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RESEARCH NOTE

EARLY COLOR DEPRIVATION AND SUBSEQUENT COLOR VISION IN A DICHROMATIC MONKEY

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Abstract—A squirrel monkey (*Saimiri sciureus*) was reared for the first 4 months of life in a dim, colorless environment. Following an additional 10 months of normal visual experience, tests of color vision and spectral sensitivity were run on this animal and a control subject. The results suggest that the adult expression of dichromatic color vision does not depend on color experience during the first 4 months of life.

Primate color vision Development Squirrel monkey

INTRODUCTION

Two general paradigms have been used to investigate the development of primate color vision. One involves repetitive testing of color vision during the early postnatal period; the other examines whether some systematic bias in the early visual environment might influence subsequent color vision. Studies of human color vision are naturally limited to the first of these approaches (reviewed by Boothe *et al.*, 1985), but with other primates it is possible to control the visual environment and assess its effect. The results of this latter approach have been almost uniformly negative. Results from an early experiment by LeGros Clark (1940) suggested that rearing rhesus monkeys in a "blue-free" light environment produced significant structural changes in the lateral geniculate nucleus. Chow (1955) conducted a replication and extension of this study, however, and could find none of the changes suggested by LeGros Clark's experiment. Boothe *et al.* (1975) placed a pig-tailed macaque monkey in complete darkness from 2 weeks to 3 months of age. This manipulation was without effect on subsequently assessed color vision. Recently, Brenner *et al.* (1985) reared a macaque monkey for the first 3 months of life under deep red light. This selective rearing did not appear to affect the animal's ability in later tests of spectral sensitivity and color vision.

In this report we describe an experiment involving the effects of an unusual early environment on color vision in a monkey. In the face of the array of negative results summarized above, one might be inclined to question the fruitfulness of further work of this sort. One justification is that most of the previous experiments were not, strictly, color deprivation experiments. Rather, they involved rearing animals in highly spectrally biased environments. We thought that there is at least one difference between color deprivation and color bias in the rearing environment that might be important. The locations in the visual system where deprivation conditions have their effects are most often regions of synaptic interaction. In the case of color vision these would be sites of spectrally opponent interactions. Consider the effects of a spectrally biased environment on such opponent sites. Deep red illumination, for instance, would provide a substantial tonic signal to such an opponent site, but the strength of that input would be sharply modulated by increases or decreases in luminance (see, for example, De Valois, 1971; Gouras and Eggers, 1983). Such changes are inevitable in any spatially structured environment. Although the inputs to these spectrally opponent sites under chromatic rearing conditions would be highly biased toward the cone type receiving maximal stimulation, they still might be sufficiently variegated to

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allow the development or maintenance of the connections required for functional opponent cells. A different approach would be to rear animals in an environment where the outputs from the photoreceptors are not sufficiently robust to produce any signals from opponent cells. Such a condition is indeed "color deprivation." One way to achieve this would be to rear animals in total darkness, but that condition can pose its own unique difficulties. As an alternative, in the present experiment a monkey was reared in dim achromatic light, bright enough to allow vision but too feeble to yield color vision. Such an environment would be expected to produce minimal activity from any spectrally opponent cells in the developing visual system.

METHODS

Rearing conditions

A pregnant squirrel monkey (*Saimiri sciureus*) was placed in a rearing cage about 6 weeks prior to parturition. The cage was constructed by joining two standard monkey cages with a small runway thus allowing the animals considerable freedom of movement. All of the illumination in the rearing room came from a fluorescent tube (40 W cool white, 4200 K) mounted in a 1.2 m long light box located behind the cage. The box had a small adjustable slit that ran along its length. Light emerged from the slit and passed through a series of diffusers into the room. The intensity of light from the box was adjusted upwards until a human fully adapted (i.e. for greater than 45 min) to the ambient level could discriminate considerable spatial detail, but could not detect any color. The average illuminance in the test chamber at this point was $1.4 \cdot 10^{-2}$ lx. Under these conditions a human with normal acuity could just resolve a high-contrast square-wave grating of 2.6 c/deg; it was possible to discern the finest mesh in the cage wall and see individual digits on resident monkeys. To verify the absence of color, each of two normal human trichromats attempted to sort the Farnsworth-Munsell 100-Hue test at this light level. The resulting performances were at change levels. We were additionally unable to correctly name the colors of highly saturated paint and fabric samples brought into the test environment, and an attempt to match to sample four adjacent pairs drawn from the full range of the FM 100-Hue test was likewise a complete failure. Finally, a normal human trichromat was tested on the H-R-R Pseudoisochromatic Plates. This individual was unable to detect any "colored designs" as the instructions require in any of the 20 plates although one of the symbols for the most severe protan diagnosis (Plates 15 and 16) could be discerned by their brightness differences. Rod and cone thresholds are quite similar for squirrel monkeys and humans (Jacobs, 1973), as are their visual acuities (Merigan, 1976), and thus we assumed that this environment was also sufficiently bright to allow the squirrel monkey considerable visual stimulation, but no possibility of color vision. The light in the rearing room was set to a normal 12:12 light:dark cycle.

