# Photopigments and colour vision in New World monkeys from the family Atelidae

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Most New World monkeys have an X-chromosome opsin gene polymorphism that produces a variety of different colour vision phenotypes. Howler monkeys (*Alouatta*), one of the four genera in the family Atelidae, lack this polymorphism. Instead, they have acquired uniform trichromatic colour vision similar to that of Old World monkeys, apes and people through opsin gene duplication. In order to determine whether closely related monkeys share this arrangement, spectral sensitivity functions that allow inferences about cone pigments were measured for 56 monkeys from two other Atelid genera, spider monkeys (*Ateles*) and woolly monkeys (*Lagothrix*). Unlike howler monkeys, both spider and woolly monkeys are polymorphic for their middle- and long-wavelength cone photopigments. However, they also differ from other polymorphic New World monkeys in having two rather than three possible types of middle- and long-wavelength cone pigments. This feature directly influences the relative numbers of dichromatic and trichromatic monkeys.

**Keywords:** New World monkeys; colour vision; photopigment polymorphism; opsin evolution

## 1. INTRODUCTION

Grether (1939) was the first to suggest that there might be significant variations in colour vision among New World monkeys. In recent years that topic has come under renewed study and a number of platyrrhine species have been shown to have polymorphic colour vision that arises from the sorting of allelic versions of X-chromosome cone opsin genes at a single gene locus (Jacobs 1998). The result is a mixture of trichromatic and dichromatic phenotypes in which all male monkeys are dichromatic while females may be either dichromatic or trichromatic. The study of these animals is important, both because it serves as a prime example of the interlinked relationships between opsin genes, photopigments and colour vision, and because it can provide unique insights into the evolution and use of primate colour vision.

In his comparative study Grether (1939) examined colour vision in a female spider monkey. In contrast to other New World monkeys tested, this animal showed excellent wavelength discrimination ability, having thresholds comparable to those equivalently measured in Old World monkeys and people and it was concluded that she had trichromatic colour vision (Grether 1939). That interpretation was supported by tests subsequently run on a pair of spider monkeys in which both a male and a female showed evidence of trichromatic colour vision, although the two had different visual capacities and neither seemed identical to normal human trichromats (Blakeslee & Jacobs 1982).

It was against this background and the modern understanding of platyrrhine colour vision that we set out to measure photopigments in Atelid monkeys by making spectral sensitivity measurements in various representatives from this family, including spider monkeys. In the course of these experiments we discovered that one of the four genera in Atelidae, the howler monkeys (*Alouatta*), have opsin gene and photopigment complements that predicts that all of the members of this genus, male and female alike, should have trichromatic colour vision (Jacobs *et al*. 1996b). That conclusion has been reinforced by further examinations of howler monkey opsin genes (Kainz *et al*. 1998; Dulai *et al*. 1999). This paper summarizes results obtained from measurements of spectral sensitivity in animals from two other genera of Atelid monkeys—spider monkeys (*Ateles*) and woolly monkeys (*Lagothrix*). Contrary to the results obtained from howler monkeys and from expectations based on earlier behavioural studies, these monkeys appear to have a photopigment polymorphism generally similar to that of many other platyrrhine species. An abstract reporting preliminary results has appeared (Jacobs & Deegan 1993).

## 2. METHODS

Recordings of 47 juvenile and adult spider monkeys (18 male and 29 female) were made. Of these, 12 were brown-headed spider monkeys (*Ateles fusciceps robustus*) and 18 were black-handed spider monkeys (*Ateles geoffroyi*). The remaining 17 spider monkeys were from a colony in which hybridization had occurred making accurate species identification impossible. Nine common woolly monkeys were also examined. All of these were adult males—eight were *Lagothrix lagotrica poeppigii* and one was classified as *Lagothrix lagotrica lugens*.

The use of electroretinogram (ERG) flicker photometry for measuring spectral sensitivity and inferring photopigment complements in individual monkeys has been fully described elsewhere (Jacobs *et al*. 1996a; Jacobs & Neitz 1987a; Jacobs & Deegan 1999). In brief, the cornea was anaesthetized by topical application of proparacaine hydrochloride (0.5%) and ERGs were differentially recorded from a contact-lens electrode installed in the eye of a sedated monkey. The recordings were conducted at a variety of test sites and the anaesthetic regime varied somewhat according to the local veterinary practice. An

