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Visual Sensitivity: Significant Within-Species Variations in a Nonhuman Primate

Abstract. *Among squirrel monkeys (*Saimiri sciureus*) there are significant sex-related differences in visual sensitivity. As measured behaviorally in an increment-threshold task, a sample of males was found to be substantially less sensitive to long-wavelength (640-nanometer) light than a group of females tested in the same way, although the two groups showed no significant differences in sensitivity to a middle-wavelength (540-nanometer) light. The two groups also differed on a test designed to measure the effects of chromatic adaptation.*

The presence of significant variations in sensory capacity among human populations has been documented for a number of sensory dimensions. Particularly well known, and by far the most extensively studied, are those variations collectively categorized as defective color vision (*1*). The differences in visual capacity between so-called color-defective observers and those with normal color vision can be substantial. For example, sensitivity to long test wavelengths may be on the order of 1 log unit or more higher in individuals with normal color vision than in those having one of the most common types of color-defective vision, protanopia (*2*). Study of these naturally occurring differences has occupied a prominent position in vision research, primarily because of the possibility of obtaining useful inferences about biological mechanisms through a comparison of normal and defective systems. However, because it is difficult to directly test hypotheses about mechanisms in human subjects, it would be useful if significant within-species variations in visual capacity could be identified in a nonhuman species. I have recently found such differences in the South American squirrel monkey and now report the results of behavioral tests of members of this species to indicate the nature and the magnitude of their variation in visual capacity (*3*). One of the interesting aspects of this variation is that it appears to be linked to gender.

All behavioral tests were conducted in the context of a forced-choice discrimination task. Three stimulus panels were transilluminated by light sources located outside a small test chamber. Each of these circular panels subtended 18° to 35° of visual angle, depending on the position of the unrestrained monkey. The interior of this chamber was continuously illuminated with an achromatic light (mean illuminance of 60 lux). Animals were deprived of food for 22 hours before each daily test session. Through an operant shaping procedure they were initially taught to receive a food reinforcement—a 97-mg banana-flavored pellet—by pressing a lever mounted adjacent to that stimulus panel which was differently illuminated from the other two. Between test trials the three panels were identically illuminated. A test trial consisted of opening a shutter which added light to one of the three panels. A cueing tone was used to demark the occurrence of this observation interval. A noncorrection procedure was used. The position of the positive panel (that is, the panel to which light was added) was random within the constraint that all three panels were positive an equal number of times in each test session.

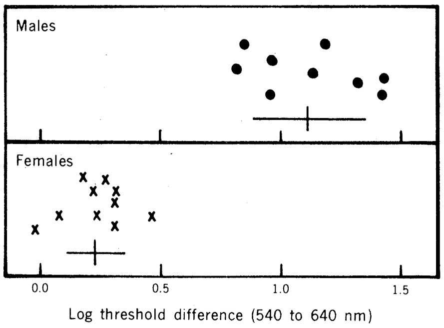

Fig. 1. Visual sensitivity of squirrel monkeys as measured in an increment-threshold task. The values plotted represent differences between the thresholds for 540- and 640-nm test lights. Each symbol represents one animal. These symbols are positioned arbitrarily on the ordinate for ease of viewing. The vertical line indicates the mean difference for each group, and the horizontal line encloses two standard deviations.

The subjects were adult squirrel monkeys (*Saimiri sciureus*). All were feral animals of the "Roman Arch" phenotype (*4*), but they were otherwise unselected. The first test consisted of measuring the monkeys' sensitivity to two different monochromatic lights, 540 and 640 nm (half-energy bandwidths of 10 nm). Either of the stimuli at a high-intensity level was added to one of the three panels, all of which were continuously illuminated with achromatic light (luminance = 3 cd/m^2, color temperature = 5820°K). During the initial training period, the two test lights were presented an equal number of times in each test session. Once the animal acquired the discriminations (as indicated by performing at, or close to, 100 percent correct), the intensity of each monochromatic light was decreased in steps of 0.3 log unit until a level was reached that produced chance discrimination (33 percent correct). At this point the full range of intensities for each test wave length was presented until, over test sessions, a total of 50 trials had been accumulated at each wavelength-intensity combination. From these results the intensity of the light required to produce threshold-level discrimination (arbitrarily defined as 50 percent correct) was determined. Thresholds for each test wavelength were determined twice, and if any improvement occurred between the first and second determinations, a third set of measurements was also made.

