[43] Forest dwelling animals, such as many primates, probably use colour vision to detect, segregate and discriminate unevenly illuminated objects.[33] In the case of uniform illumination, colour vision helps us to detect objects against dappled background, such as fruits on the background of differently oriented leaves.[33]

Colour also serves for the identification of object properties; for example, fruits can be categorised according to their colour.[33] While the use of colour for detection, segregation and discrimination of objects requires simple comparison of chromatic (cone ratio) signals, a more complex processing of receptor signals is needed for object identification.[54] Surface colours depend on surface reflectance and on spectral distribution of the illuminant.[54] To identify objects under conditions of changing illumination, we need to extract the information about the reflectance spectra and ignore colour changes caused by the spectral variations of the illuminant, that is, we need to perceive colours constantly.[54] Human beings and many animals have colour constancy,[54-56] and many algorithms have been proposed to explain this phenomenon.[53,54,57-59] However, we do not know how these algorithms are implemented in human retina and brain. Moreover, we do not know which algorithm(s) of colour constancy humans use.[54,60]

BENEFITS OF PRIMATE TRICHROMACY

Approximately two per cent of the human male population are cone dichromats, lacking either L (protanopes) or M (deuteranopes) cones.[61] Such vision is probably similar to that of our dichromatic ancestors. Analysis of difficulties in colour perception experienced by dichromats may reveal the benefits of trichromacy. The first detailed description of colour deficiency caused by the lack of a cone visual pigment was given at the end of the 18th Century by John Dalton, who was colour deficient. Thinking that his abnormal colour perception was caused by a blue filter in his eye, Dalton gave instructions that his eyes should be examined on his death (1844). However, Dalton's aqueous and lens appeared to be normal for a person of his age.[62] Recent molecular studies on the preserved tissue from John Dalton's eye showed that Dalton lacked the M cone pigment and therefore, was a deuteranope.[62] Dalton first suspected that his colour perception was abnormal when he was 20 years old.[62,63] Usually dichromats become aware of their colour deficiency relatively late in life or when they fail in specially designed tests. From this, we can conclude that in everyday life many visual tasks can be solved using only two spectral types of cones. Moreover, the evolutionary success of dichromatic mammals indicates that dichromacy is sufficient for solving many visual tasks in a variety of habitats.

The most obvious disadvantage of dichromacy is the inability to discriminate some colours that normal trichromats easily perceive as different, such as particular shades of green, yellow, orange and red. This leads to difficulties in detecting red, orange and yellow fruits against a dappled background of leaves. As fruits play an important role in primate diet,

trichromacy could have evolved as a specific adaptation for finding food.[33,39,40] Theoretical work also shows that trichromats must outperform dichromats in estimating the state of ripeness of fruits on the basis of their colour.[64] Another biologically important set of reddish colours is produced by the colour of blood. The inability to detect blood in stools or other samples creates difficulties for dichromatic medical practitioners.[65] Dichromats also fail to discriminate variations in skin colour related to illness.[66] As the colour of skin helps us to estimate emotional state or the state of health, the reduced ability of dichromats to perceive slight changes in skin colour may disadvantage them in social interactions. Many primates have red sexual displays. [67] For example, around the time of ovulation, females of many Old World monkeys and hominoids develop a prominent reddening of the sexual skin around the perineum.[67] Therefore, sexual selection could also play a role in evolution of primate trichromacy.