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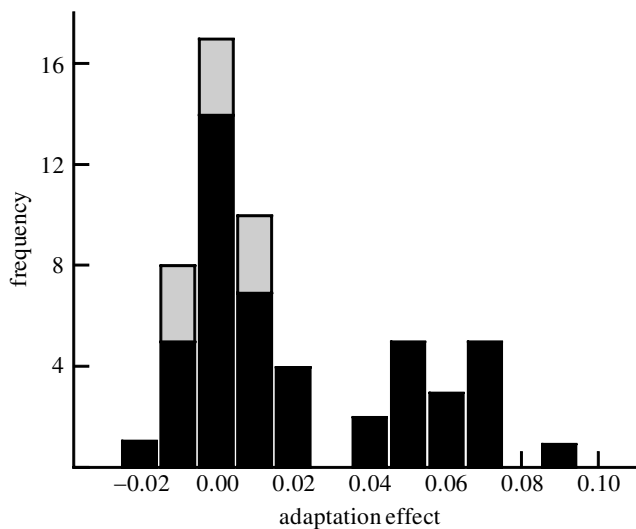
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Figure 1. Results from a test of response univariance run on spider and woolly monkeys. The adaptation effect is the difference (log units) between photometric equations made for 540 and 630 nm lights under conditions of red and green adaptation. The absence of an adaptation effect (value *ca*. 0.0) indicates the presence of a single class of middle- or long-wavelength photopigment and predicts dichromatic colour vision. Equations for spider monkeys are shown in black and equations for woolly monkeys are shown in grey. Bin width = 0.01 log units.
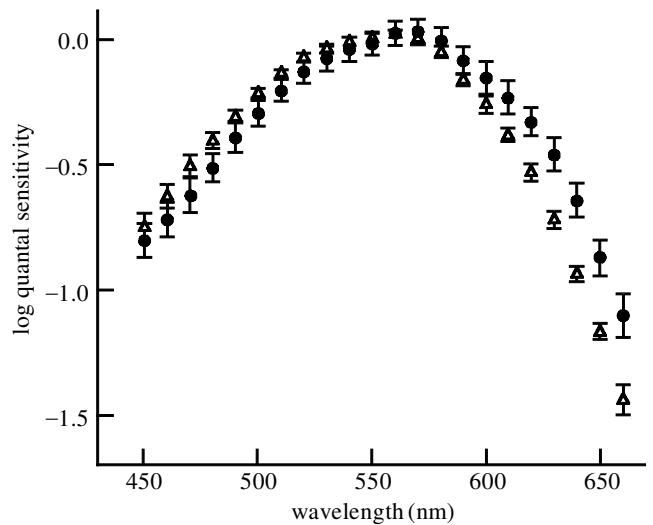


Figure 2. Spectral sensitivity functions for two types of cone found in spider monkeys determined as described in § 2. All of these animals were shown to have only a single type of middle- or long-wavelength cone. The triangles are the mean values for ten monkeys ( ± s.d.). The functions for individual animals were shifted on the vertical axis prior to averaging so that all had the same average sensitivity. Circles show the averaged data for 21 spider monkeys plotted using the same conventions.

intramuscularly injected mixture of ketamine hydrochloride ($20 \, mg \, kg^{-1}$) and acepromazine maleate ($0.2 \, mg \, kg^{-1}$) was most frequently used. The pupil was dilated by topical application of atropine sulphate (0.04%) and phenylephredine hydrochloride (10%).

A three-beam, Maxwellian view (circular spot) (59°) optical system was used. The sources were regulated tungsten–halide lamps and the three beams were the test light of the photometer that came from a monochromator (half-energy pass band = 10 nm), the photometer reference light (achromatic 2450 K) (retinal illuminance = 3.3 log td) and an adaptation light, respectively. ERGs were recorded for trains of square-wave pulses originating from the test and reference beams. These trains were interleaved and each was modulated with a 25% duty cycle. A neutral-density wedge was used for varying the radiance of the test light. The reference and adaptation lights were controlled through the use of neutral-density step filters and interference filters (Optical Thin Films, North Conway, NH, USA) (10 nm half bandwidth). The system used to process the ERG signals is described elsewhere (Jacobs *et al*. 1996*a*). The recordings were made with ambient illumination at photopic levels (ranging from 150 to 400 lux at the different recording locations).

The effectiveness of the test and reference lights in the flicker photometric procedure was equated by adjusting the intensity of a test light until the ERG it elicited was equivalent to the response produced by a reference light. These equations were made based on the average of the fundamental responses to the last 50 cycles of a total of 70 stimulus cycles. The density setting on the wedge at the point of an equation was recorded to a precision of 0.01 log units. Each test/reference light equation was completed at least twice during the course of the experiment and these individual values were subsequently averaged.

