



Research report

Color vision perception in the capuchin monkey (*Cebus apella*):
a re-evaluation of procedures using Munsell papers

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Abstract

In previous experiments based on color vision discrimination of Munsell chips, Pessoa et al. (Behav Brain Res 1997;89:285–8) presented evidence of trichromatic color vision in capuchin monkeys. However, the possibility of subjects using brightness cues was not eliminated. The purpose of the present study was to reassess the color perception in *Cebus apella* in a similar behavioral paradigm, but using a range of brightness values at each tested hue. We now report that male capuchins show a dichromatic behavior. The results are discussed in terms of the hypothesis of male dichromatism in the New World monkey, the biological role of color vision and cognitive abilities of capuchin monkeys. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Color vision; Sexual polymorphism; Capuchin monkey; Munsell paper

1. Introduction

In the last 2 decades, studies in different species of New World monkeys have indicated that their color vision is polymorphic (review in Refs. [9,10]). This polymorphism is characterized by the presence of three types of trichromacy and three types of dichromacy, males expressing only dichromatic phenotypes. Contrasting with the intra-species variation of New World monkeys, color vision of Old World monkeys is characterized by uniform trichromacy [5,19].

One exception to the polymorphic design of color vision in the New World monkeys includes the existence of homogeneous trichromatism in howler monkeys (*Alouatta caraya* and *Alouatta seniculus*) which seem to have acquired a similar genotype/phenotype arrangement to that reported for Old World monkeys [14,16]. Another variant is related to the *Aotus* (owl monkey), a nocturnal simian, which has a single type of cone, being monochromat [12]. A third exception is the

cotton-top tamarin (*Saguinus oedipus oedipus*) that makes accurate discriminations across the visible spectrum [23], although methodological issues may account for such differences [9].

Reports of trichromatism have also been provided for capuchin monkeys (*Cebus apella*). Early behavioral studies suggested an absence of dichromacy in males of *C. apella* [8], although a red-blindness has also been demonstrated for this species [17]. Later, electoretinographic measurements indicated that *C. apella* displays, as with other New World monkeys studied, a polymorphism of color vision [13].

In order to contribute to a better understanding of this question, we recently presented evidence of behavioral trichromaticity in the capuchin monkey [21]. In these studies, the ability of two males and one female to discriminate between chromatic and achromatic stimuli was tested using Munsell color chips. However, the possibility that subjects might have used brightness cues rather than hue to make the discrimination was not eliminated [11,21]. Furthermore, some discriminating pairs used in the monkey experiments were not difficult or impossible for three human dichromats, casting doubt on that claim [11].

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2. Materials and methods

2.1. Subjects

Four capuchins (three males and one female *Cebus apella*), ranging from 8 to 10 years of age, served as subjects (Ss) for this study. They were housed in cages (4 m length, 2.9 m width, 2 m height) at the Primate Center of the University of Brasilia. The animals were tested in their own home cages and were not deprived of food, except prior to an experimental session when food was removed and made available again after the test. They had ad libitum water.

Eight human subjects (two trichromats and six dichromats), aged between 21 and 30 years old, with normal or corrected vision, recruited in University campus, were also used. The objectives of the human experiments were: (1) to select pairs of Munsell chips which were difficult to tell apart by dichromats but were easily discriminated by trichromats—these pairs were used in the monkey experiments; and (2) to replicate the monkeys discriminating experiments—in this case, four individuals (two trichromats and two dichromats) from the original group were used.

2.2. Equipment and stimuli

A version of the Wisconsin General Test Apparatus was mounted on a portable table in front of the animal's home cage. A tray carried the stimuli and a wooden screen allowed the experimenter to set up problems and prevent animals observing stimuli between trials.

Plexiglass cubes were used as stimuli-holders, specially built for the adequate adjustment of the stimuli. The cubes were drained in their inferior surface to contain the reinforcement (pieces of grapes) and in posterior surface, in order to allow the placement and retreat of the stimuli. On the top of these cubes, a round window (1.2 cm diameter) permitted the subjects visualize the stimuli.

The stimuli consisted of chromatic chips (2×1.5 cm) from the Munsell Book of Color. In this system, every color patch was specified by three attributes (hue, brightness or value and saturation), arrayed in orderly scales of equal visual steps. Discrimination hues belonged to nine categories: red (R), yellow–red (YR), green–yellow (GY), green (G), blue–green (BG), blue (B), purple–blue (PB), purple (P) and red–purple (RP). Each hue category was presented with four different values. In the Munsell system, hue is represented by a number and a letter, whereas the brightness and the saturation by a fraction. For example, the notation 10YR 6/10 corresponds to a yellow-red color chip 10, with brightness 6 and saturation 10.

