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Uniformity of colour vision in Old World monkeys

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It is often assumed that all Old World monkeys share the same trichromatic colour vision, but the evidence in support of this conclusion is sparse as only a small fraction of all Old World monkey species have been tested. To address this issue, spectral sensitivity functions were measured in animals from eight species of Old World monkey (five cercopithecine species and three colobine species) using a non-invasive electrophysiological technique. Each of the 25 animals examined had spectrally well-separated middle- and long-wavelength cone pigments. Cone pigments maximally sensitive to short wavelengths were also detected, implying the presence of trichromatic colour vision. Direct comparisons of the spectral sensitivity functions of Old World monkeys suggest there are no significant variations in the spectral positions of the cone pigments underlying the trichromatic colour vision of Old World monkeys.

Keywords: colour vision; Old World monkeys; photopigment variations; evolution

1. INTRODUCTION

The presence of colour vision in rhesus macaque monkeys (*Macaca mulatta*) was established nearly a century ago (Kinnaman 1902), and subsequent experiments provided definitive evidence that the colour vision of this and several other macaque species is similar to that of normal human trichromats (De Valois *et al*. 1974; Grether 1939; Harwerth & Smith III 1985; Oyama *et al*. 1986; Trendelenberg & Schmidt 1930). Old World monkeys form a heterogeneous group that encompasses in total some 80 species whose native habitats are widely spread across Africa and south-eastern Asia and, beyond the work on the macaques, the literature contains few observations on colour vision in any of these species. Although studies of colour vision in these monkeys are scarce, recent years have seen an increasing use of a variety of biological indices that can be used to draw inferences about colour vision. Prominent among these are direct measurements of cone photopigments, electrophysiological reflections of photopigment activation and examination of genes that code for cone opsins. For example, microspectrophotometric (MSP) measurements have revealed three classes of cone pigment in the following Old World monkeys: baboons (*Papio*), four species of guenon (*Cercopithecus*), and talapoin (*Miopithecus*) and Patas monkeys (*Erythrocebus*) (Bowmaker 1990; Bowmaker *et al*. 1991). These results strongly imply the presence of trichromatic colour vision in each of these primates.

Although it has become common to assume that trichromatic colour vision is characteristic of all Old World monkeys, there are reasons to withhold a final judgement. First, there is the example provided by studies of New World monkeys. With only two known exceptions, all New World monkey genera have been found to have highly polymorphic colour vision, individual animals having any of several distinct types of dichromatic and trichromatic colour vision (reviewed in Jacobs 1997, 1998). Colour vision polymorphism of this kind could be easily overlooked in small samples. Although a large number of macaque monkeys (Jacobs & Deegan II 1997; Jacobs & Harwerth 1989) have been shown to be uniformly trichromatic, only restricted samples of other Old World monkeys have been examined. It is possible that significant polymorphisms of colour vision in Old World monkeys might have escaped detection. A second reason the understanding of colour vision in Old World monkeys is incomplete is simply that only a few monkey species have been examined. Old World monkeys are divided into two subfamilies, Cercopithecinae and Colobinae. All of the species of Old World monkey examined to date in experiments dealing with vision and the visual system have been from the former group. This bias is intriguing in light of the long-standing hypothesis that the trichromatic colour vision of primates may have coevolved with coloured tropical fruits (Mollon 1991; Polyak 1957). While cercopithecine monkeys are substantially frugivorous (Fleagle 1998), colobine monkeys are mainly foliovores (Davies & Oates 1995). If the suggested linkage between food gathering and colour vision is correct, one might imagine that if there are variations in colour vision among Old World monkeys it would be between monkeys of these two subfamilies.

In this investigation a non-invasive electrophysiological measure was used to obtain spectral sensitivity functions from several species of Old World monkey and thus provide information to draw inferences about colour vision. We were particularly interested in comparing results obtained for cercopithecine and colobine monkeys.

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2. METHODS

Measurements were made on 14 cercopithecine monkeys drawn from five species: five red-tailed monkeys (*Cercopithecus ascanius*—two males, three females); three Diana monkeys (*Cercopithecus diana diana*—one male, two females); three blue monkeys (*Cercopithecus mitis*—one male, two females); one male DeBrazza monkey (*Cercopithecus neglectus*); one female mustached guenon (*Cercopithecus cephus*); one male Mona monkey (*Cescopithecus mona*); and on 11 colobine monkeys from three species: five black and white colobus monkeys (*Colobus guereza*—four males, one female); four Angolan colobus (*Colobus angolensis*—three males, one female); two silvered langurs (*Presbytis cristata*—one male, one female). To provide a comparative baseline, data obtained from 44 male macaque monkeys (*Macaca mulatta* and *Macaca fascicularis*) were examined. Most of the results from the macaques have been presented elsewhere (Jacobs & Deegan II 1997). All of the monkeys were in captive collections and were tested on the occasion of routine physical examinations.