Two sets of data were collected from each monkey. We first measured a spectral sensitivity function by varying the test light

over the spectral range from 450 to 660 nm in steps of 10 nm (stimulus pulse rate = 31.25 Hz). Second, a test for response univariance was conducted in order to determine whether the retina contained more than one type of middle- or long-wavelength-sensitive photopigment and, consequently, whether the monkey would be predicted to have dichromatic or trichromatic colour vision (Jacobs & Neitz 1987*a*). In this case photometric equations were established for a 540 nm test light and a 630 nm reference light (flicker rate = 31.25 Hz) as the eye was first adapted to a 540 nm light and then to a 630 nm light. The intensities of the two adaptation lights were set such that each elevated the threshold of a 560 nm test light by an equal amount (0.5 log units). One type of New World monkey (*Aotus*) has been found to lack a functional short wavelength-sensitive cone (Jacobs *et al*. 1993*a*). Consequently, we tried to obtain an objective indication of the presence of a viable short-wavelength cone pigment for representative animals from each species by measuring spectral sensitivity with test conditions previously demonstrated effective for this purpose (Jacobs & Deegan 1999). These test conditions included (i) a stimulus pulse rate of 12.5 Hz, (ii) a 460 nm reference light, and (iii) concurrent adaptation of the eye to a bright long-wavelength light that was produced by inserting a high-pass filter (50% transmission at 585 nm) into the adaptation beam. Sensitivity measurements were then made for short-wavelength test lights (usually 430–510 nm taken at 10 nm steps).

## 3. RESULTS

### (a) *Spider monkeys*

Although spectral sensitivity functions were measured prior to the test for response univariance, the results from that test served to organize the spectral measurements so that they were presented first. A majority of the spider monkeys (31 out of 47 animals) showed no consistent
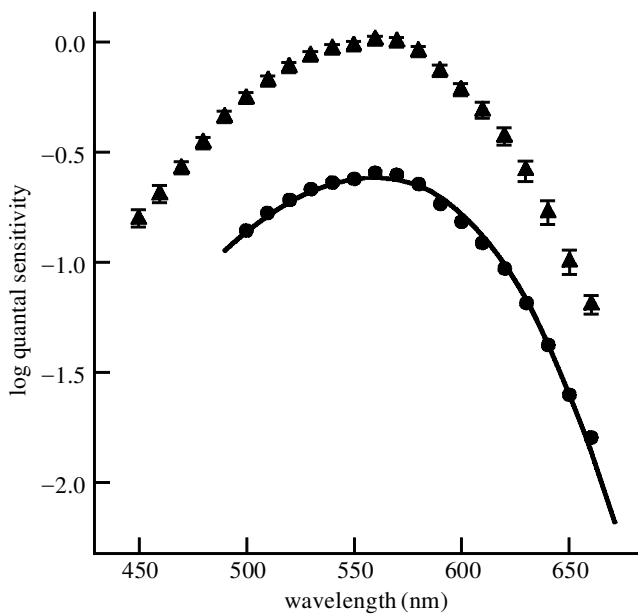
Figure 3. Top line: spectral sensitivity functions for 16 trichromatic spider monkeys. All other details are as given in figure 2. Bottom line: the sensitivity values from the trichromatic spider monkeys for wavelengths of 500 nm and longer have been best fitted (continuous line) with a summative combination of absorption curves for pigments having $\lambda_{\max}$ values of 562 and 550 nm.
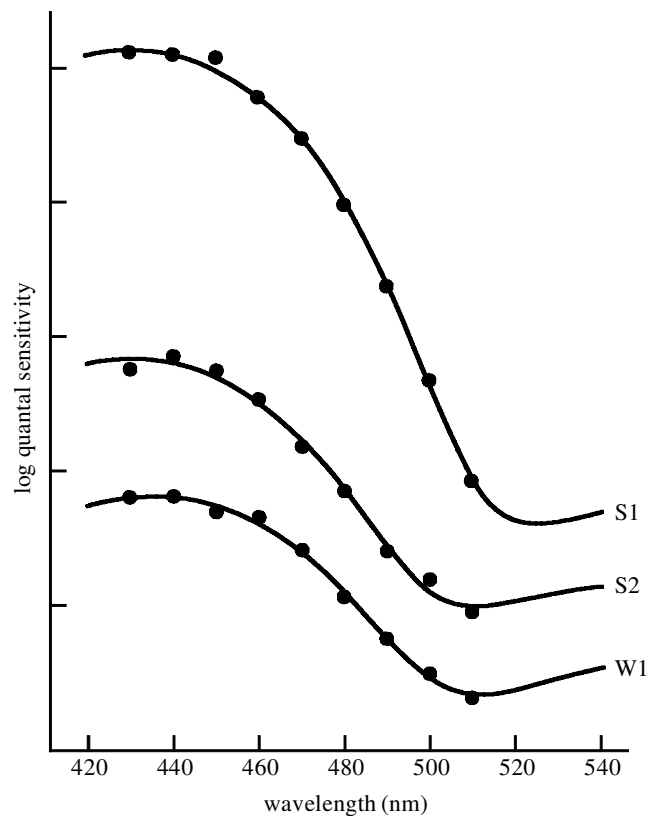


Figure 4. Spectral sensitivity measurements that illustrate the presence of short-wavelength cones in spider (S) and woolly (W) monkeys. Each function was obtained from a single animal using test conditions that were designed in order to suppress contributions from middle- and long-wavelength cones (see § 2). The continuous lines are the best-fitting linear sums of the absorption curves for the middle- or long-wavelength cone previously measured for each animal ($\lambda_{\max}$ values, S1 = 550 nm, S2 = 562 nm and W1 = 562 nm) and a short-wavelength cone, the peak value of which was derived from the fitting procedure. The functions for the three animals have been arbitrarily positioned on the sensitivity axis where each scale division equals 0.5 log units.