The pairs of Munsell color chips used in this study were selected in an experiment with seven human males, 01 trichromat and 06 dichromats (three deutans and three protans, diagnosed by the Ishihara test). Subjects were initially required to organize 150 different Munsell chips (of varying hues, brightness and saturations) in as many groups as desired, according to color appearance. Afterwards, they were required to pair similar chips in each group. Any odd pairing detected by the experimenter (a trichromat) was interpreted as a range of spectral confusion. Besides these pairs, which produced similar perception by the dichromat humans, stimuli of easy discrimination by protans and deutans were also paired in monkeys' discrimination experiments. Furthermore, to estimate the degree of difficulty of each pair of stimuli, four humans (one protan, one deutan and two trichromats) served as subjects in a two choice color discrimination test, using the same proceedings (and apparatus) from monkey experiments.

2.3. Procedures

The experimental sessions were conducted three times a week, between 14:00 and 16:30 h, under daylight diffuse illumination. Tests started with the presentation of one pair of stimuli at a time. On any given trial, the subjects were faced with a choice between two discrimination stimuli. The reward was placed under the cube containing the positive discriminating stimulus (SD +) and was accessed by the monkey only if its choice was correct; the other cube, without reward, was the negative discriminating stimulus, SD –. The position of the reinforcement was determined according to the Gellerman table of random numbers. The delay between the trials lasted 10 s. Fifteen pairs of stimuli were selected from an experiment with protan and deutan humans.

Aiming at intra- and intersubject comparisons of performances, discrimination tests were conducted in two stages: training and testing.

To make sure that discriminations were based on color rather than brightness cues, four brightness values of the SD + were paired to four brightness values of the SD –, making a total of 16 possible pairings. Each possible pairing was presented four times, making a total of 64 trials per experimental session. Based on these 64 trials, a percentage of correct responses were determined. Once finished the testing phase, the subjects were introduced into another training phase, with a different SD +.

The binomial test constructed the 95% confidence limits around chance performance based on the number of test trials. Thus, for 64 trials, the upper limit was calculated as 63%. The performance of all subjects was compared to these confidence limits and any performance above the upper limit was considered significant ($P < 0.025$). In human experiments, the number of tri-

als was 16 and below chance performance was determined according to the binomial test for $\alpha = 0.05$ and $\alpha = 0.01$.

As mentioned before, 15 test blocks were related to the pairs selected in human studies. To exemplify, the 2.5 YR block was composed of four pairs of easy discrimination (2.5 YR $n/14$ versus 10BG $n/6$, 5PB $n/6$, 7.5P $n/8$ or 5B $n/6$; n stands for 4, 5, 6 and 7) and one pair of difficult discrimination (2.5YR $n/14 \times 7.5GY n/10$; n stands for 4, 5, 6 and 7), obtained in the human experiment. Each block began with a training situation, where the animal learns the SD + (in the given example, 2.5YR). This phase ended when the animal hit the criterion of 80% of correct responses in one session consisting of 100 trials. Then, the animal proceeded to the testing phase, where the subject was submitted to three discriminative tests with three pairs of easy discrimination, in three different sessions. A fourth test always involved the pair of difficult discrimination (obtained in the test with humans). Finally, during a fifth and last session, the animal accomplished the easy pair. If subjects were dichromats, they must show a decrease in performance during the fourth test, below the upper limit and then performance grew up in the fifth pair.

As a control for not visual cues, an impossible discriminating pair constituted by a color against itself (5YR $n/14$ paired with 5YR $n/14$), was presented between two easy discriminating pairs in a block of five tests.

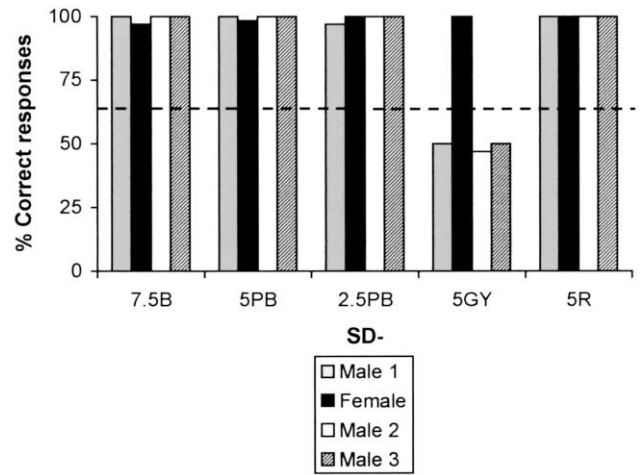


Fig. 2. Color discrimination performance by 04 individual capuchin monkeys with 10YR as the positive discriminating stimulus (SD +). The negative discriminating stimuli (SD -) are disposed along the x-axis. The horizontal line indicates the upper limit of 95% confidence interval for color discrimination.