Spectral sensitivity functions were measured with a non-invasive electrophysiological technique, electroretinogram (ERG) flicker photometry. General features of the recording and analysis procedures and their specific application to Old World monkeys have been reported (Jacobs & Deegan II 1997; Jacobs *et al*. 1996*b*). ERGs were differentially recorded from a contact lens electrode placed on the eye of a sedated monkey. Prior to installation of the electrode the cornea was anaesthetized by topical application of proparacaine hydrochloride. Experiments were conducted at several different test sites and the anaesthetic regime varied somewhat according to local practice. Most commonly, monkeys were sedated with intramuscular (IM) injections of a mixture of ketamine hydrochloride and acepromazine maleate. On occasion this was supplemented by intravenous (IV) administration of diazepam. Four of the colobine monkeys received initial IM injections of ketamine hydrochloride and were then transferred to an inhalant mixture of isoflurane and oxygen. There is no evidence that variation in anaesthetic agents in any way influenced the recordings.

The output from a three-beam optical system was imaged in Maxwellian view (circular, 59°) through a pupil dilated by application of atropine sulphate (0.04%) and phenylephedrine hydrochloride. The three beams originated from tungsten halide lamps; these were the test light of the photometer (derived from a monochromator with a half-energy passband of 10 nm), the reference light of the photometer and an accessory adaptation light. High-speed electromagnetic shutters controlled the timing of stimulus presentation. ERGs were elicited by an interleaved train of square-wave pulses originating from test and reference lights, each modulated with a 25% duty cycle. A 3.0 log unit circular, neutral-density wedge was used to control the radiance of the test light. The reference and adaptation lights were altered by using neutral-density step filters and interference filters (10 nm half-bandwidth). The signal processing procedure is described elsewhere (Jacobs *et al*. 1996*b*).

Experiments were conducted in illuminated rooms that varied in light level at the several test locations over a range from about 150 to 300 lux. The effectiveness of the test and reference light were equated by iteratively adjusting the intensity of the test light until the ERG it elicited was equal to that produced by a constant reference light. Equations were made between the test and reference light based on the average of the stimulus-locked ERG responses to the last 50 cycles of a total of 70 stimulus cycles. The wedge density value at the point of equation was recorded to a precision of 0.01 log unit. Equations were made twice during the session for each test–reference light combination and the average of the two was subsequently used for analysis.

Complete photopic spectral sensitivity functions were obtained from each monkey using a stimulus pulse rate of 31.25 Hz. The test light was varied in 10 nm steps from 440 to 660 nm. The reference light was achromatic (2450 K) and yielded a retinal illuminance of 3.3 log td (trolands). A second experiment was designed to ascertain whether the retina contained one or more than one middle (M)- to long (L)-wavelength photopigment and so served as an explicit test of whether the monkey might be expected to have dichromatic or trichromatic colour vision (Jacobs & Neitz 1987). For this purpose an ERG flicker-photometric equation was made between a 540 nm test light and a 630 nm reference light. The stimulus pulse rate was 31.25 Hz. These photometric equations were made while the eye was alternately adapted to 540 nm and 630 nm lights. The intensities of these two adaptation lights were adjusted so that the presence of each elevated the threshold of a 560 nm flickering (31.25 Hz) test light by an equal amount (0.5 log unit). Other details for obtaining these equations were as described previously (Jacobs & Deegan II 1997). Finally, as time permitted, we also attempted to obtain evidence for the existence of a spectral mechanism with maximum sensitivity in the short wavelengths. The test conditions were those previously established as favourable for eliciting ERG signals from short-wavelength-sensitive (S) cones (Jacobs *et al*. 1996*a*). For this purpose, the stimulus pulse rate was slowed to 12.5 Hz, a 460 nm reference light was used, and the eye was concurrently adapted to an intense long-wavelength light produced by inserting a high-pass filter (50% transmission at 585 nm) into the adaptation beam. Spectral sensitivity measurements were made at 10 nm intervals, usually from 430 to 510 nm.