The loss of a spectral type of cone impairs the ability to categorise colours. In general, trichromacy is advantageous for identification of objects on the basis of their colour. John Dalton wrote: 'I was always of the opinion, though I might not often mention it, that several colours were injudiciously named. The term *pink,* in reference to the flower of that name, seemed proper enough; but when the term *red* was substituted for pink, I thought it highly improper; it should have been *blue*, in my apprehension, as pink and blue appear to me very nearly allied; whilst pink and red have scarcely any relation'.[63] Dichromats cannot fully appreciate common colour naming, because they lack a perceptual dimension in their vision. Trichromatic colour has attributes of hue, saturation (chroma) and brightness (lightness). Lightness scales colours from dark to light, saturation scales colours from achromatic (shades of grey) to saturated colours, such as colours of monochromatic lights; hue gives the perceptual attribute of colour that remains relatively invariant when their lightness and chroma change.[54,68] Basic colour terms, such as red, green and blue, specify hue. Exceptions
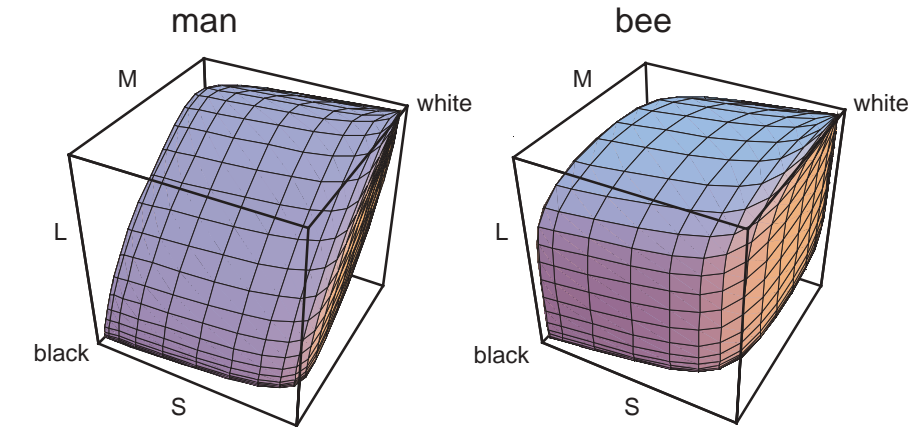
Figure 2. The spread of object colours in the colour spaces of a human and a bee. A colour is represented as a point in the space where the quantum catches of S, M and L photoreceptors are placed along the co-ordinate axes. Object colours occupy a part of this space—an object colour solid.[23,68] The volume of the object colour solid can be related to the total number of colours that a visual system can discriminate.[23] The object colour solid has one apex at the origin, which corresponds to an ideal black surface and the other at the corner corresponding to an ideal white reflector. If receptor sensitivities do not overlap, the object colour solid fills the entire cubic volume between these apexes. For overlapping receptor sensitivities, the object colour solid fills only a limited part of the cubic volume, so a visual system with largely non-overlapping photoreceptor sensitivities, such as that of bees,[45] is able to discriminate colours better than the visual system of a human. This approach does not take into account that some colours may be more important than others.

from this general rule are rare. For example, brown may be different from yellow only in its lightness; in Russian, unsaturated blue has a special term—'goluboy', while saturated blue is termed 'siniy'.[69]

In the colour space of dichromats, the colour of a spectrally flat light (achromatic) can be matched by a monochromatic light of a particular wavelength; this wavelength corresponds to the dichromatic confusion point.[68] Also, spectrally pure lights can be matched by the sum of a light of a particular wavelength and of a spectrally flat light.[68] Therefore, dichromats are able to categorise colours into only two hue categories. These two categories correspond either to the wavelengths shorter than that of a dichromatic confusion point or to those longer than this point. In contrast, trichromats are able to perceive a continuum of hues.

Of the three perceptual attributes of colour, hue gives the most reliable infor-

mation about the material properties of a reflecting surface. In conditions of patchy illumination, lightness is unreliable, because it may depend on the spatial distribution of the illuminant.[33] Saturation may also vary strongly depending on viewing conditions. Most objects have either rough or shiny surfaces, which means that, depending on the angles between the surface, illumination and observer, the amount of non-selectively (specularly) reflected light varies.[70] Therefore, the ability of trichromats to perceive a continuum of hues gives a reliable way to identify and categorise objects when illumination and viewing conditions vary.

Finally, primate trichromacy may be beneficial in conditions of dim light. Natural light has typically low photon flux in the short-wavelength part of the spectrum. Therefore, S cone mechanisms are insensitive in dim light,[68] so, at the light intensity where S cone mechanisms are insensi-

tive, dichromats cannot use chromatic vision, that is, utilise the L-S signal. Trichromats having both M and L cones potentially can compare signals of these cones and enjoy chromatic vision when the light is too dim for S cones. However, in conditions of dim light the increased photon noise might corrupt the opponent L–M signal and negate any advantage in chromatic vision enjoyed by trichromats. It is important to note that during dawn and dusk, the relative amount of the quantum flux in the short-wavelength part of the spectrum is high.[71] Therefore, it has been suggested that in twilight, mammals use S cones to maximise the contrast.[72]

COST OF TRICHROMACY FOR SPATIAL VISION

In dichromatic mammals, the density of L cones is significantly higher than the density of S cones. Hence, spatial vision is mediated either solely or mainly by L cones.[3] In humans, both L and M cones contribute to luminosity vision. This may be disadvantageous for spatial vision for two reasons.