change in the 540/630 nm equations under the two conditions of chromatic adaptation. The photometric equations for the remainder of the animals did change consistently, i.e. more 540 nm light was required when the eye was adapted to 540 nm light and less 540 nm light was required when the adaptation light was changed to 630 nm. These results are summarized as a frequency histogram in figure 1. The differences in the equation values for the two adaptation conditions obtained from animals showing no consistent chromatic adaptation (mean ± s.d. = 0.004 ± 0.009 log units) are very similar to those obtained from human dichromats tested in exactly the same fashion (mean ± s.d. = 0.014 ± 0.015 log units) ($n = 27$) (Jacobs & Deegan 1997). The remainder of the sample all showed a small but consistent adaptation effect (mean ± s.d. = 0.056 ± 0.015 log units). This experiment thus indicates that some spider monkeys have only a single type of medium- or long-wavelength cone photopigment while others have more than one.

The spectral sensitivity functions for those spider monkeys that failed to give a chromatic adaptation effect fell into two spectrally discrete groups. These are shown in figure 2. The majority (21 out of 31) (data points indicated by circles in figure 2) had spectral sensitivity functions that peaked at longer wavelengths than the remainder (data points indicated by triangles in figure 2). The individual variations in spectral sensitivity within each group were quite small. The spectral sensitivity functions for those spider monkeys that did show significant chromatic adaptation effects are illustrated in a similar fashion in figure 3. The individual variations in spectral sensitivity among animals of this group were likewise small and their spectral sensitivity functions were

consistently broader than those of the monkeys whose data are given in figure 2.

There were no obvious differences in the representations of animals from the two species of spider monkey in the groups identified separately in the results of figures 2 and 3, but there was a clear difference between the sexes. None of the male monkeys tested showed any systematic effects of chromatic adaptation. Consequently, the spectral sensitivity functions for all of the males are included in figure 2. On the other hand, approximately half of the female monkeys fell into each of the two groups (16 out of 29 showed significant chromatic adaptation effects). Thus, all of the spectral sensitivity functions in figure 3 are from female spider monkeys.

Verifying the presence of a short-wavelength cone in spider monkeys was straightforward. Figure 4 shows the spectral sensitivity functions obtained from two subjects (S1 and S2) in the presence of long-wavelength adaptation. Exposure to long-wavelength light greatly reduced the monkeys' sensitivity to middle and long wavelengths while at the same time revealing contributions to the ERG signal from a population of short-wavelength cones.
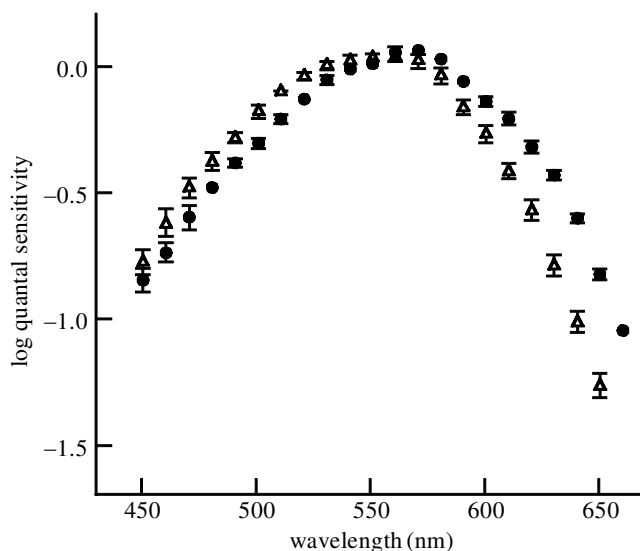
Figure 5. Spectral sensitivity functions for two types of dichromatic woolly monkey. Triangles represent the mean values for five monkeys and circles represent the mean values for four monkeys. All other conventions are the same as those for figure 2. Note that, in a number of cases, the error bars are smaller than the size of the data points.

## (b) *Woolly monkeys*

None of the nine woolly monkeys tested showed evidence of differential chromatic adaptation over the middle- to long-wavelength portion of the spectrum. The changes in the photometric equations between the two conditions of chromatic adaptation were insignificant (see figure 1) (mean shift ± s.d. = 0.003 ± 0.003 log units). In accord with the discussion above, this suggests that none of these animals would be expected to have trichromatic colour vision.

The spectral sensitivity functions for the woolly monkeys also fell into two groups and their averaged values are shown in figure 5. Again, individual variability within the groups was quite small and, as was the case for the dichromatic spider monkeys, the two groups can be seen to differ systematically, one group having spectral sensitivity that peaked at somewhat longer wavelengths than the other. The presence of an active short-wavelength cone mechanism in woolly monkeys was verified by measuring spectral sensitivity under adaptation and test conditions that were designed in order to minimize contributions from the middle- and long-wavelength cones. Figure 4 (labelled W1) shows such a function.