3. RESULTS

Figure 1 shows the averaged spectral sensitivity functions obtained from representatives of five species of cercopithecine monkey; figure 2 provides a similar summary of the results from three species of colobine monkey. Error bars are shown (± 1 s.d.) for each of the species where data were obtained from three or more animals. The variation in sensitivity among animals of a species was relatively small, e.g. for *C. mitis* ($n = 3$) the mean standard deviation for the 23 wavelengths tested was 0.051 log unit. Variations of similar size were obtained in each of the other cases.

Results from the test to determine if the retinas of these Old World monkeys contained more than one type of M/L photopigment were clear-cut. For every animal, more 540 nm light was required to complete the ERG photometric equation when the eye was concurrently exposed to 540 nm, while less 540 nm light was required when the adaptation was shifted to 630 nm. An implication is that each animal has multiple M/L cone pigments. The magnitude of the change in the equation value derived for the two adaptation conditions provides a convenient index for a test of this type (Jacobs & Neitz 1987). The average change for 24 subjects (the test was not completed on one *C. diana* monkey) was 0.188 log unit (s.d. = 0.075). To put this in comparative context, the average shift in the equation earlier obtained from 44

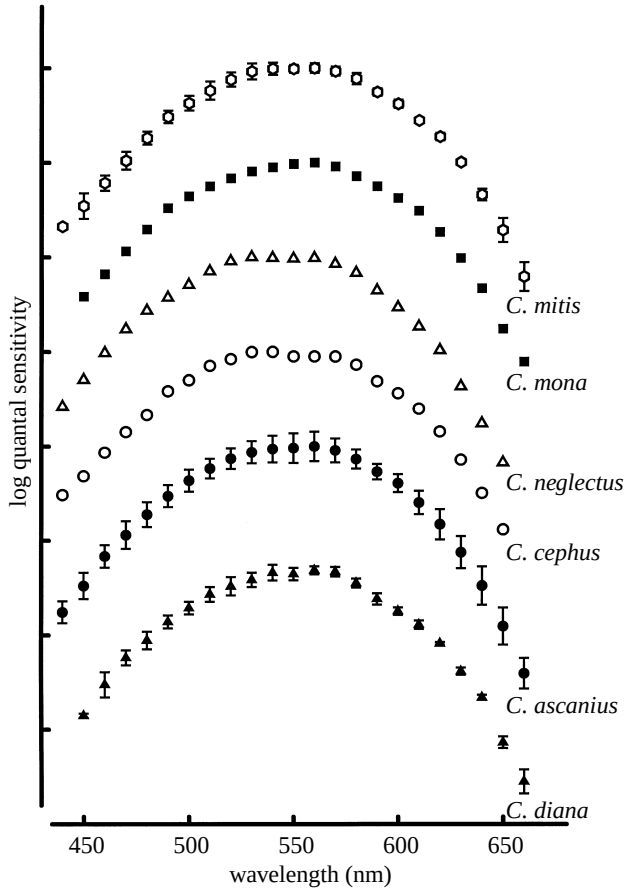

Figure 1. Spectral sensitivity functions for five species of cercopithecine monkey. Each function was measured using ERG flicker photometry. The symbols represent mean sensitivity values. Error bars (± 1 s.d.) are shown for each sample that included three or more animals. The functions for the various species have been arbitrarily positioned on the sensitivity axis where each scale division equals 0.5 log unit.