1. In humans, the optics of the eye is matched to the resolution of the L–M cone mosaic.[73] Thus, the highest spatial resolution can be mediated by a single L or M cone. As L and M cones have different spectral sensitivities, the luminance signal depends on whether it is mediated by the L or the M cone. This adds noise to the high resolution luminance vision.[73] Random fluctuations in cone densities may also create noise for spatial vision at lower spatial resolutions.[73]

2. Due to chromatic aberrations, it is impossible at the same time to optimally focus light for cones peaking in different parts of the spectrum.[68] Therefore, where more than one spectral type of cone is used for spatial vision, the spatial resolution can be impaired.

It has also been suggested that dichromats may outperform trichromats in scotopic conditions,[74] although scotopic thresholds of dichromats appear to be similar to those of trichromats.[75] The advantage of dichromacy in mesopic conditions has not been excluded.[75]
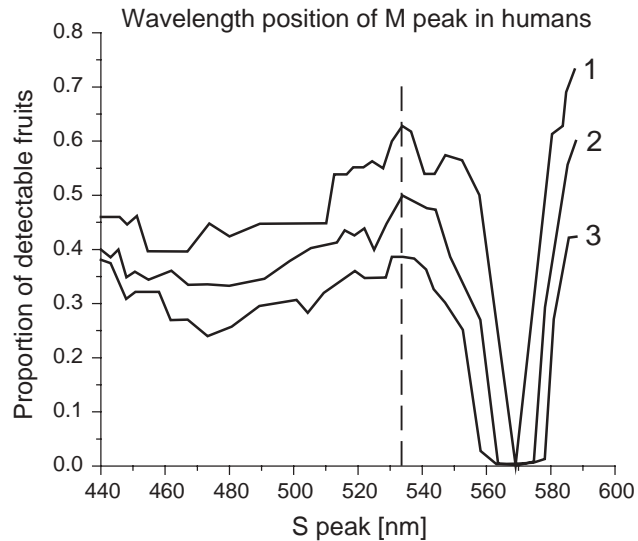
Figure 3. Detection of fruits against the dappled background of leaves by a dichromatic eye.[44] The L peak is held constant and the S peak is varied. The spectra of fruits available in European food stores were measured. A fruit was counted as detectable if its chromatic distance from every leaf is greater than a threshold distance. Calculations were for three thresholds corresponding to distances of 1, 2 and 3. With a fixed L pigment the number of detectable fruits reaches a maximum when the spectral position of the S cone is close to the position of the human M cone. Thus the spectral separation of L and M cones in humans is close to optimal for fruit detection using the signal of the [L–M] chromatic mechanism.

TUNING OF VISUAL PIGMENTS

While the sensitivities of primate L and M cones strongly overlap, most animals have largely non-overlapping spectral sensitivities.[26] For example, in diurnal birds and reptiles, cone sensitivities are narrowed by filtering the incident light with coloured oil droplets, which reduces the overlap between the spectrally adjacent cones.[8,10,21] Also, in bees the peaks of photoreceptor spectral sensitivities are placed roughly uniformly along the spectrum,[51] an arrangement that minimises the overlap between photoreceptor sensitivities. Mathematical modelling shows that reduction of spectral overlap generally increases the number of colours that can be discriminated (Figure 2).[22,23,45,76] Thus, the largely non-overlapping photoreceptor sensitivities of many animals could have been favoured by natural selection.

The overlap of primate L and M cones can be explained in several ways.

1. It can be a consequence of constraints imposed on the evolution of visual pigments. Because L and M visual pigments diverged relatively recently from the ancestral mammalian LWS/MWS pigment, their wavelength positions could not yet reach the optimal wavelength positions. Also, it could be impossible to evolve from the ancestral mammalian LWS/MWS pigment an M pigment peaking further towards the shorter wavelengths.[26] However, these explanations seem to be invalid, first, because the study of cone sensitivities in closely related fish species shows that the shift of spectral sensitivities can occur fast during evolution[28] and second, because some mammals have L cone pigment, the peak of which is shifted to the shorter wavelength, compared to human M peak (530 nm). For example, in rats it peaks at 510.[77]

Thus, it is likely that the spectral overlap of primate L and M cones was favoured by natural selection. As most animals have non-overlapping cone sensitivities,[26] the selective pressures determining the spectral positions of primate cones are likely to differ from those imposed on the evolution of colour vision in other animals.

