

## RESEARCH NOTE

# COLOR VISION IN SQUIRREL MONKEYS: SEX-RELATED DIFFERENCES SUGGEST THE MODE OF INHERITANCE

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**Abstract**—Behavioral tests of vision in squirrel monkeys (*Saimiri sciureus*) reveal that there are widespread individual variations in color vision in this species. The variation has a sex-related component: whereas both trichromatic and dichromatic color vision occurs among female monkeys, males appear exclusively dichromatic. This finding suggests that, unlike humans, squirrel monkeys have only a single photopigment locus on the X chromosome.

Squirrel monkeys (*Saimiri sciureus*)    Color vision    Genetics

Over the past several years we have accumulated evidence indicating there are significant individual variations in color vision in the platyrrhine species *Saimiri sciureus* (the squirrel monkey) (Jacobs, 1984). Behavioral tests of color vision show some of these monkeys have trichromatic color vision, while others have dichromatic color vision. Within each of these categories several subvarieties can be discerned, and it presently appears that as many as six different color vision phenotypes may be required to characterize color vision in this species. Unlike the human, where significant color vision variations involve only a small proportion of the population, the color vision variations in squirrel monkeys are widespread. Indeed, it is as yet not possible to say which of the several color vision types, if any, is predominant. In concurrent experiments, measurements of retinal photopigments have been made in squirrel monkeys using the technique of microspectrophotometry (Mollon *et al.*, 1984). These measurements reveal the presence of four classes of cone photopigments having absorbance peaks at about 433, 535, 550 and 564 nm. Although the 433 nm photopigment is probably common to all animals, there are considerable variations between animals in the presence of the latter three types. The photopigment measurements correlate well with the behavioral results in that monkeys judged dichromatic have only one of the latter three types while those tested as trichromatic had two. Thus in the squirrel monkey, as is usual in the human, there appears to be a direct correspondence between the retinal photopigments and color vision phenotype. Although the details of the distribution of color vision phenotypes among squirrel monkeys are not yet known, we have found there are striking differences in the variations in color

vision in the two sexes. These differences are summarized here and their implications for the inheritance of color variation in this species are considered.

Color vision was established in behavioral tests involving a three-alternative, forced-choice discrimination, the details of which are given elsewhere (Jacobs, 1984). Of interest here was whether any given monkey had dichromatic or trichromatic color vision. That distinction was made on the basis of the animal's performance on one or more of three color vision tests: wavelength discrimination, Rayleigh matches, and a search for a spectral neutral point. Figure 1 illustrates the results obtained from typical dichromatic and trichromatic monkeys on each of these three tests. An animal was judged dichromatic if (1) its wavelength discrimination function was U-shaped with a single minimum around 500 nm, (2) it was unable to discriminate both a monochromatic red and a monochromatic green light from a yellow light (i.e. failed to make a Rayleigh match), and (3) it was unable to discriminate some monochromatic light in the wavelength range from 485 to 510 nm from an equiluminant white light. Alternatively, monkeys were judged trichromatic if their wavelength discrimination functions had twin minima at about 500 and 580 nm, if they were able to set a unique Rayleigh match, and if they showed no evidence of a neutral point. All of these criteria have been classically employed to distinguish between human dichromats and trichromats (Boynton, 1979; Pokorny *et al.*, 1979).

Data from a total of 36 squirrel monkeys were examined. Using the phenotypic and karyotypic criteria established by Ariga *et al.* (1978), these animals were judged to have the following geographical

orgins: Peru (27 monkeys), Colombia (4), Bolivia (4), Guayana (1). Twenty of these completed more than one of the tests; in those cases there was agreement between the outcome of the separate tests. Detailed results for these animals are presented elsewhere (Jacobs, 1984; Jacobs and Blakeslee, 1984).

The outcome of this survey is given in Table 1 from which it can be seen that although a majority of the

female monkeys had trichromatic color vision, none of the males did. The difference in occurrence of trichromacy and dichromacy in the two sexes is highly significant ( $\chi^2 = 20.57$ , d.f. = 1,  $P < .001$ ).

Of particular interest here is the fact that none of the males had trichromatic color vision. Although the total number of such animals tested is still somewhat limited (15 monkeys), less individually compelling observations made on additional monkeys also yield no evidence for male trichromacy. For instance, the results of both visual sensitivity tests (Jacobs, 1983a) and electrophysiological measurements (Jacobs, 1983b) are compatible with this conclusion. Accordingly, it presently appears that all male squirrel monkeys have dichromatic color vision.