The lighting regimen was in effect from 4 weeks prior to the birth of the animal to 4 months after birth. During that time great care was taken to assure that no additional light ever reached the subject. At the end of 4 months the light level in the room was gradually increased over a several day period until it reached normal levels. Mother and offspring were then returned to a large colony cage where they subsequently lived as members of a social group. At 14 months of age the subject was transferred to an individual cage and tests of vision were initiated.

Subjects

The subject was a male (identified here as TX). Squirrel monkeys have a color vision polymorphism based on individual variation in the middle wavelength cone pigment (Jacobs, 1984). The color vision phenotype of TX was revealed by the results of tests reported below. An adult male monkey, PH, served as a control subject. His color vision had been categorized in earlier experiments; it was of the same phenotype as that of TX.

Apparatus and procedure

The apparatus and procedures used for evaluating vision in the squirrel monkey have been described in detail in recent publications (Jacobs 1983; 1984). The test was a three-alternative, forced-choice discrimination in which the animal was trained to select a uniquely illuminated stimulus panel from among three such panels. Over trials the nature of the illumination difference between the positive and negative panels was varied so as to permit the measurement of discrimination threshold. Three tests were run. (1) We first measured increment-threshold spectral sensitivity. The three stimulus panels were continuously and equally illu-

minated with achromatic light (4800 K, 20 cd/m^2). On a test trial a 2 sec flash of monochromatic light (half energy pass-band = 16 nm) was added to one of the panels. Thresholds were measured for test wavelengths from 440 to 660 nm in steps of 10 nm by varying the intensity of each test light in steps of 0.3 log unit over a range sufficient to produce discrimination between 90 and 100% correct and chance. This procedure was continued until 25 test trials had been run at each intensity/wavelength combination. Threshold was taken as the intensity necessary to maintain performance at the 95% confidence level (57% correct). (2) The second test was of color vision. All male squirrel monkeys are dichromats having neutral points in the 490–500 nm portion of the spectrum (Jacobs, 1984). A search was made for such a neutral point in the region from 475 to 514 nm. For this test the two negative panels were achromatic (4800 K) having a luminance of 5 cd/m^2. The test light was varied from 475 to 514 nm in steps of 3 nm. At each tested wavelength, intensity was varied in steps of 0.1 log unit over a total range of $\pm$0.6 log units around the human brightness match. Testing continued until 25 trials had been run at each wavelength/intensity setting. (3) In a third test spectral sensitivity was measured for rapidly flickering lights. The apparatus and procedure were essentially identical to those used in test (1) except that the positive stimulus was 30 Hz square wave flicker. The two negative stimuli were of identical spectral content and had the same time-averaged luminance as the positive stimulus. At each test wavelength the intensity of all three panels was varied in steps of 0.3 log unit, threshold being determined by the intensity required to maintain performance at an average level of 57% correct. Threshold measurements were made at 18 test wavelengths taken at 10 nm steps from 460 to 630 nm. PH was not tested in this experiment.

RESULTS

TX developed normally under the reduced light regimen and upon removal to normal lighting and group living showed no overt evidence of any visual deficit. His behavior following the four-month period of color deprivation was of the same frenetic quality as that typically observed in other young squirrel monkeys.

Complete increment-threshold spectral sensitivity functions for TX (circles) and the control subject PH (squares) are shown in Fig. 1. Absolute differences in sensitivity between the two subjects have been preserved in that plot. The spectral sensitivity functions for the two monkeys are remarkably similar, both in absolute sensitivity and spectral shape. These facts are emphasized by the single curve drawn through the data points for the two animals. Both subjects produced the double-humped spectral sensitivity function characteristically obtained from dichromats of this species when they are tested at increment threshold; that is, they show a region of high sensitivity at the shortest test wavelengths (*ca* 440 nm), a second region of high sensitivity broadly peaked from about 520 to 580 nm, and a sharply defined intermediate region of depressed sensitivity centered at about 490 nm.

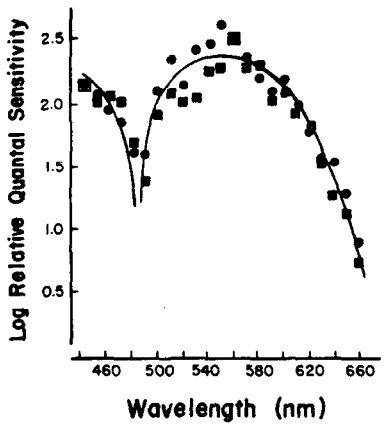

Fig. 1. Increment-threshold spectral sensitivity functions for squirrel monkeys TX (circles) and PH (squares). Background luminance = 20 cd/m^2. The sensitivity values for the two animals have not been adjusted relative one to another. The solid lines drawn through the data represent the best fitting subtractive combination of two wavelength dependent visual pigment nomograms having λ_{max} values of 433 and 550 nm. The proportions required for this best fit were: 433 nm (58%) and 550 nm (42%).

