

## Color Vision in New World Monkeys: Di- and/or Trichromaticity ?

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### Abstract

*Research carried out by various investigators has indicated significant differences in color vision perception between Old World and New World monkeys. While the former seem evenly trichromatic, the New World monkeys show color vision polymorphism with at least 06 different phenotypes and an absence of trichromacy amongst the males of the Saimiri and Callithrix genera. In this report we summarize the studies of color vision in New World monkeys, including our own data, showing inconsistencies in the outcomes of these experiments, the interspecific differences and the numerous non - tested species. The results are discussed according to the neurobiological hypothesis of male dichromatism in New World monkeys, to the hypothesis that the major function of color vision in primates is its role as an adaptation to feeding ecology, as well as to aspects regarding primates evolution. In conclusion, the available data points to the necessity of further work on this problem - including behavioral, electrophysiological and genetical approaches - before definitive proofs are possible.*

Since the experiments of Young, in the beginning of 19th century, trichromatic color vision has been explained as dependent upon distinct classes of resonators (lately identified as cone photoreceptors) in the retina [1]. The central idea of trichromacy is that the visual pathway contains three distinct mechanisms that are sensitive to different, but overlapping, regions of the spectrum [2]. Thus, lights of different spectral composition will be distinguishable by the distinct patterns of excitations in the three mechanisms.

The correlation between number of cone types (photopigment types) and the dimensionality of the resultant human color vision, estimated by color-matching

experiments, has contributed to the assumption that one implies the other. Therefore, an animal species with two types of photopigments must be dichromatic and one with three types of pigment must be trichromatic. However, three constraints should make one cautious about inferences between mechanisms and the dimensionality of color vision. The first is the sampling inadequacy or sensitivity limitation of microspectrophotometrical and electrophysiological methods. The second is the contribution of rod based signals to produce color. The third is the fact that color vision is a result of active operations carried out in the nervous system as a whole. As a consequence, dimensionality of non-human color vision systems should be established through appropriate behavioral studies [3].

Amongst the mammals, human and non-human primates are the species that seem to enjoy a trichromatic color vision [4], [5], [6]. On the other hand, the existence of multiple forms of human color vision has raised the hypothesis that the variations were preserved in some contemporaneous species [7]. Therefore, In some early behavioral studies [8] it was found that although several species of Old World monkeys behaved much like normal trichromatic humans, members of the genus Cebus, a New World monkey species, showed a markedly deficient hue discrimination in the long wavelength end of the spectrum, as it happens for the protanopic type of human color vision. These pioneering investigations stimulated the interest in New World monkeys color vision.

The utility of color vision in the natural world is another aspect which has motivated comparative studies in different species of monkeys. Color can be used for perceptual segregation of targets. In case of fructivorous primates, one of the most important functions of trichromatic color vision must be to judge the state of ripeness of fruit from the external appearance. Similarly, variations in the color of ground-covering vegetation can reveal at a distance the presence of water [9]. Since in

these two situations, the variations in lightness and spectral composition of the illuminant may be substantial, we should expect the animal to exhibit color constancy: it ought to be able to recognize the spectral reflectance of a surface independently of the composition of the illuminant [10]. Daylight is also strongly modified in its spectral composition as it penetrates dense jungle, becoming dominated by green light that escapes absorption by foliage. This spatial heterogeneity of environment might serve as a selective pressure for occupation of different ecological niches by primates with diverse color abilities. For example, protan animals might occupy niches where long-wave light is more attenuated, whereas deutan animals would choose the canopy or relatively open areas at the forest edge, where long-wave light is less attenuated [11]. In addition, visual recognition is one of the most challenging problems of contemporary neurophysiology and experimental psychology, with significant implications for mathematical and computer modeling of perceptual phenomena.

Therefore, in the past several years, electrophysiological, molecular genetics, microspectrophotometrical and behavioral studies in different species of New World monkeys, have characterized their color vision types. Table 1 presents a summary of the literature regarding color vision studies in these animals. For two widely studied callitrichid monkeys - *Callithrix jacchus* and *Saguinus fuscicollis* - color vision is polymorphic. It is characterized by a presence of three types of trichromacy and three types of dichromacy, males expressing only dichromatic phenotypes. However, some inconsistencies shall be considered. Thus, while the saddle-backed tamarin - *Saguinus fuscicollis* follows the trend and shows a sex-linked polymorphism [23 - 25], the cotton-top tamarin - *Saguinus oedipus oedipus* makes accurate discriminations across the visible spectrum [26]. Interspecific and/or methodological differences may account for such differences.