2. While for colour vision it is beneficial to increase the spectral separation between cone sensitivities, the needs of spatial vision could lead to a decrease in the spectral separation between L and M cones. An analysis of spectra from natural scenes shows that the spectral position of human L and M cones reduces the difference between luminance signals yielded by L and M cones (see above) and hence, reduces the noise of high resolution luminance vision.[78] Chromatic aberrations could also keep the spectral positions of L and M cones close together (see above). It is important to note that fish[79] and birds[80] probably use only one spectral type of cone for luminance vision, namely the cone containing the long-wavelength sensitive (LWS) pigment. Hence, the spectral positions of other cones in fish and birds are not constrained by the needs of luminance vision.

3. Primate visual pigments could be tuned for looking at a particular set of objects. According to the hypothesis of Allen,[41] primate trichromacy is a specific adaptation for finding fruits.[33,39,40,44,46-48] An analysis of the spectra of fruits eaten by humans showed that the separation of L and M cones is close to optimum for detection of fruits against foliage[44] (Figure 3). This result was later confirmed by the analysis of spectra of primate edible fruits collected in the rainforest.[46-48] Having a reddish colour, young leaves also constitute an important component of the primate diet.[81] It has been suggested that primate trichromacy evolved as an adaptation for finding red leaves, rather than fruits.[82] Indeed, the only New World primate that evolved uniform trichromacy, the howler monkey,[34] forages predominantly on leaves.[81] However, as both fruits and leaves generally play an important role in primate diet, it is more likely that spectra of both fruits and red leaves affected the tuning of primate visual pigments.[83]

WHY NON-PRIMATE PLACENTAL MAMMALS ARE DICHROMATS

Primates are the only mammals that evolved trichromacy by duplication of a gene coding L pigment. This may indicate either that trichromacy is particularly useful for primates, that primates are unique among placental mammals in their ability to utilise the signals of three spectrally distinct types of cones, or both. Among mammals only primates have in their retina midget ganglion cells.[84] While in dichromatic primates these cells convey information about fine spatial details of the image, in trichromats they also convey colour opponent L–M signals.[85,86] The centre of the receptive field of midget ganglion cells may receive input from only one L or M cone, but its surroundings receive input from both L and M cells.[85,86] The comparison of the signal from the centre with that of the surrounding gives the colour opponent L–M signal. Thus, a neural pathway originally used for spatial vision has been utilised by trichromatic primates for the purpose of colour vision.[85,86] The absence of midget ganglion cells from the eyes of non-primate placental mammals[84] could have precluded them from evolving trichromacy.

COLOUR VISION IN NEW WORLD PRIMATES

Unlike Old World primates, most New World primates (platyrrines) do not have uniform trichromacy. Instead, they have polymorphic genes coding for M and L cone pigments.[32,35-37] Because the polymorphic gene is located on the X chromosome, males of New World primates (having only one X chromosome) are natural dichromats. They possess S cones and one type of M or L cone. Heterozygote females of New World primates, having two X chromosomes, possess, in addition to S cones, two spectrally different M and L cones.[32,35-37] One species of New World primate, the howler monkey, evolved uniform trichromacy by duplication of the gene coding L–M pigment independently from Old World primates.[34] In other New World primates, the polymorphic gene codes from

three to five L/M pigments.[32] Combinations of these pigments give several types of trichromacy in heterozygotic females. The trichromatic individuals having a broad spectral separation between L and M visual pigments are analogous to normal human observers; trichromats having narrow spectral separation between L and M pigments are analogous to human colour deficient trichromatic observers.

As in all primates, New World monkeys have midget ganglion cells in their retinae.[86] Thus, the signals of spectrally distinct L and M cones can be compared. Indeed, behavioural and physiological studies show that heterozygote females of New World primates have trichromatic vision.[86,87,89] The polymorphism of L/M visual pigments, rather than uniform trichromacy, in other New World monkeys, may indicate that this polymorphism is beneficial.[33] Alternatively, constraints other than the lack of midget ganglion cells may explain the absence of uniform trichromacy in New World primates and prosimians.

A possible benefit of the polymorphism of L–M pigments is that a population consists of individuals having different visual systems, which can have advantages in detecting different fruits. Hence, a polymorphic population may outperform a population of trichromats having identical cones.[33,47,48] However, analysis of spectra of fruits consumed by a New World monkey, the tamarine, showed that trichromatic individuals with a broad spectral separation between L and M visual pigments must detect better all fruits, indicating that a group of normal trichromats would detect fruits better than a polymorphic group (Osorio, Smith, Vorobyev, Buchanan-Smith, unpublished data). Therefore, the lack of uniform trichromacy in New World primates can be better understood as a consequence of evolutionary constraints.

To use trichromatic vision, it is essential to have:

1. An appropriate set of cones.
2. Retinal mechanisms that compare signals of different spectral types of cones and convey reliable opponent signals to the brain.