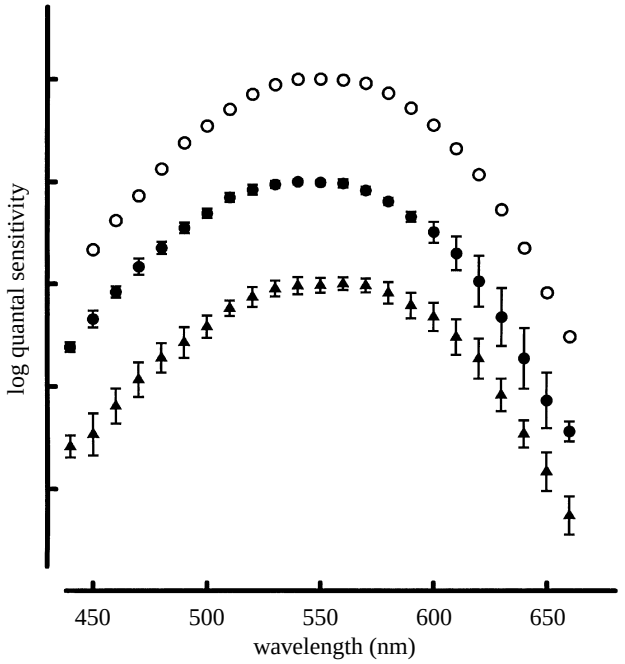

Figure 2. Spectral sensitivity functions for three species of colobine monkey. Open circles: *Presbytis cristata*; filled circles: *Colobus angolensis*; filled triangles: *Colobus guereza*. All the conventions are the same as those for figure 1. On the sensitivity axis each scale division equals 0.5 log unit.

macaque monkeys who were identically tested was 0.197 (s.d. = 0.050), while 27 human dichromats gave an average value of 0.014 (s.d. = 0.015) (Jacobs & Deegan II 1997). Although the number of subjects is small in some cases, there was no indication of any systematic variations in the magnitude of this value, either for individual species or between the groups of cercopithecine and colobine monkeys.

Evidence for the presence of an S-cone mechanism was obtained from nine animals. Figure 3 shows the averaged spectral sensitivity functions obtained from this group (seven cercopithecine monkeys; two colobine monkeys.) For these test conditions spectral sensitivity is highest in the short wavelengths; in fact, the adaptation light so depressed sensitivity in the long wavelengths that it was not possible to complete measurements for test wavelengths longer than about 500 nm. Note that there is only modest individual variation in spectral sensitivity for the larger sample (solid circles) and that results from cercopithecine and colobine monkeys are similar.

4. DISCUSSION

These measurements significantly expand the number of primate species for which inferences can be drawn about colour vision. The important result is the strong support for the conclusion that trichromatic colour vision is routinely present in Old World monkeys.

(a) *Variations in spectral sensitivity among Old World monkeys*

Given that all of the Old World monkeys examined to date appear to be trichromats, might there still be some systematic variations in their retinal photopigments and, therefore, in some details of their colour vision? Inspection of the spectral sensitivity functions obtained from various cercopithecine and colobine monkeys (figures 1 and 2) reveals no compelling indication of interspecies variations. Based on molecular comparisons and examination of fossil evidence, it appears that the two groups diverged about 14 million years ago (Stewart & Disotell 1998) and it is worth specifically inquiring whether some differences in photopigment complement may have accumulated in the two separate lines over that time. Figure 4 plots the averaged spectral sensitivity functions obtained from 11 colobine monkeys (filled circles) and 14 cercopithecine monkeys (open circles). The inset at the bottom of the figure shows the wavelength-by-wavelength difference in average sensitivity between the two functions after the two functions were shifted so as to have the same average height on the sensitivity axis. The comparison shows a remarkable degree of similarity in spectral sensitivity between the two—the average difference in sensitivity amounts to only 0.024 log unit. This suggests that any differences in photopigment complement between these two groups of catarrhine monkeys are likely to be very small.

There have been extensive measurements of cone pigments and spectral sensitivity, as well as studies of