**TABLE 1**  
**SUMMARY OF COLOR VISION STUDIES IN NEW WORLD MONKEYS**

Animal Species	Technique	Evidence of Trichromacy in males	Reference
<i>Alouatta caraya</i>	ERG	Yes	12
<i>Ateles ater</i>	B	Yes	8
<i>Ateles belzebuth</i>	B	Yes	13
<i>Callithrix jacchus</i>	B, MEP, G	No	5, 14 - 16
<i>Callicebus molloch</i>	ERG	No	17
<i>Cebus albifrons</i>	B	Yes	18
<i>Cebus apella</i>	B, ERG	No	17, 19
<i>Cebus apella</i>	B	Yes	20, 21
<i>Cebus griseus</i>	B	Yes	22
<i>Saguinus fuscicollis</i>	B, G	No	23 - 25
<i>Saguinus oedipus oedipus</i>	B	Yes	26
<i>Saimiri sciureus</i>	B	Yes	27
<i>Saimiri sciureus</i>	B, MEP, ERG, G	No	11, 28 - 34

Abbreviations: B = Behavior; ERG = Electoretinography; MEP = Microspectrophotometry;  
G = molecular genetics.

Regarding the family Cebidae, the numerous studies of color vision in squirrel monkeys - *Saimiri sciureus* [28 - 34], which report a sex-linked polymorphism, are in contrast with a fragmentary knowledge of color vision in capuchin monkeys - *Cebus apella*. In this last species, the behavioral studies suggest, amongst the males, a dichromacy of protanopic type [19], or an absence of dichromatism but an anomalous trichromatism [20]. While measurements made on cones from a single male *Cebus apella* show a single class of middle wavelength cone having an average  $\lambda_{\max}$  value of 534 nm [35], spectral sensitivity functions determined in eight males of the same species, by electroretinogram flicker photometry [17], show that each monkey had only a single type of the middle wavelength cone having  $\lambda_{\max}$  values of either 550 or 562 nm.

It is important to mention that in these last group of experiments only male *Cebus* monkeys were available for examination. There appears to be no further work in *Cebus* color vision since that last investigation [17]. Thus, as a contribution to better understand this question, we [21] investigate the ability of males and a female *Cebus* monkeys in discriminating chromatic and achromatic stimuli using a behavioral discrimination learning paradigm. The subjects were tested in a simplified version of the Wisconsin General Test Apparatus in their home cage environment. The color stimuli consisted of Munsell color chips and three protocols were used: (1) a simple color discrimination test where the stimuli had different hues but the same brightness and saturation; (2) a test pairing each hue with achromatic chips of different values; (3) a test pairing different achromatic chips. On any given trial, the subject was faced with a choice between two discriminating color chips. The results indicated that all *Cebus* monkeys tested were capable of discriminations along five major spectral locations used (red, yellow, green, blue and purple). Furthermore, the subjects had no problem discriminating the pairs of hues *versus* grays. These data strongly suggest that capuchin monkeys can be trichromats. However, further studies using a broad range of brightness values at each discriminable hue is necessary to eliminate the possibility of subjects using brightness cues rather than hue to make the discrimination.

Regarding the uses of color vision in the natural environment, the presence of several forms of color vision in *Cebus* monkeys or the existence of an exclusive trichromacy are both

plausible hypothesis. Selective pressures favor considerable enhancement of the visual apparatus, including accurate color vision, thereby helping primates to easily discern the presence of ripe fruits [21]. On the other hand, where animals live in a troop it might be advantageous to the group to have members with multiple types of color vision. Camouflaged predators and cryptic food are likely to be visible to some subset of the group, who can then attract the attention of other members of the group. It is also possible that different phenotypes occupy diverse locations within the jungle, enhancing overall foraging success [4].

The key to understand any adaptive trait, such as color vision, comes not only from a knowledge of current selective pressures but also from the past evolutionary history of the species in question. New adaptations are not creations *sui generis* but rather are modifications of past adaptations [36]. Early primate studies were largely concerned with the behavior of savanna-living primates since these were thought to offer possible analogues for hominid evolution. But, to understand the origins and uses of color vision in hominids we must look also at life in tropical forests, for it is here that the first steps toward an increasing dependence on mental abilities must have been taken.

Behavioral experiments, as we performed in our investigation and field studies of food eaten habits surely will contribute to a better understanding of this phenomena. Ongoing experiments in our laboratory are investigating the accuracy of *Cebus* monkeys in discriminating Ishihara plates, frequently used as screening tests for color vision in human primates. In such pseudoisochromatic plates a figure is seen even though that figure is defined only by spatially separated colored dots in a field of dots that otherwise vary randomly in lightness. Data obtained from such studies will help to formulate neurobiological hypothesis of color vision in New World monkeys as well as to understand aspects concerning feeding ecology and primate evolution.

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