3. A brain capable of analysing trichromatic colour.

Comparative studies of the brain anatomy in an Old World primate (macaque) and a New World primate (marmoset) reveal the differences in the complexity of the cortical areas[89] that, in Old World primates, are involved in categorical colour perception (V4 and higher).[90] Such differences may explain the absence of uniform trichromacy in New World primates. The complexity of cortical areas can be estimated by counting the number of neurones and synapses.[89] As New World primates are small, their brains generally contain fewer neurones. While the density of synapses in the areas used for the lower level processing of visual information (V1, V2) is similar in Old and New World primates, the density of synapses in areas involved in categorical colour perception (V4 and higher) in an Old World primate is higher than the density in the corresponding areas of a New World primate.[89] In humans, categorical colour perception probably requires long-lasting maturation of synaptic connections—children learn colour names after they learn the names of basic shapes.[91] This may indicate that, in primates, categorical colour perception requires sophisticated processing of visual information. Complex area V4 of the visual cortex in Old World primates may provide a necessary neural basis for categorical colour perception of trichromatic colour.

CONCLUSION

Primate trichromacy could have evolved as a specific adaptation for finding colourful food or as an adaptation for a variety of visual tasks. The observation that primates forage on colourful fruits, while non-primate diurnal mammals mostly eat dull objects (for example, squirrels eat brown and grey nuts) favours the hypothesis that primate colour vision evolved as a specific adaptation for finding colourful food.[33,39,40] However, the fact that most non-mammalian diurnal vertebrates have more than two spectral types of cone indicates that well-developed colour vision is beneficial for many tasks. Non-primate

mammals could have failed to evolve trichromacy because of the constraints imposed on the processing of receptor signals. Among mammals, only primates have in their retina midget ganglion cells.[86] These cells form a pre-existing pathway for colour opponent L–M signals.

As the structure of the retina in New and Old World primates is similar, the absence of uniform trichromacy in New World primates cannot be explained by the constraints imposed at the level of retina. Also, it is unlikely that the differences between New and Old World primates can be explained by the differences in the colour of the food they eat. The less complex visual cortex could reduce the benefits of trichromacy for New World primates and preclude them from evolving uniform trichromacy. It is also possible that the gene duplication is a rare event that simply did not occur in the majority of New World primates.