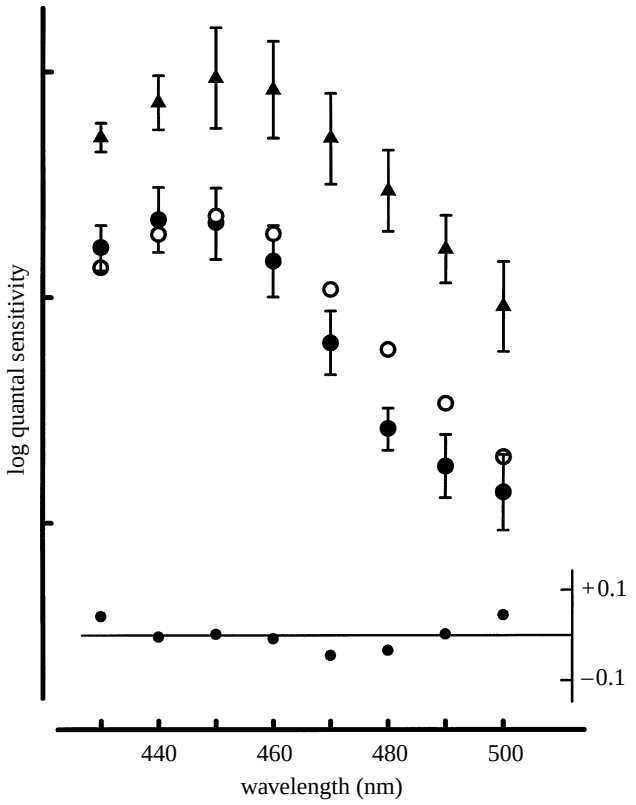

Figure 3. Spectral sensitivity functions for three groups of Old World monkeys. The symbols represent mean sensitivity values obtained from each of the groups as recorded in the presence of an intense long-wavelength adaptation (see text for details). Triangles: macaque monkeys ($n=8$); filled circles: cercopithecine monkeys ($n=7$); open circles: colobine monkeys ($n=2$). Error bars are 1 s.d. On the sensitivity axis each scale division represents 0.5 log unit. The inset at the bottom shows wavelength-by-wavelength differences in spectral sensitivity between the mean values for the macaque function and the combined function for cercopithecine and colobine monkeys. The scale values for the inset (right) are in log units.

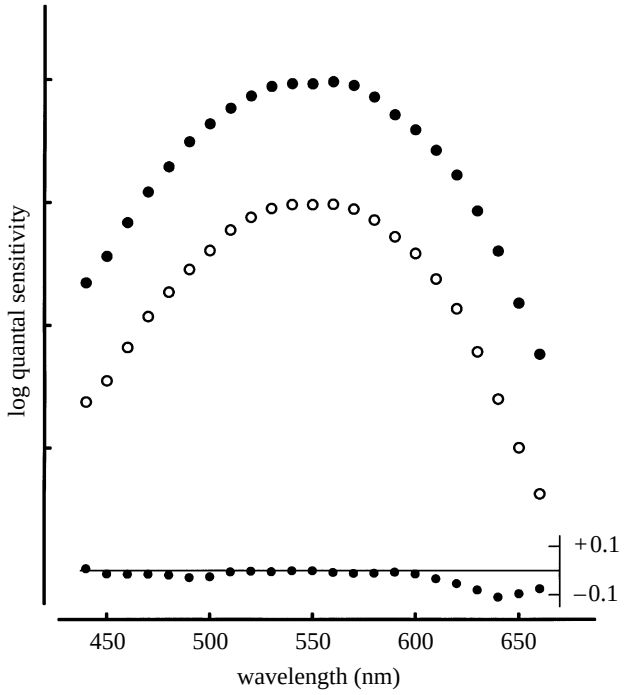

Figure 4. The averaged spectral sensitivity functions for all the colobine monkeys (filled circles, $n=11$) and cercopithecine monkeys (open circles, $n=14$) tested. The scale divisions on the sensitivity axis represent 0.5 log unit. The inset at the bottom gives the wavelength-by-wavelength differences in sensitivity between the two spectral sensitivity functions.

colour vision, for macaque monkeys. They can thus serve as a useful comparative baseline against which to evaluate the present measurements. It is particularly appropriate to do this because spectral sensitivity measurements were recently made on a large sample of macaque monkeys using techniques identical to those employed here (Jacobs & Deegan II 1997). Figure 5 shows the average ERG flicker photometric spectral sensitivity functions obtained from all the species tested in this experiment (open circles, $n=25$) and the corresponding averaged data for a group of rhesus (*M. mulatta*) and long-tailed (*M. fascicularis*) macaque monkeys (filled circles, $n=42$). The inset at the bottom of the figure shows wavelength-by-wavelength comparison of the sensitivities of these two groups of monkey, computed in the same fashion as for figure 4. These sensitivity differences are again slight, the mean difference for 23 test wavelengths being 0.045 log units. Even though these differences are small, there is the hint of a systematic deviation in spectral sensitivity between macaques and the other catarrhine monkeys with the macaques being slightly but consistently less sensitive to wavelengths longer than about 600 nm.