## (c) *Photopigments of Atelid monkeys*

Evidence was obtained for the presence of three separate cone mechanisms in both spider and woolly monkeys. The spectral sensitivities of those monkeys having only a single middle- or long-wavelength mechanism can provide an estimate of the absorption properties of the cone pigments, but doing so requires that some assumptions be made. Although there is no published evidence on the presence of any pre-retinal filters in either spider or woolly monkeys, it seems certain that they, like all other diurnal primates, have both lens and macular pigments that significantly absorb short-wavelength lights and can thus condition the spectral sensitivity functions.

Truncating the spectral sensitivity functions to include only the longer wavelengths is one strategy that is used to minimize the potential effects of these filters (Sharpe *et al*. 1998). Figure 6*a* shows the averaged spectral sensitivity functions for the two groups of dichromatic spider monkeys. Test wavelengths shorter than 500 nm were omitted from this analysis. A variety of different absorption curves have been proposed as best accounting for photopigments. Curves previously employed in characterizing photopigments from New World monkeys have been best fit to the data arrays in figure 6 (Jacobs & Neitz 1987*a*,*b*; Jacobs *et al*. 1987). These functions provide a good account of the two sets of data for peak values ($\lambda_{max}$) of 551 (left-hand panel) and 562 nm (right-hand panel). The dispersion of the results from monkeys in each of the two groups was examined by computing peak values for each subject individually. These were as follows for the two groups: mean ± s.d. = 550.2 ± 1.32 and 561.2 ± 2.20 nm.

Since only two different middle- or long-wavelength pigments were detected in the sample of spider monkeys tested, it is reasonable to assume that these two are present in the animals whose retinas contained more than one middle- or long-wavelength pigment. The averaged data for the 17 animals falling in this category have been fitted with the best-fitting linear sum of two middle- or long-wavelength pigments having peak values of 550 and 562 nm in figure 3 (bottom curve). Before fitting, the short-wavelength points were truncated from the functions for the reasons given above. The combination of 550 (44%) + 562 nm (56%) is a best fit for the spectral sensitivity of these putative trichromatic monkeys.

The data obtained from the nine woolly monkeys were analysed in the same fashion as described above and the results are shown in figure 6*b*. In this case, the best-fitting photopigment absorption curves had peak values of 548 (left-hand panel) and 563 nm (right-hand panel). Fits made to the data from individual animals again showed only small variation (the mean values for the two groups were 546.8 ± 1.00 and 562 ± 0.58 nm). The spectral positioning of the longer of the two middle- or long-wavelength pigments did not differ for spider and woolly monkeys as judged from $\lambda_{max}$ estimates ($t = 0.67$, d.f. = 23 and $p > 0.05$; figure 6, right-hand panels) but, by the same reckoning, the spectral positions of the other middle- or long-wavelength pigment did differ significantly for the two types of monkey ($t = 4.96$, d.f. = 13 and $p < 0.01$; figure 6, left-hand panels).