REFERENCES
1. Bowmaker JK, Astell S, Hunt DM, Mollon JD. Photosensitive and photostable pigments in the retinae of Old World monkeys. *J Exp Biol* 1991; 156: 1-19.
2. Jacobs GH. Uniformity of colour vision in Old World monkeys. *Proc R Soc Lond B* 1999; 266: 2023-2028.
3. Jacobs GH. The distribution and nature of color vision among mammals. *Biol Rev* 1993; 68: 413-471.
4. Yokoyama S. Molecular evolution of vertebrate visual pigments. *Prog Retin Eye Res* 2000; 19: 385-419.
5. Jacobs GH, Rowe P.W. Evolution of vertebrate color vision. *Clin Exp Optom* 2004; 87: 206-216.
6. Bowmaker JK. Visual pigment absorbance and scotopic spectral sensitivity in the goldfish, *Carassius auratus. Rev Can Biol* 1979; 38: 185-187.
7. Bowmaker JK, Thorpe A, Douglas RH. Ultraviolet-sensitive cones in the goldfish. *Vision Res* 1991; 31: 349-352.
8. Loew ER, Govardovskii VI. Photoreceptors and visual pigments of the red-eared turtle, *Pseudemis scripta elegans. Visual Neurosci* 2001; 18: 753-757.
9. Govardovskii VI, Zueva LV. Visual pigments of chicken and pigeon. *Vision Res* 1977; 17: 150-159.
10. Hart NS. The visual ecology of avian photoreceptors. *Prog Retin Eye Res* 2001; 20: 675-703.
11. Neumeyer C. An ultraviolet as a fourth receptor type in goldfish colour vision. *Naturwissen* 1985; 72: 162-163.
12. Arnold K, Neumeyer C. Wavelength discrimination in the turtle *Pseudemys scripta elegans. Vision Res* 1987; 27: 1501-1511.
13. Palacios AG, Varela FJ. Color mixing in the pigeon (*Columba livia*), II: A psychophysical determination in the middle, short and near-UV wavelength range. *Vision Res* 1992; 32: 1947-1953.
14. Osorio D, Vorobyev M, Jones C. Colour vision in domestic chick. *J Exp Biol* 1999; 202: 2951-2959.
15. Cronin TW, Marshall NJ. A retina with at least ten spectral types of photoreceptors in a mantis shrimp. *Nature* 1989; 339: 137-140.
16. Marshall NJ, Oberwinkler J. The colourful world of the mantis shrimp. *Nature* 1999; 401: 873-874.
17. Long JA. The Rise of Fishes. Sydney: University of New South Wales Press; 1995.
18. Shu DG, Morris SC, Han J, Zhang ZF, Yasui K, Janvier P, Che L, Honeycutt RL, Tsao H, Li WH, Chen L, Zhang XL, Liu JN, Li Y, Liu HQ. Head and Backbone of the early Cambrian vertebrate *Haikouichthys. Nature* 2003; 421: 526-529.
19. Collin SP, Knight MA, Davies WL, Potter IC, Hunt DM, Trezise AEO. Ancient colour vision: multiple opsin genes in the ancestral vertebrates. *Curr Biol* 2003; 13: R864-R865.
20. Collin SP. The origins of colour vision in vertebrates. *Clin Exp Optom* 2004; 87: 217-223.
21. Walls GL. The Vertebrate Eye and Its Adaptive Radiation. Granbrook Institute of Science; 1942.
22. Govardovskii VI. On the role of oil drops in color vision. *Vision Res* 1983; 23: 1739-1740.
23. Vorobyev M. Coloured oil droplets enhance colour discrimination. *Proc R Soc Lond B* 2003; 270: 1255-1261.
24. Robinson SR. Early vertebrate color vision. *Nature* 1994; 367: 121.
25. Marshall NJ, Collin SP, Hart NS, Vorobyev M, Bales HJ. Visual ecology of the Australian lung fish *Neoceratodus forstery*. In: Proceedings of the Australian Neuroscience Society 2004; 15: ORAL-02-0.
26. Goldsmith TH. Optimization, constraint, and history in the evolution of eyes. *Q Rev Biol* 1990; 65: 281-322.
27. Lythgoe JN. The Ecology of Vision, Oxford: Claredon Press; 1979.
28. Bowmaker JK, Govardovskii VI, Shukolyukov SA, Zueva LV, Hunt DM, Sideleva VG,

Smirnova OG. Visual pigments and the photic environment: the cottoid fish of Lake Baikal. *Vision Res* 1994; 34: 591-605.

29. 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 B Biol Sci* 1996; 263: 705-710.

30. Fasick JI, Cronin TW, Hunt DM, Robinson PR. The visual pigments of the bottlenose dolphin (*Tursiops truncatus*). *Vis Neurosci* 1998; 15: 643-651.

31. Wang D, Oakley T, Mower J, Shimmin LC, Yim S, Honeycutt RL, Tsao H, Li WH. Molecular evolution of bat color vision genes. *Mol Biol Evol* 2004; 21: 295-302.

32. Hunt DM, Dulai KS, Cowing JA, Julliot C, Mollon JD, Bowmaker JK et al. Molecular evolution of trichromacy in primates. *Vision Res* 1998; 38: 3299-3306.

33. 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.

34. Jacobs GH, Neitz M, Deegan JF, Neitz J. Trichromatic colour vision in New World monkeys. *Nature* 1996; 382: 156-158.

35. Jacobs GH, Bowmaker JK, Mollon JD. Behavioural and microspectrophotometric measurements of colour vision in monkeys. *Nature* 1981; 292: 541-543.

36. Mollon JD, Bowmaker JK, Jacobs GH. Variations in colour vision in a New World primate can be explained by polymorphism of retinal photopigments. *Proc R Soc Lond B* 1984; 222: 373-399.

37. Bowmaker JK, Jacobs GH, Mollon JD. Polymorphism of photopigments in the squirrel monkey: a sixth phenotype. *Proc Soc Lond B* 1987; 231: 383-390.

38. Tan Y, Li WH. Trichromatic vision in prosimians. *Nature* 1999; 402: 36.

39. Allen G. The Colour-sense: Its Origin and Developement. London: Trubner & Co; 1879.

40. Polyak S. The Vertebrate Visual System. Chicago: University of Chicago Press; 1957.

41. Jacobs GH. Comparative Color Vision. New York: Academic Press; 1981.

42. Rubin JM, Richards WA. Color vision and image intensities: when are changes material? *Biol Cybern* 1982; 45: 215-226.

43. Maximov VV. Environmental factors which may have led to the appearance of colour vision. *Phil Trans R Soc Lond. B* 2000; 355: 1239-1242.