The results from tests of 19 monkeys (nine males, ten females) are shown in Fig. 1. In order to minimize the effects of individual differences in response criterion, the data plotted are the differences in threshold for the 540- and 640-nm test lights. The male monkeys show a much greater difference in sensitivity to the 540- and 640-nm lights than the females do. The mean threshold difference between these two wavelengths for the females is 0.23 log unit, whereas for the males, the corresponding comparison is 1.12 log units ($t = 4.56$, $P < .001$). There is in this sample no overlap between the two groups; that is, the most sensitive male was less sensitive to the long test wavelength than the least sensitive female. On the other hand, the two groups showed no significant differences in threshold to the 540-nm test wavelength ($t = 0.79$, $P > .05$).

It seemed unlikely that the large differences shown in Fig. 1 could be due to any systematic differences in response criteria or to some sort of preretinal filter present in some, but not all, animals. Nevertheless, these possibilities were evaluated by redetermining thresholds for several animals using the same two test wavelengths, but with the panel and house lights extinguished and the animals completely dark-adapted. Under conditions of light adaptation the threshold difference for a representative male was 1.42 log units, that for a representative female, 0.02 log unit. However, when the same two animals were tested under conditions of dark adaptation, the threshold differences were 2.16 and 2.28 log units, respectively; that is, the large differences seen under conditions of light adaptation disappeared when the animals were dark-adapted. This result shows that the differences seen in Fig. 1 cannot be due to any sort of preretinal filtering, and it suggests that they are not explicable on the basis of any systematic wavelength-related differences in response criteria. Rather, they must be due to differences in visual system mechanisms located in the retina or beyond, which operate only when the eye is light-adapted.

In another experiment, I sought to determine to what extent the visual sensitivity of these animals could be altered by chromatic adaptation. To do this, sensitivity thresholds were measured in the manner described but with the important difference that the panels were continuously illuminated with chromatic rather than with achromatic light. The effects of two different lights (having dominant wavelengths of 540 and 640 nm and luminances of 20 and 25 cd/m^2 respectively) on the thresholds for 540- and 640-nm test lights were determined. From the four measured thresholds, an index ($\bar{\eta}$) can be derived, which indicates whether the subject tested has two or more spectral mechanisms that are differentially affected by the adapting lights. This index is the difference between the sum of the two heterochromatic threshold values (for example, a 540-nm test light on a 640-nm background), given logarithmically, and the sum of the two homochromatic threshold values (for example, a 540-nm test light on a 540-nm background). If the subject shows differential chromatic adaptation over this spectral range, an index value greater than zero is obtained; if not, the value approximates zero (*5*, *6*).

Table 1 shows the results of this experiment for 14 monkeys. The index values for the male monkeys were uniformly clustered around zero, whereas the mean value for the females was 0.49. The values obtained from individual female subjects varied considerably, but only one animal gave an $\bar{\eta}$ value of less than 0.30. For purposes of comparison, the results from a number of human subjects tested in the same situation are also shown. In confirmation of previous measurements (*6*), a human protanopic dichromat showed no differential chromatic adaptation over this spectral range. On the other hand, individuals classified as normal human trichromats all gave significant values of $\bar{\eta}$. Although there was a substantial overlap between the two groups, the mean for the normal group was somewhat higher than that for the female squirrel monkeys. In sum, this experiment shows that male squirrel monkeys differ from female monkeys in showing much less differential chromatic adaptation over the 540- to 640-nm portion of the spectrum.

Table 1. Effects of chromatic adaptation on visual sensitivity. The tabled index values were derived from four increment-threshold measurements, two homochromatic and two heterochromatic; S.D., standard deviation.