The study of the inheritance of color vision in humans suggests a possible explanation for the squirrel monkey results. From examinations of pedigrees it was established over a hundred years ago that the common (red-green) color vision defects among humans are inherited as X-chromosome linked recessive traits, and hence the incidence of defective color vision is very much higher in males than in females (Kalmus, 1965; Jaeger, 1972). It is currently believed that the retinal photopigments absorbing maximally in the middle to long wavelengths arises from the activity of two genes, both located on the X chromosome. Multiple alleles at each locus specify directly the type of photopigment produced (Piantanida, 1974). Thus, if a human male has alleles at each locus that code for the same type of middle to long wavelength photopigment, then only that photopigment will be produced and he will have dichromatic color vision.

We examined whether an X-linked, two-locus model could account for the observed frequencies of trichromatic and dichromatic color vision in male and female squirrel monkeys. Two assumptions were made: (a) that only three photopigments absorbing maximally in the middle to long wavelengths are available in this species, and (b) that the same photopigment gene is required at all loci to yield dichromatic color vision. To determine whether the observed frequencies of male and female dichromats and trichromats (Table 1) are in accord with the models requires that they be compared with expected frequencies. These expected frequencies are a function of the proportions of the three photopigment genes in the population. These proportions are unknown, and, thus, for each possible proportion of the three photopigments in the population a computer was used to generate a set of expected frequencies for: (1) males receiving the same photopigment gene at both X-chromosome loci (male dichromats), (2) males receiving different photopigment genes at both X-chromosome loci (male trichromats), (3) females receiving the same photopigment genes at both loci on both their X-chromosomes (female dichromats), and (4) females receiving at least two different X-chromosome photopigment genes (female trichro-

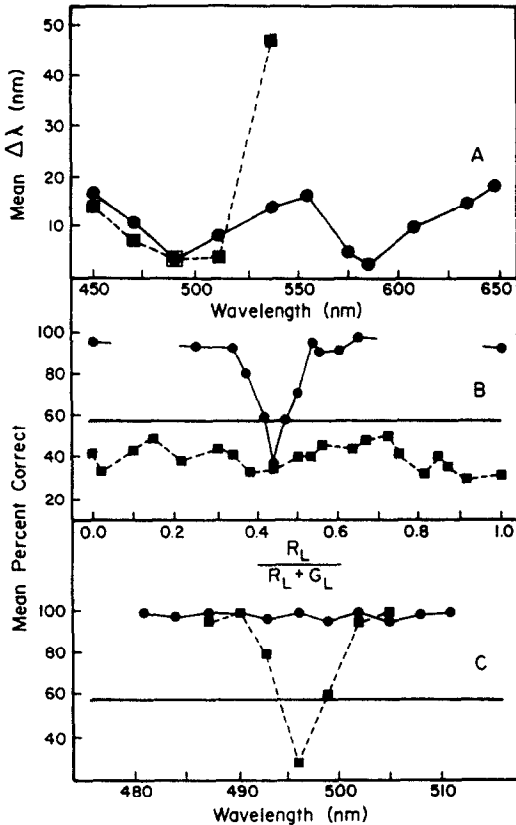


Fig. 1. Examples of the results obtained from squirrel monkeys on three tests of color vision. Each panel illustrates the outcome on one test for a typical dichromatic (●---●) and a typical trichromatic (●—●) monkey. Complete details about these tests are given elsewhere (Jacobs, 1984). **Panel A:** Wavelength discrimination functions. Each point plots the wavelength difference ( $\Delta\lambda$ ) required for successful discrimination at the indicated wavelength. A total of 18 monkeys (8 males, 10 females) completed this test. **Panel B:** Rayleigh matches. Each point shows the asymptotic performance achieved in a three-alternative forced choice test in which the monkey was required to discriminate a light composed of mixture of red and green light from a standard yellow light. Performance is based on a total of 25 test trials/mixture. The horizontal line indicates the 95% confidence level for successful discrimination. Note that the dichromatic subject failed the discrimination for all of the red/green mixture settings, whereas the trichromatic subject failed only for a restricted range of settings. A total of 25 monkeys (7 males, 18 females) completed this test. **Panel C:** Neutral point test. Each plotted point indicates the asymptotic performance level achieved by the subject in a test involving a discrimination between a monochromatic light and an equiluminant achromatic light. Performance is based on 25 trials/wavelength; the horizontal line again indicates the 95% confidence level. A total of 17 monkeys (10 males, 7 females) completed this test.