44. Osorio D, Vorobyev M. Colour vision as an adaptation to frugivory in primates. *Proc Roy Soc Lond B* 1996; 263: 593-599.

45. Vorobyev M, Menzel R. Flower advertisement for insects. In: Archer S, Partridge J, eds. Adaptive Mechanisms in the Ecology of Vision. Dortrecht: Kluwer Academic Publishers; 1999. p 537-553.

46. Sumner P, Mollon JD. Catarrhine photopigments are optimised for detecting targets against a foliage background. *J Exp Biol* 2000; 203: 1963-1986.

47. Regan BC, Julliot C, Simmen B, Vienot F, Charles-Dominique P, Mollon JD. Frugivory and colour vision in Alouatta seniculus, a trichromatic platyrrhine monkey. *Vision Res* 1998; 38: 3321-3327.

48. Regan BC, Julliot C, Simmen B, Vienot F, Charles-Dominique P, Mollon JD. Fruits, foliage and the evolution of primate colour vision. *Phil Trans R Soc Lond B* 2001; 356: 229-283.

49. Bowmaker JK The evolution of vertebrate visual pigments and photoreceptors. In: Cronly-Dillon JR, ed. Vision and Visual Dysfunction, Vol.2. Evolution of the Eye and Visual System. London: MacMillan Press; 1991. p 63-81.

50. Kelber A, Vorobyev M, Osorio D. Animal colour vision—behavioural tests and physiological concepts. *Biol Reviews* 2003; 78: 81-118.

51. Peitsch D, Fietz A, Hertel H, Souza JD, Ventura D, Menzel R. The spectral inputs of hymenopteran insects and their receptor based colour vision. *J Comp Physiol A* 1992; 433: 561-581.

52. Beck CB. Origin and Early Evolution of Angiosperms. New York: Columbia University Press; 1976.

53. Foster DH, Nascimento SM. Relational colour constancy from invariant cone-excitation ratios. *Proc R Soc Lond B Biol Sci* 1994; 257: 115-121.

54. Pokorny J, Shevell SK, Smith VC. Colour appearance and colour constancy. In: Cronly-Dillon JR, ed. Vision and Visual Dysfunction. Vol.6. The Perception of Colour. London: MacMillan Press; 1991. p 43-61.

55. Neumeyer C. Chromatic adaptation in the honeybee: successive color contrast and color constancy. *J Comp Physiol* 1981; 144: 543-553.

56. Neumeyer C, Dorr S. The goldfish—a colour-constant animal. *Perception* 1996; 25: 243-250.

57. Land EH. Recent advances in Retinex Theory. *Vision Res* 1986; 26: 7-21.

58. Brainard DH, Freeman WT. Bayesian color constancy. *J Opt Soc Am A* 1997; 14: 1393-1411.

59. Buchsbaum, GJ. A spatial processor model for object colour perception. *J Franklin Inst* 1980; 310: 1-26.

60. Foster DH. Does colour constancy exist? *Trends Cogn Sci* 2003; 7: 439-443.

61. Pokorny J, Smith VC, Veriest G, Pinkers AJLJ. Congenital and Acquired Color Vision Defects. New York: Grune and Stratton; 1979.

62. Mollon JD, Dulai KS, Hunt DM. Dalton's colour blindness: an essay in molecular bi-

ography. In: Dickinson C, Murray I, Carden D, eds. John Dalton's Colour Vision Legacy. Bristol: Taylor&Francis; 1997. p 15-36.

63. Dalton J. Extraodinary facts relating to the vision of colours: with observations by Mr John Dalton. In: Dickinson C, Murray I, Carden D, eds. John Dalton's Colour Vision Legacy, Bristol: Taylor&Francis; 1997. p 7-15.

64. Sumner P, Mollon JD. Chromaticity as a signal of ripeness in fruits taken by primates. *J Exp Biol* 2000; 203 Pt 13: 1987-2000.

65. Spalding JA. Medical students and congenital colour vision deficiency: unnoticed problems and the case for screening. *Occup Med (Lond)* 1999; 49: 247-252.

66. Steward JM, Cole BL. What do color vision defectives say about everyday tasks? *Optom Vis Sci* 1989; 66: 288-295.

67. Dixson AF. Primate Sexuality—Comparative Studies of the Prosimians, Monkeys, Apes and Human Beings. Oxford: Oxford University Press; 1998.

68. Wyszecki G, Stiles WS. Color Science: Concepts and Methods, Quantitative Data and Formulae. 2nd ed. New York: Wiley; 1982.