Subject	*N*	Mean	S.D.
Squirrel monkeys			
Male	6	.028	.036
Female	8	.494	.369
Human			
Normal trichromats	8	.525	.172
Protanope	1	.025	

The results from several earlier experiments on squirrel monkey vision suggested that, as a species, these animals possess protanomalous color vision (*7*). Although my results do not constitute direct measurements of color vision, these indices would be expected to covary with other, direct measurements of color vision. Specifically, an abnormally large decline in sensitivity to the long wavelengths is one of the prominent characteristics of the protanopic and protanomalous color defects. Male squirrel monkeys thus seem to differ from females of the same species at least in the degree, and perhaps in the nature of their color deficiency (*8*). Although there is already some evidence to show that male squirrel monkeys are not so severely affected as to be dichromatic (*9*), further testing will be required to determine the details of color vision in these two groups and to ascertain how completely the sexes are separated along these and other dimensions of visual capacity. Also remaining to be determined are the mechanisms underlying these differences and what significances these differences may hold for normal visual behavior. Nevertheless, it is apparent that this species provides a range of possibilities for investigating visual mechanisms on a within-species basis (*10*).

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References and Notes

1. For reviews of this topic, see, for example, F. H. C. Marriott [in *The Eye*, H. Davson, Ed. (Academic Press, New York, 1962), vol. 2, pp. 273–297]; Y. Hsia and C. H. Graham [in *Vision and Visual Perception*, C. H. Graham, Ed. (Wiley, New York, 1965), pp. 395–413]; L. M. Hurvich [in *Handbook of Sensory Physiology*, vol. 7, part 4, *Visual Psychophysics*, D. Jameson and L. M. Hurvich, Eds. (Springer-Verlag, Berlin, 1972), pp. 582–624].
2. W. D. Wright, *Researches on Normal and Defective Color Vision* (Mosby, St. Louis, 1947).
3. The first indication that such an intraspecific variation might exist was reported by G. H. Jacobs [*J. Comp. Physiol. Psychol.* **77**, 425 (1972)]. Verification of the possibility was later reported in an abstract [G. H. Jacobs, *Physiologist* **17**, 254 (1974)].
4. That squirrel monkeys are separable into groups on the basis of their physical appearance has been known for some time [P. D. MacLean, *Science* **146**, 950 (1964)]. MacLean suggested descriptive names based on the shape of the white fur patch located above the eyes. Those showing the so-called Roman Arch phenotype have been exported through Iquitos, Peru, while those having the so-called Gothic Arch phenotype have been exported through Leticia, Colombia [R. W. Cooper, in *The Squirrel Monkey*, L. A. Rosenblum and R. W. Cooper, Eds. (Academic Press, New York, 1968), pp. 1–29]. Recently, cytogenetic differences have been shown to exist between these two groups [R. C. Jones and N. S. F. Ma, *Fed. Proc. Fed. Am. Soc. Exp. Biol.* **34**, 1646 (1975)]. In our laboratory, we have tested a few monkeys of Colombian origin, but it is not yet clear whether these animals show the same kind of differences as those reported here.
5. This is an adaptation of a test developed by Boynton and his colleagues for use on human subjects (*6*).
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7. R. C. Miles, *J. Comp. Physiol. Psychol.* **51**, 328 (1958); G. H. Jacobs, *ibid.* **56**, 616 (1963); R. L. DeValois and H. C. Morgan, *Vision Res.* **14**, 69 (1974).
8. In humans, the most common types of defective color vision are hereditarily transmitted by recessive genes located on the X chromosome [see, for example, W. Jaeger, in *Handbook of Sensory Physiology*, vol. 7, part 4, *Visual Psychophysics*, D. Jameson and L. M. Hurvich, Eds. (Springer-Verlag, Berlin, 1972), pp. 625–642]. This mode of inheritance could not be used as an explanatory mechanism to account for the results reported here if, as the data suggest, all male squirrel monkeys differ from all female squirrel monkeys in visual capacity.
9. In our laboratory, male squirrel monkeys have been trained to successfully discriminate between two monochromatic lights (555 and 620 nm), which were equated so as to be equiluminant for the subject. A dichromatic individual, at least a protanope or a deuteranope, would not be expected to be able to make such a discrimination.
10. There is some evidence to suggest that another species of platyrrhine primate, the Cebus monkey, may also show sex-linked variations in visual capacity [F. Lepore, M. Lassonde, M. Ptito, B. Cardu, *Percept. Mot. Skills* **40**, 783 (1975)].
11. I thank D. McFadden, R. L. De Valois, and D. Birch for their helpful comments on this report. Supported by grants from the National Eye Institute (EY 00105) and the National Science Foundation (GB 23551).

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