3. Results

Figs. 1 and 2 show the monkeys' color vision performance, based on percentage of correct responses, when SD + was 2.5YR and 10YR, respectively. In both test blocks, the female subject exhibited a performance well above the upper confidence limit for all pairs presented. However, the three male monkeys showed a fortuity response for orange versus green pairs, that is, for 2.5YR versus 7.5GY (Fig. 1) and for 10YR versus 5GY (Fig. 2). These results indicate that, in contrast with the female, male capuchin monkeys behaved like dichromats.

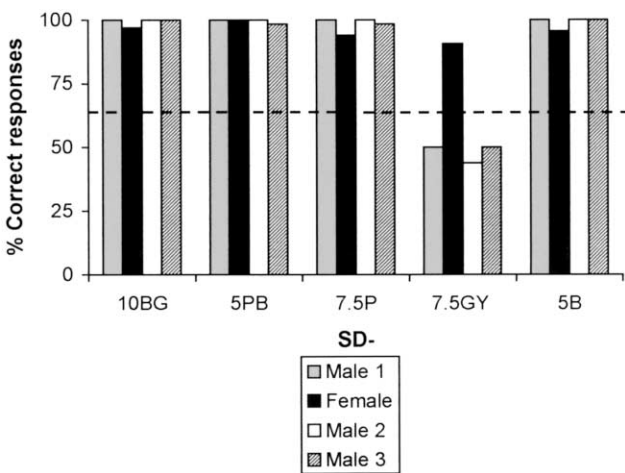


Fig. 1. Color discrimination performance by 04 individual capuchin monkeys with 2.5YR as the positive discriminating stimulus (SD +). The negative discriminating stimuli (SD -) are disposed along the x-axis. The horizontal line indicates the upper limit of 95% confidence interval for color discrimination.

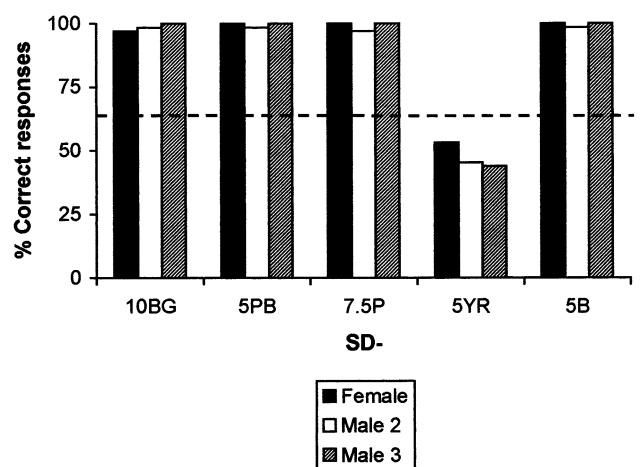


Fig. 3. Color discrimination performance by 03 individual capuchin monkeys with 5YR as the positive discriminating stimulus (SD +). The negative discriminating stimuli (SD -) are disposed along the x-axis. The horizontal line indicates the upper limit of 95% confidence interval for color discrimination.

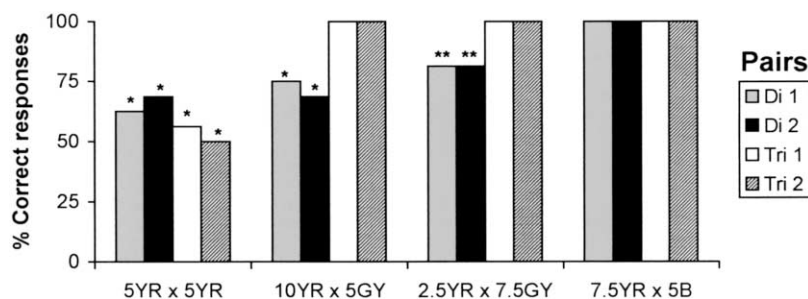


Fig. 4. Color discrimination performance by 04 human subjects—two dichromats (Di 1, Di 2) and two trichromats (Tri 1, Tri 2). One asterisk (*) indicates a below chance performance for $\alpha = 0.05$; two asterisks (**) indicate a below chance performance for $\alpha = 0.01$.