A short-wavelength cone mechanism was present in both spider and woolly monkeys. It was not possible to specify its spectral positioning precisely because details of the short-wavelength filters in the eyes of these New World monkeys are unknown and because the chromatic adaptation technique used to reveal short-wavelength cone contributions could not be automatically assumed to have eliminated all contributions to spectral sensitivity from the middle- or long-wavelength cones. In the face of these uncertainties we attempted to account for the spectral sensitivity functions in figure 4 by first assuming that absorption in the lens of these large New World monkeys might be like that measured for the similarly sized Old World macaque monkeys (Boettner 1967). The spectra for
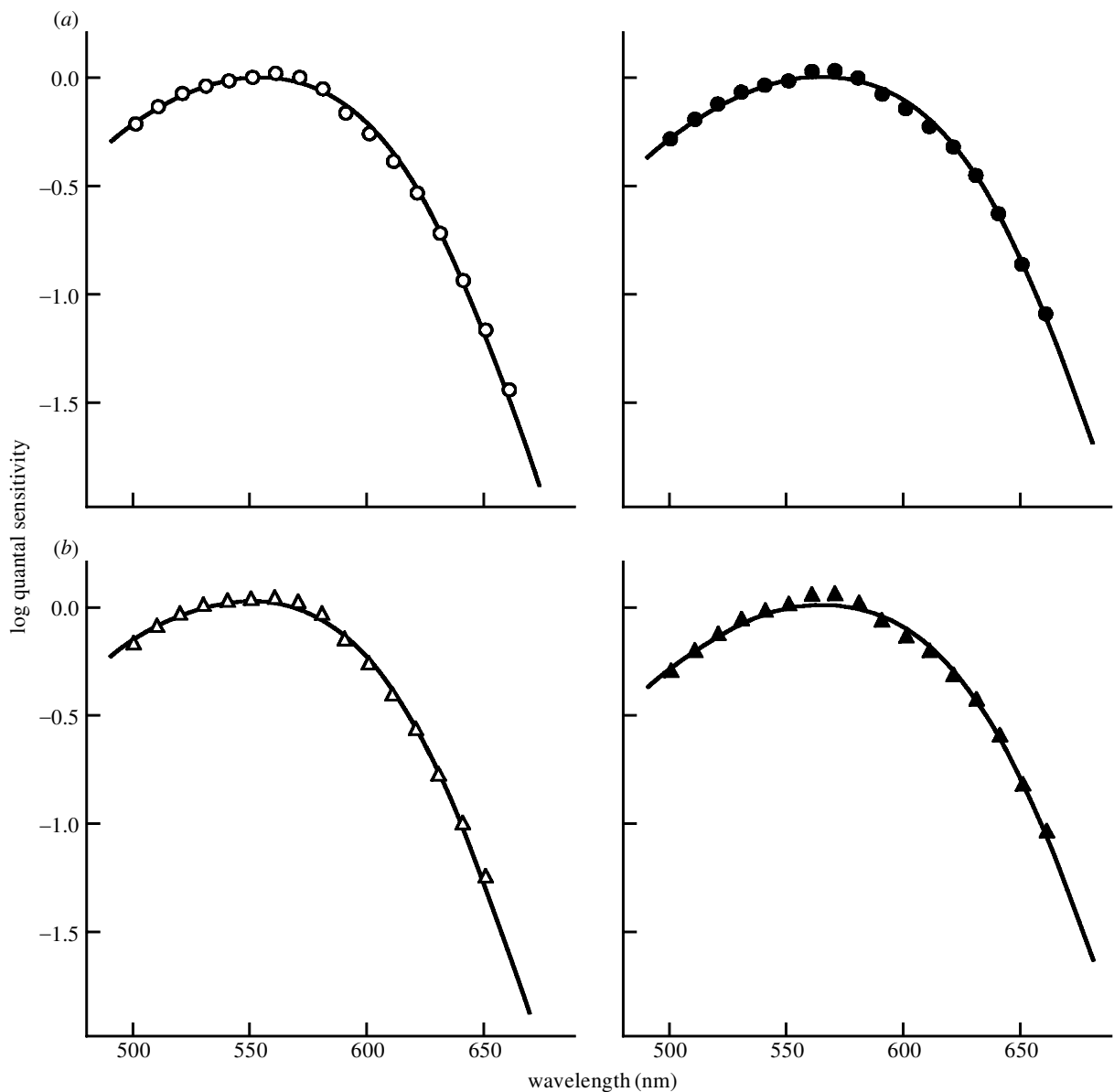
Figure 6. Average spectral sensitivity functions for spider (*a*) and woolly (*b*) monkeys. The two types of dichromatic monkey have been best fit with photopigment absorption curves having peak values of 551 and 562 nm (spider monkeys) and 548 and 563 nm (woolly monkeys). For other details see the text.

the middle- or long-wavelength cones determined in each of these Atelid monkeys were measured directly. In order to account for the measured spectral sensitivity function we determined what linear sum of the identified middle- or long-wavelength pigment spectrum and a second pigment having peak sensitivity somewhere in the short wavelengths would best account for the data array. In order to accomplish this the short-wavelength cone absorption curve was stepped from 420 to 460 nm in 1 nm steps and the best fitting summation of the putative short-wavelength and known middle- or long-wavelength pigment was calculated for each position. The best fits (continuous lines in figure 4) were obtained by assuming short-wavelength cone $\lambda_{max}$ values of 432 nm (spider monkeys) and 437 nm (woolly monkey), respectively. These values are close to the spectral peaks of short-wavelength cones measured directly in squirrel monkeys (Mollon *et al*. 1984).

## 4. DISCUSSION

ERG measurements of spectral sensitivity provide a consistent picture of the photopigment arrangements characteristic of spider monkeys and, although the sample size was more limited, the results obtained here indicated that woolly monkeys are not substantially different.

### (a) *Comparisons to other New World monkeys*

There are variations in the cone photopigment complements of individual animals for the majority of New World monkeys so far studied and these variations translate directly into significant differences in visual sensitivity and colour vision. Although the extent and nature of the evidence varies for different types of monkey, this general arrangement holds for various callitrichid monkeys (Jacobs *et al*. 1987; Travis *et al*. 1988; Tovée *et al*. 1992; Jacobs & Deegan 1994) as well as for familiar

cebids such as squirrel and capuchin monkeys (Jacobs 1984; Mollon *et al.* 1984; Jacobs & Neitz 1987*b*). In each case, these variations reflect the presence of polymorphic middle- or long-wavelength cone opsin genes at single X-chromosome sites (Jacobs & Neitz 1987*a*; Williams *et al.* 1992; Hunt *et al.* 1993; Jacobs *et al.* 1993*b*; Shyue *et al.* 1995). The most prominent diagnostic feature of this polymorphism is the presence of only a single middle- or long-wavelength pigment in all males. Of the 27 male spider and woolly monkeys studied, each had only one middle- or long-wavelength pigment. It seems quite clear that these two genera of New World monkey must have an opsin gene/cone photopigment polymorphism that is similar to that previously documented for several other types of New World monkey. This conclusion is consistent with genetic examinations that have detected only a single X-chromosome opsin gene in male spider and woolly monkeys (Hagstrom *et al.* 1993; Boissinot *et al.* 1997).