MSP measurements of M and L cones have revealed no systematic differences in the photopigment positions of macaque monkeys and several other catarrhine species (Bowmaker 1990; Bowmaker *et al*. 1991). That conclusion is supported by the fact that there are also no variations among some of these same species in the codons that specify the amino acids believed crucial for spectral tuning in the M- and L-cone opsins (Dulai *et al*. 1994). We fitted the spectral sensitivity data of figure 5 using linear summations of photopigment absorption spectra having peak values of 535 nm and 562 nm. This choice is based on the presumption that all of these catarrhine monkeys share in common the M and L-cone positions of macaque monkeys (Jacobs & Deegan II 1997). It was also assumed that the spectral absorption properties of the lens in all of these catarrhine species are similar to those earlier catalogued for the rhesus macaque monkey (Boettner 1967). With these assumptions the data for both sets of monkeys can be well fit, but they require somewhat different L/M-cone weights—1.08 for the sample of macaque monkeys, 1.94 for the other catarrhines. It was earlier argued that this L/M weighting may reflect the overall proportion of L and M cones in the macaque retina, suggesting that the ratio of their representation is close to unity (Jacobs & Deegan II 1997). By analogy, this might be taken to predict that the cercopithecine and colobine species tested here have higher average L/M-cone ratios. Although that could be true, two facts would encourage caution. First, direct MSP measurements provide no support for the idea that the relative incidence

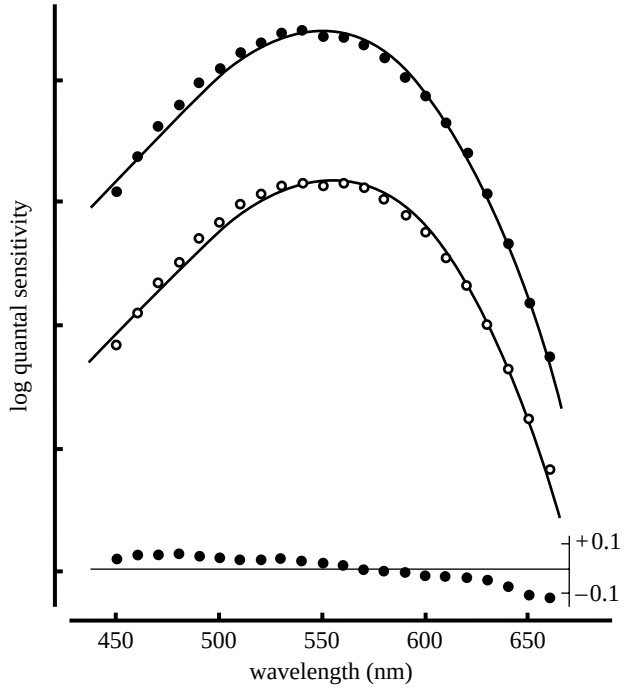

Figure 5. Combined spectral sensitivity functions for all of the colobine and cercopithecine monkeys (filled circles, $n = 25$) and for a sample of macaque monkeys identically tested (open circles, $n = 42$). The sensitivity values have been corrected for pre-retinal absorption (see text). Sensitivity scale divisions are 0.5 log unit. In each case the continuous lines are the best-fitting linear summation of two M/L pigment absorption curves having respective peak values of 535 and 562 nm. The inset at the bottom plots the differences in sensitivity of the two spectral sensitivity functions.

of M and L cones varies among the catarrhine monkeys studied so far (Bowmaker 1990). Second, very small differences in the fitting assumptions can greatly influence this outcome. For instance, a shift of a few nm in the spectral positioning of the L pigment will significantly alter the fitting proportions. The important outcome of this comparison is not the small differences in spectral sensitivity among colobine and cercopithecine monkeys, but, rather, their great similarities. Indeed, the similarity goes beyond the present results: in conjunction with earlier measurements made on Old World monkeys (Jacobs & Deegan II 1997; Jacobs *et al*. 1991) we have now detected no evidence for significant variations in spectral sensitivity among 81 Old World monkeys drawn from 12 different species. It is noteworthy that most of these monkeys (86%) were male, which would increase the likelihood of detecting any significant X-chromosome-related variations in colour vision.

(b) *S cones in Old World monkeys*

The spectra of S cones have been measured directly in the retinas of some Old World monkeys with MSP and single-receptor recordings (Bowmaker *et al*. 1991; Mansfield *et al*. 1984; Schnapf *et al*. 1988). Such cones are sparse in number (<10% of the total) and contain a photopigment with an average peak absorption of about 430 nm. Here the presence of S cones is inferred from the appearance of the spectral sensitivity function recorded under conditions designed to optimize the detection of S-cone contributions (figure 3). Since the chromatic adaptation used to enhance S-cone contribution cannot be assumed to eliminate entirely signals from the M/L cones, the resulting spectral sensitivity function is necessarily complex, quite possibly containing a mixture of signals originating in all three cone classes. These functions thus cannot provide any compelling indication of the spectral positioning of the S cones. What can be done is to ask whether there are any obvious variations in S-cone positioning among Old World monkeys. Figure 3 includes measurements made on macaque monkeys as well as on the cercopithecine and colobine monkeys that are the focus of this experiment. All of the subjects were tested in the identical fashion. The shapes of the spectral sensitivity functions that are dominated by contributions from S cones are similar for all of these monkeys. Just how similar can be seen at the bottom of figure 3 where wavelength-by-wavelength differences in sensitivity are plotted for the sample of macaques ($n = 8$) and the combined results from guenons and colobine monkeys ($n = 9$). Those differences are small and non-systematic across the tested wavelengths suggesting that all of these Old World monkeys share in common their S-cone pigment.