Figure 2 summarizes the results from the color vision test. Plotted for each subject is the asymptotic discrimination performance recorded for the final 25 test trials at each test wavelength. These values reflect the poorest discrimination recorded at each test wavelength. In each case these were produced by stimuli lying in the middle of the test intensity range; we presume these values define discrimination performance at points of equal luminance. Both animals show high levels of correct performance for test wavelengths shorter than about 485 nm and longer than 500 nm and for both discrimination between these two points becomes considerably poorer. The zone of poorest discrimi-

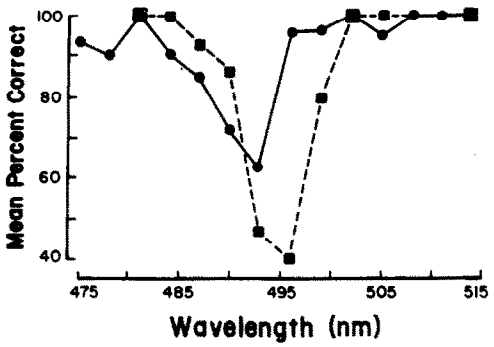

Fig. 2. Neutral point test results for TX (circles) and PH (squares). Each plotted point represents the performance achieved in a discrimination between achromatic and equiluminant monochromatic lights (see text for details).

nation is centered at 492–495 nm. The asymptotic performance level of TX at the spectral location of poorest performance was somewhat superior to that of PH.

Figure 3 shows the spectral sensitivity function for TX obtained from the flicker discrimination experiment. The individual points define a smooth spectral sensitivity function absent of secondary peaks. The solid line in Fig. 3 is a curve derived from that wavelength dependent visual pigment nomogram that best fits this data array (Neitz and Jacobs, 1984). The λ_{max} of that function is 552 nm.

DISCUSSION

Male squirrel monkeys have dichromatic color vision based on the presence of two types of cone photopigment, one having λ_{max} at about 433 nm, the other peaking at either 538, 550, or 563 nm (Mollon *et al.*, 1984). The subject of this experiment, TX, fell into the second of these categories (Fig. 3) as did the control subject PH.

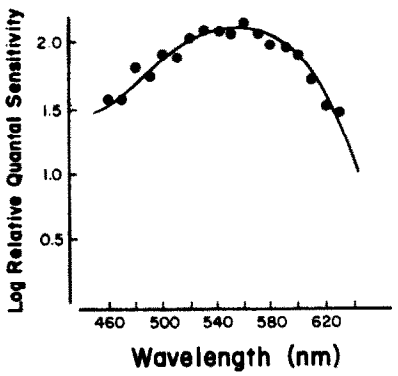

Fig. 3. Flicker spectral sensitivity function for TX. The solid line is the best fitting visual pigment nomogram (λ_{max} = 552 nm). Flicker rate: 30 Hz.

The results summarized in Figs 1 and 2 argue that adequate stimulation of spectrally opponent sites in the visual system is not required over the first 4 months of life for subsequent color vision in adult, dichromatic squirrel monkeys. The differences in performance of TX and PH are well within the range of variability measured on many other squirrel monkeys in these same test situations (Jacobs, 1983; 1984). Spectral sensitivity functions measured at increment threshold are traditionally interpreted as reflecting the operation of spectrally opponent mechanisms (Sperling and Harwerth, 1971). The fact that TX's increment threshold function was virtually identical to that of the control subject suggests that his visual system has a normal complement of spectrally opponent cells. Figure 2 reports a direct test of color vision. The result summarized there shows that TX has a color vision capacity. Since the location of the neutral point of TX is characteristic for this type of dichromacy (Jacobs, 1984), the result further indicates that the quality of his color vision is normal for this color vision phenotype.

This color deprivation experiment suggests, as did the earlier studies involving the use of spectrally biased environments, that normal color experience during early life is not a prerequisite for normal color vision in the adult primate. Two caveats to that conclusion may be noted. First, it is possible that the 4-month period of color deprivation was insufficient to produce an effect. We believe this to be unlikely in light of the fact that color vision in both humans and macaques appears to have developed by about 3 months of age (Booth *et al.*, 1975; Hamer *et al.*, 1982). A second possibility is that although color experience may not be required for the normal development of dichromatic color vision in primates, such experience might be necessary for the normal development of trichromatic color vision. It is well established that there are a number of differences between the short-wavelength cone mechanism and the other middle and long wavelength cone mechanisms (reviewed by Mollon, 1982). Perhaps these cone types even differ to the extent that the arrangement of their outputs into opponent circuits are specified genetically. On the other hand, the great similarity between middle and long wavelength cone types might mean that some early color experience is required for the formation of opponent interactions between them.

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