Two different photopigment patterns have emerged from studies of polymorphic New World monkeys. Although estimates of the spectral positioning of the photopigments vary somewhat as a function of the nature of the measurement employed and the means used to characterize the spectra, representative callitrichid species have a total of three middle- or long-wavelength photopigments with $\lambda_{max}$ values of *ca.* 543, 556 and 562 nm (Jacobs *et al.* 1987; Travis *et al.* 1988). One of the three middle- or long-wavelength pigments ($\lambda_{max} = ca.$ 562 nm) appears to be the same in other New World monkeys, but the other two occupy different spectral positions in cebid monkeys ($\lambda_{max} = ca.$ 535 and 550 nm). The spectral positions of the two middle- or long-wavelength pigments identified in spider and woolly monkeys are thus more similar to two of those found in the cebids. In the ERG measurements the shorter of the two middle- or long-wavelength pigments assumes slightly different spectral positions in woolly and spider monkeys, the former shifted *ca.* 3 nm towards the shorter wavelengths. This difference is not large and rests on a relatively small sample. Beyond that, it could reflect an opsin sequence variation at one of the tuning sites known to yield small shifts in the spectral positioning of primate middle- or long-wavelength cone photopigments (Shyue *et al.* 1998).

Unlike the other polymorphic monkey species examined earlier, we found evidence for only two middle- or long-wavelength pigments in spider and woolly monkeys. This is a potentially important difference, but needs to be treated cautiously. Obviously, the failure to find a third pigment type could simply be a sampling problem. For instance, it might be that the animals studied were drawn from restricted breeding groups and the absence of a potential third middle- or long-wavelength opsin gene reflects that genetic bias. The latter possibility seems unlikely, at least for the spider monkeys since they were tested at seven different sites, each of which derived their animals from different (and varied) sources. It might also be that these monkeys have a third middle- or long-wavelength pigment, but that the allele specifying that pigment is present at an unusually low frequency in the population. Middle- or long-wavelength photopigments have been characterized earlier in approximately the same number

of dichromatic squirrel monkeys as were identified in the present study (Jacobs *et al.* 1993*b*). Among squirrel monkeys, the three middle- or long-wavelength pigments were detected at approximately equal frequency. Assuming equal incidence of the middle- or long-wavelength gene alleles to be characteristic of New World monkeys and using the Poisson approximation to the binomial theorem, the probability of our failing to detect any animals having a third type of middle- or long-wavelength pigment is $5 \times 10^{-6}$. The same approach can be used to estimate the maximum incidence of this third pigment in spider and woolly monkeys given the sample size examined. The value thus obtained ($p = 0.05\%$) is 9%. This suggests that, at the least, the presence of a third type of middle- or long-wavelength cone pigment in spider and woolly monkeys must be rare. A major practical implication of this restriction is that the number of females heterozygous at the opsin gene site (and, hence, potential trichromats) would be expected to be lower than for species that maintain three allelic versions of this gene. That difference was in fact observed—55% (16 out of 29) of the female spider monkeys in this sample had two middle- or long-wavelength pigments while 63% of female squirrel monkeys had earlier been found to have two middle- or long-wavelength pigments (Jacobs *et al.* 1993*b*).

Although a variety of different phylogenetic arrangements have been proposed for New World monkeys, the alternative versions all agree on the close association of howler monkeys, spider monkeys and woolly monkeys (Hugot 1998). The current results support the view that the latter two have only a single X-chromosome opsin gene and, thus, that they are similar to most New World monkeys and distinctly different from howler monkeys. As noted above, howler monkeys have two X-chromosome genes specifying separate middle- and long-wavelength cone pigments. As in the case of the catarrhine primates, the two separate middle- and long-wavelength opsin genes of the howler monkey emerged as a result of opsin gene duplication, but sequence comparisons also show that the gene duplication in howler monkeys occurred independently of the analogous event in Old World primates (Boissinot *et al.* 1997; Hunt *et al.* 1998; Kainz *et al.* 1998; Dulai *et al.* 1999). A phylogeny derived from comparisons of ε-globin gene sequences places the divergence date for howler monkeys, woolly and spider monkeys at *ca.* 13 million years ago (Harada *et al.* 1995). The difference in the opsin gene arrangements of these two lines suggests that the gene duplication rendering the colour vision of howler monkeys unique among all other New World monkeys has occurred since that time.