Table 1. Distribution of trichromatic and dichromatic color vision among 36 squirrel monkeys

	Type of color vision	
	Trichromatic	Dichromatic
Males	0	15
Females	16	5

The classification was based on each animal's performance on one or more of three behavioral tests of color vision.

mats). Each set of expected frequencies was compared to the observed frequencies of Table 1 and a goodness of fit was assessed by computing the least sum of squared differences between the two. The best fit was achieved for three photopigments in the proportions of 0.00: 0.23: 0.77. Even if this most-optimal proportion of photopigments actually characterized the present sample, a statistical test shows that the two-locus model is inadequate to account for the observed proportions of trichromatic and dichromatic squirrel monkeys ( $\chi^2 = 9.47$ , d.f. = 2,  $P < 0.01$ ).

An alternative explanation of the squirrel monkey results is the following: Assume that, as in the human, the gene(s) responsible for the production of middle to long-wavelength photopigments are located on the X chromosome. Now, if, unlike the human, there is only a single photopigment locus, and there are three alleles corresponding to three possible classes of photopigments, then the males will perforce have only one of the three possible pigment types and be dichromatic. On the other hand, two X chromosomes allow females the possibility of inheriting alleles which code for two different middle to long-wavelength photopigments. X-chromosome inactivation would yield two populations of photoreceptors in the retinas of females whose maternal and paternal alleles differ, and they would be trichromatic. If the alleles occur with equal frequency in the population, and the fact that we so far find no predominant color vision phenotype in either the males or the females suggests this is the case, then the single locus model predicts a 2:1 ratio of trichromatic to dichromatic females. The observed proportion of trichromatic and dichromatic female squirrel monkeys (Table 1) is compatible with that possibility ( $\chi^2 = 0.86$ , d.f. = 1, n.s.), although some others cannot yet be excluded.

Whether this simple model can be used to account for the heritability of color vision in the squirrel monkey or not will be eventually established through

an examination of color vision pedigrees in this species. It is for the present clear that both color vision variation and color vision inheritance in this primate differ in fundamental ways from that found in man. Interestingly, there is some evidence to suggest that the within-species variations in color vision established for the squirrel monkey may also be present in other neotropical monkeys, whereas various Old World monkeys seem to show no greater color vision variations than those found in man (Jacobs, 1983c). The evolution of color vision in these two groups of primates would appear to be at clearly distinguishable stages.

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#### REFERENCES

- Ariga S., Dukelow W. R., Emley G. S. and Hutchinson R. R. (1978) Possible errors of identification of squirrel monkeys (*Saimiri sciureus*) from different South American points of export. *J. med. Primat.* **7**, 139–135.
- Boynton R. M. (1979) *Human Color Vision*. Holt, Rinehart and Winston, New York.
- Jacobs G. H. (1983a) Within-species variations in visual capacity among squirrel monkeys (*Saimiri sciureus*): Sensitivity differences. *Vision Res.* **23**, 239–248.
- Jacobs G. H. (1983b) Differences in spectral response properties of LGN cells in male and female squirrel monkeys. *Vision Res.* **23**, 461–468.
- Jacobs G. H. (1983c) Variations in color vision among nonhuman primates. In *Colour Vision: Physiology and Psychophysics* (Edited by Mollon J. D. and Sharpe L. T.). Academic Press, London.
- Jacobs G. H. (1984) Within-species variations in visual capacity among squirrel monkeys (*Saimiri sciureus*): Color vision. *Vision Res.* **24**, 1267–1277.
- Jacobs G. H. and Blakeslee B. (1984) Individual variations in color vision among squirrel monkeys (*Saimiri sciureus*) of different geographical origin. *J. comp. Psychol.* **98**, 347–357.
- Jaeger W. (1970) Genetics of congenital colour deficiencies. In *Handbook of Sensory Physiology*, Vol. VII/4, *Visual Psychophysics* (Edited by Jameson D. and Hurvich L. M.). Springer, Berlin.
- Kalmus H. (1965) *Diagnosis and Genetics of Defective Colour Vision*. Pergamon, Oxford.
- Mollon J. D., Bowmaker J. K. and Jacobs G. H. (1984) Variations of colour vision in a New World primate can be explained by polymorphism of retinal photopigments. *Proc. Roy. Soc. Lond. B.* **222**, 373–399.
- Piantanida T. P. (1974) A replacement model of X-linked recessive colour vision defects. *Ann. Hum. Gen.* **37**, 393–404.
- Pokorny J., Smith V. C., Verriest G. and Pinckers A. J. L. G. (1979) *Congenital and Acquired Color Vision Defects*. Grune & Stratton, New York.