As a control for visual cues (Fig. 3), all monkeys, including the female, showed chance level performance when the chip (5YR) were presented against another chip of the same hue (5YR), composing an impossible pair.

Similar results were obtained in a replication of these experiments with 04 humans (Fig. 4). In this case, the responses of two dichromatic males were compared with the discriminating abilities of two trichromats (one male and one female). All subjects discriminated a pair (7.5 YR \times 5B) that did not pose problems to dichromats and trichromats. However, while dichromatic humans failed to discriminate the same pairs that were difficult for male monkeys (10YR \times 5GY; 2.5 YR \times 7.5 GY), trichromatic humans discriminated all pairs but one (the impossible discrimination pair, 5YR \times 5YR).

4. Discussion

A fundamental feature of the polymorphic color vision in a number of New World monkeys is that male monkeys are routinely dichromatic (reviewed in Ref. [10]). In previous experiments, Pessoa et al. [21] found that one female and two male capuchin monkeys were capable of discriminations along major spectral locations of the Munsell color system. These results have been interpreted as evidence of homogeneous trichromatism in *C. apella* and that this species could be another exception to the sex linked polymorphism in New World monkeys. However, the results of the present study using brightness variations of each discriminable hue show that all male monkeys tested did not discriminate oranges versus greens pairs of hues. It is important to mention that these pairs of stimuli were selected on the basis of an experiment with human subjects and that dichromatic humans failed to discriminate the same pairs.

It is crucial in tests of color vision that they exclude the influence of cues other than spectral differences per se. Our results stress the importance of brightness control when testing color vision in non-human species. This is even more critical when dealing with Munsell

papers, where perceptual dimensions are specified in psychophysical scaling by trichromatic human observers [11]. We believe that an experimental protocol employing random variation of brightness values for each pair, as in the present study, eliminate brightness factors as cues for the discriminations.

It has been suggested that the major advantage of trichromatic over dichromatic color vision in primates is to enhance detection of food items, such as yellow/orange fruits [22] or red young leaves [4], against a background of mature foliage [24]. The feeding hypothesis was recently tested in a study comparing the foraging ability of dichromatic and trichromatic marmosets (*Callithrix geoffroy*) for orange- and green-colored cereal balls in a naturalized captive setting [3]. The results support an advantage for trichromatic females in detecting orange colored food items against foliage. Similarly, our female capuchin monkey posed no problem in discriminating orange versus green stimuli, a condition which male capuchins were unable to solve.

It is possible that male capuchin monkeys may compensate the reduced color vision by some peculiar organizational arrangement of the visual system or by some cognitive mechanism. Regarding the first possibility, studies of photoreceptor topography in *C. apella* show a high ratio of rod to cone at the dorsal portion of the retina, a feature that may retain a gain in light sampling at low luminance levels [1]. Therefore, it is inciting to propose a possible contribution of rods to color vision in dichromatic capuchin monkeys. In this respect, it has been demonstrated that dichromatic marmosets exhibit strong rod input to parvocellular cells (the chromatic channel) even at high levels of illuminance [26]. Rod contribution for color perception has been also suggested in studies with dichromatic humans (e.g. Ref. [20]).

Secondly, a dichromatic vision may also be outweighed by the observer's knowledge of scene content. Such cognitive mechanisms have long been recognized in color-science literature [6]. Visual memory can compensate, for instance, for reduced chromatic information of X-chromosome dichromats when viewing and analyzing complex color images of natural scene [7].

Taking the case of capuchin monkeys, it is known that these animals feed mainly from fruit trees that are fixed in space and produce food over an extended period of the year [15]. Thus, *C. apella* should benefit greatly by knowing the spatial locations and phenological states of important fruit sources [15]. Regarding that, studies in this species have demonstrated a highly developed recognition memory [25] and an extremely high level of problem-solving ability [2], which suggest a capacity for integrating time and space in a mental map of food resources.

In conclusion, the data obtained in this present study indicate that *Cebus* monkeys seem to follow the trend, as suggested by other approaches (e.g. Ref. [13]), of an obligatory or widespread presence of dichromatic color vision in male subjects of this species. In spite of this, we cannot discard the possibility that, in natural occurrence situations, dichromatic *Cebus* could expand color discrimination in the red-green range by using rod signals. Nevertheless, as discussed above, dichromatism would not be considered a disadvantage since this condition helps to identify cryptic predators and/or food with color-based camouflage [18].

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