(c) *Colour vision in Old World monkeys and the feeding hypotheses*

Among all mammals only primates have trichromatic colour vision (Jacobs 1993). One explanation for this uniqueness is that primate trichromacy evolved as a specialization for finding food. The most popular version of this idea suggests that primate trichromacy coevolved with coloured fruits (Mollon 1991; Polyak 1957) and assumes that this capacity is particularly advantageous in the discrimination and identification of tropical fruits, particularly those that are orange and yellow in colour. This idea has garnered support, both from observations of the spectral properties of tropical fruits harvested by monkeys and from recent modelling studies that demonstrate the spectral positioning of the M and L cones in trichromatic non-human primates to be near optimal for the detection and identification of such fruits (Osorio & Vorobyev 1996; Regan *et al*. 1998). A second version of the feeding hypothesis has a different focus, suggesting that many monkeys eat leaves as a significant part of their diet and in so doing preferentially select edible young leaves that can best be detected by those colour cues available to the trichromatic viewer (Lucas *et al*. 1998).

Both alternatives of the feeding hypothesis have been argued to speak to potential differences in colour vision between cercopithecine and colobine monkeys. The latter are more typical foliovores and, depending on the version of the feeding hypothesis preferred, this is taken to predict either that colobines should have uniform trichromatic colour vision (Lucas *et al*. 1998) or that if variant or polymorphic forms of catarrhine colour vision do exist, they will be in these foliovorous species (Bowmaker *et al*. 1991). The present results show a distinct lack of variation between cercopithecine and colobine monkeys. Nor is there any indication of polymorphic variation in any of these Old World species, although the sample is admittedly still limited. It seems doubtful, however, if either of these facts can be used as evidence for the competing versions of the feeding hypothesis. Contemporary

adaptations have to be understood in the light of their evolutionary history and the best evidence is that the opsin gene duplication believed to be crucial for providing the photopigment basis of routine primate trichromacy occurred early in catarrhine history (Nathans *et al*. 1986), long before divergence of the cercopithecine and colobine lines (Stewart & Disotell 1998). It has been further conjectured that even after the divergence the early colobines were still predominant fruit eaters, with adaptation towards increasing use of plant foods arising later (Oates & Davies 1994). It is worth recalling that for any diurnal animal there are a significant number of advantages that may accrue from having trichromatic colour vision, both for behaviours that are based on colour discriminations *per se* and for other visual tasks (Jacobs 1999; Mollon 1991). Given that, it may not be surprising that the trichromacy invented by earlier catarrhines has been so conservatively maintained.

Finally, it would be remiss not to caution that although the present measurements expand considerably the grounds for assuming that Old World monkeys are routine trichromats, there are numerous species in this group whose photopigments and colour vision remain unknown.

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REFERENCES

Boettner, E. A. 1967 Spectral transmission of the eye. *University of Michigan Contract AF41 (609)-2966*. USAF School of Aerospace Medicine, Brooks Air Force Base, TX, USA.

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

Bowmaker, J. K., Astell, S., Hunt, D. M. & Mollon, J. D. 1991 Photosensitive and photostable pigments in the retinae of Old World monkeys. *J. Exp. Biol.* **156**, 1–19.

Davies, A. G. & Oates, J. F. E. 1995 *Colobine monkeys: their ecology, behaviour and evolution*. Cambridge University Press.

De Valois, R. L., Morgan, H. C., Polson, M. C., Mead, W. R. & Hull, E. M. 1974 Psychophysical studies of monkey vision. I. Macaque luminosity and color vision tests. *Vision Res.* **14**, 53–67.

Dulai, K. S., Bowmaker, J. K., Mollon, J. D. & Hunt, D. M. 1994 Sequence divergence, polymorphism and evolution of middle-wave and long-wave visual pigment genes of great apes and Old World monkeys. *Vision Res.* **34**, 2483–2491.