69. Lyons J. Colour in language. In: Lamb T, Bouriau J. eds. Colour: Art and Science. UK: Cambridge University Press; 1995. p 194-224.

70. Zaidi Q. Color constancy in a rough world. *Color Res Applic* 2001; 26: S192-S200.

71. Munz FW, McFarland WN. The significance of spectral position in the rhodopsins of tropical marine fishes. *Vision Res* 1973; 33: 1829-1874.

72. Peichl L, Kunzle H, Vogel P. Photoreceptor types and distributions in the retinae of insecivores. *Vis Neurosci* 2000; 17: 937-948.

73. Williams DR, Sekiguchi N, Haake W, Brainard D, Packer O. The cost of trichromacy for spatial vision. In: Valberg A, Lee BB, eds. From Pigments to Perception: Advances in Understanding Visual Process. New York: Plenum; 1991. p 11-22.

74. Verhulst S, Maes FW. Scotopic vision in colour-blinds *Vision Res* 1998; 38: 3387-3390.

75. Simunovic MP, Regan BC, Mollon JD. Is color vision deficiency an advantage under scotopic conditions? *Invest Ophthalmol Vis Sci* 2001; 42: 3357-3364.

76. Vorobyev M, Osorio D, Bennett ATD, Marshall NJ, Cuthill IC. Tetrachromacy, oil droplets and bird plumage colours. *J Comp Physiol A* 1998; 183: 621-633.

77. Neitz J, Jacobs GH. Reexamination of spectral mechnisms in the rat. (*Rattus norvegicus*). *J Comp Physiol* 1986; 100: 21-29.

78. Osorio D, Ruderman DL, Cronin TW. Estimation of errors in luminance signals encoded by primate retina resulting from sampling of natural images with red and green cones. *J Opt Soc Am A Opt Image Sci Vis* 1998; 15: 16-22.

79. Schaerer S, Neumeyer C. Motion detection in goldfish investigated with the optomotor response is 'color blind'. *Vision Res* 1996; 36: 4025-4034.

80. Jones CD, Osorio D. Discrimination of oriented visual textures by poultry chicks. *Vision Res* 2004; 44: 83-89.

81. Lucas PW, Dominy NJ, Riba-Hernandez P, Stoner KE, Yamashita N, Loria-Calderon, Petersen-Pereira W, Rogas-Dural Y, Salas-Pena R, Solis-Madrigal S, Osorio D, Darvell BW. Evolution and function of routine trichromatic vision in primates. *Evolution Int J Org Evolution* 2003; 57: 2636-2643.

82. Dominy NJ, Lucas PW. Ecological importance of trichromatic vision to primates. *Nature* 2001; 410: 363-366.

83. Sumner P, Mollon JD. Did primate trichromacy evolve for frugivory or folivory? In: Mollon JD, Pokorny J, Knoblauch K, eds. Normal and Defective Colour Vision. Oxford: Oxford University Press; 2003; p 21-30.

84. Tompson I. Considering the evolution of vertebrate neural retina. In: Cronly-Dillon JR, Gregory RL, eds. Evolution of the Eye and Visual System. London: MacMilan; 1991. p 306-319.

85. Lee BB. Receptor inputs to primate ganglion cells. In: Gegenfurtner KR, Sharp LT, eds. Color Vision. From Genes to Perception. UK: Cambridge University Press; 1999. p 203-217.

86. Martin PR. Colour processing in the primate retina: recent progress. *J Physiol* 1998; 513: 631-638.

87. Tovée MJ, Bowmaker JK, Mollon JD. The relationship between cone pigments and behavioural sensitivity in a New World monkey *(Callithrix jacchus jacchus)*. *Vision Res* 1992; 32: 867-878.

88. 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: 7892-7904.

89. Elston G. Cortical heterogeneity: Implications for visual processing and polysensory integration. *J Neurocytol* 2002; 31: 317-335.

90. Zeki S. A Vision of the Brain. Oxford: Blackwell Scientific publication; 1993.

91. Bornstein MH. On the development of color naming in young children: data and theory. *Brain Lang* 1985; 26: 72-93.

92. Smith VC, Pokorny J. Spectral sensitivities of human foveal cone photopigments between 400 and 500 nm. *Vision Res* 1975; 15: 161-171.

93. Hart NS, Partridge JC, Cuthil IC, Bennet AT. Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the blue tit (*Prus caeruleus L.*) and the blackbird *(Turdus merula L.)*. *J Comp Physiol A* 2000; 186: 375-387.

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