## (b) *ERG spectral measurements and behavioural results*

Although the earlier diagnosis of trichromatic colour vision that emerged from discrimination tests run on two female spider monkeys is consistent with the results of this investigation (Grether 1939; Blakeslee & Jacobs 1982), the claim for trichromacy in a single male spider monkey is not. Re-examination of the procedures and results from that experiment did not reveal any obvious reasons for what now seems an unlikely outcome. Some post hoc hypotheses might be advanced for explaining this discrepancy, but from this remote vantage point none can

be seriously evaluated. For the present the earlier conclusion seems either misled for some reason or it represents the occurrence of a serious anomaly in the arrangement of cone photopigments and colour vision in spider monkeys suggested by the current results.

### (c) *Atelid monkeys and the use of primate colour vision*

There remain gaps in our understanding of colour vision in New World monkeys. Even so, it seems apparent that a vast majority of the 70 or so species that comprise this group of primates have polymorphic middle- or long-wavelength cone opsin genes leading to a mixture of trichromatic and dichromatic individuals. The maintenance of these gene polymorphisms implies that trichromacy must be advantageous. Over the years a number of potential advantages have been suggested (Mollon *et al.* 1984; Mollon 1991; Jacobs 1997), but the only empirical evidence on the matter comes from a recent experiment claiming that trichromatic tamarins are more apt at foraging for food in a semi-natural environment than their dichromatic colleagues (Caine & Mundy 2000).

Not surprisingly, food harvesting figures prominently in discussions of primate trichromacy. It has long been an article of faith that the detection and discrimination of coloured fruits in a foliage background provides a framework for the evolution of trichromatic colour vision (Allen 1879; Polyak 1957) and recently this idea has been expanded to include the possibility that trichromatic colour vision might also prove advantageous in discriminations between the leaves preferentially selected as food items by some primates (Lucas *et al.* 1998). The fruit selection hypothesis has support from modelling studies that have demonstrated that the middle- and long-wavelength pigments of trichromatic primates are spectrally well positioned for the task of discriminating objects having the reflectance properties of orange and yellow fruits from foliage backgrounds (Osorio & Vorobyev 1996; Regan *et al.* 1998). These investigations indicated that primate trichromacy can provide a useful tool in the detection and discrimination of fruits and this could well serve as an advantage that reinforces and maintains trichromatic arrangements. There are probably other advantages as well since the gene duplication that allowed universal trichromatic colour vision in early catarrhine primates seems to have been very conservatively maintained across what is now a diverse group of animals. For instance, the trichromacy of contemporary species with highly frugivorous life styles, such as the cercopithecine monkeys of West Africa, is no different to that of colobine monkeys, who are dedicated foliovores (Jacobs & Deegan 1999). Indeed, a recent examination of the spectral properties of fruits and leaves concluded that catarrhine trichromacy may prove advantageous for finding either fruits or leaves against foliage backgrounds (Sumner & Mollon 2000).

The photopigments and colour vision of Atelid monkeys may provide an illustration of the difficulty in attempting to link colour vision capacities to any single aspect of visual behaviour. Both spider and woolly monkeys are described as primary frugivores with fruits comprising as much as 80–90% of their diet (Kinzey 1997). Spider monkeys are further characterized as specializing in ripe fruits: 'immature fruit are eaten only when mature fruit are unavailable' (Kinzey 1997, p. 195). Colour would seem likely as providing a useful cue in guiding such selective behaviour. On the other hand, although the diet of howler monkeys clearly includes an assortment of fruit (Regan *et al.* 1998), members of this genus are much less consistent fruit eaters than spider and woolly monkeys, being described as either foliovore–frugivores or frugivore–foliovores depending on the season (Kinzey 1997). Significantly too, howler monkeys have been reported 'to feed on more immature fruits than other sympatric primates' (Kinzey 1997, pp. 179–180). On the surface these observations might suggest that it is spider and woolly monkeys that would be best served by having trichromatic skills, but howler monkeys are the ones apparently enjoying universal trichromatic colour vision while no more than approximately one-quarter of all woolly and spider monkeys are trichromats. From both the commonality of trichromacy among highly diverse catarrhine primates and comparison of these closely related Atelid monkeys it is hard to escape the idea that trichromatic colour vision must allow a significant range of visual advantages that could potentially serve to maintain the adaptation.

Finally, the developing understanding of primate middle- or long-wavelength cone opsin genes provides an excellent example of how the timing of gene duplication can have a significant impact. Opsin gene duplication happened early in catarrhine history and, as a result, all contemporary species are endowed with trichromatic colour vision. On the other hand, the analogous event seems to have occurred only relatively recently in platyrrhine history and, consequently, only a single genus of New World monkey currently enjoys universal trichromacy.

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