Fleagle, J. G. 1998 *Primate adaptation and evolution*. San Diego, CA: Academic Press.

Grether, W. F. 1939 Color vision and color blindness in monkeys. *Comp. Psychol. Monogr.* **29**, 1–38.

Harwerth, R. S. & Smith III, E. L. 1985 The rhesus monkey as a model for normal vision of humans. *Am. J. Optom. Physiol. Opt.* **62**, 633–641.

Jacobs, G. H. 1993 The distribution and nature of colour vision among the mammals. *Biol. Rev.* **68**, 413–471.

Jacobs, G. H. 1997 Color-vision polymorphisms in New World monkeys: implications for the evolution of primate trichromacy. In *New World primates: ecology, evolution and behavior* (ed. W. G. Kinzey), pp. 45–74. New York: Aldine de Gruyter.

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

Jacobs, G. H. 1999 Vision and behavior in primates. In *Adaptive mechanisms in the ecology of vision* (ed. S. N. Archer, M. B. A. Djamgoz, E. R. Loew, J. C. Partridge & S. Vallerga), pp. 629–650. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Jacobs, G. H. & Deegan II, J. F. 1997 Spectral sensitivity of macaque monkeys measured with ERG flicker photometry. *Vis. Neurosci.* **14**, 921–928.

Jacobs, G. H. & Harwerth, R. S. 1989 Color vision variations in Old and New World primates. *Am. J. Primatol.* **18**, 35–44.

Jacobs, G. H. & Neitz, J. 1987 Inheritance of color vision in a New World monkey (*Saimiri sciureus*). *Proc. Natl Acad. Sci. USA* **84**, 2545–2549.

Jacobs, G. H., Neitz, J., Crognale, M. A. & Brammer, G. T. 1991 Spectral sensitivity of vervet monkeys (*Cercipthecus aethiops sabeus*) and the issue of catarrhine trichromacy. *Am. J. Primatol.* **23**, 185–195.

Jacobs, G. H., Deegan II, J. F. & Moran, J. L. 1996*a* ERG measurements of spectral sensitivity of common chimpanzees (*Pan troglodytes*). *Vision Res.* **36**, 2587–2594.

Jacobs, G. H., Neitz, J. & Krogh, K. 1996*b* Electroretinogram flicker photometry and its applications. *J. Opt. Soc. Am.* A **13**, 641–648.

Kinnaman, A. J. 1902 Mental life of two Macacus rhesus monkeys in captivity. *Am. J. Psychol.* **13**, 98–148.

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

Mansfield, R. J. W., Levine, J. S., Lipetz, L. E., Collins, B. A., Raymond, G. & MacNichol, E. F. 1984 Blue-sensitive cones in the primate retina: microspectrophotometry of the visual pigment. *Exp. Brain Res.* **56**, 389–394.

Mollon, J. D. 1991 Uses and evolutionary origins of primate colour vision. In *Evolution of the eye and visual system* (ed. J. R. Cronly-Dillon & R. L. Gregory), pp. 306–319. Boca Raton, FL: CRC Press.

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

Oates, J. F. & Davies, A. G. 1994 Conclusions: the past, present and future of the colobines. In *Colobine monkeys: their ecology, behaviour and evolution* (ed. A. G. Davies & J. F. Oates), pp. 347–358. Cambridge University Press.

Osorio, D. & Vorobyev, M. 1996 Colour vision as an adaptation to frugivory in primates. *Proc. R. Soc. Lond.* B **263**, 593–599.

Oyama, T., Furusaka, T. & Kito, T. 1986 Color vision tests of Japanese and rhesus monkeys. In *Current perspectives primate biology* (ed. D. M. Taub & F. A. King), pp. 253–269. New York: Van Nostrand Reinhold.

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

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

Schnapf, J. L., Kraft, T. W., Nunn, B. J. & Baylor, D. A. 1988 Spectral sensitivity of primate photoreceptors. *Vis. Neurosci.* **1**, 255–261.

Stewart, C.-B. & Disotell, T. R. 1998 Primate evolution—in and out of Africa. *Curr. Biol.* **8**, R582–R588.

Trendelenberg, W. & Schmidt, I. 1930 Untersuchungen über das Farbensystem des Affen. *Z. Vergl. Physiol.* **12**, 249–278.