Assessing Ecological Advantages to Color Vision and Color Blindness in Capuchin Monkeys Under Controlled Conditions

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An abstract of
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Abstract

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Prior research into *Sapajus [Cebus] apella* (capuchin monkey) color vision has established that some females and all males are dichromats (red-green colorblind), while other females are trichromats (full color vision). One proposed trichromat advantage is in fruit foraging, while a proposed dichromat advantage is in hunting cryptic prey. This study, composed of two dichotomous choice tasks, intended to determine if these hypotheses, supported by previous observational studies, are still apparent in a controlled environment without other sensory/social cues. The first task was designed to determine if color vision influences efficiency in identifying red objects in green images. The second was designed to determine if color vision influences the ability to identify objects in red-green camouflaged images. Many subjects were unable to pass the training stages, including most males, so we were unable to make an overall comparison between sexes. However, females displayed an overall preference for images with red apples on green backgrounds over green apples on green backgrounds, while the one male tested showed no preference, supporting a trichromat ability in finding red objects on green backgrounds. The training data also supports a trichromat advantage over dichromats found in the literature, though we require genotype data or more male data to strengthen this claim. Results of the camouflage task indicates a floor effect, suggesting that the task may have been too complex to assess the effects of color vision on camouflage effectiveness.

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Introduction

Color vision is a product of evolution. Sometime after New World primates split from Old World primates, a gene duplication at a mid/long wave spectrum opsin gene resulted in Old World primates gaining trichromacy, the possession of three independent channels for color information (Pessoa et. al., 1997; Smith et. al., 2003). This meant a newfound ability to differentiate between red and green. The fact that all Old World primates are now trichromats supports the idea that this mutation was extremely evolutionarily advantageous. However, New World primates, with the exception of howler monkeys (Jacobs et.al., 1996) and owl monkeys (Jacobs et. al., 1993), remained mostly dichromatic. Of these New World Monkey species, only heterozygous females are trichromats (Carvalho et.al., 2017; Gomes et. al., 2002). The evolutionary advantages of a species balance between being partially dichromatic and partially trichromatic as a species is hotly contested, but important in understanding reasons behind the evolution of color vision in humans. It is possible that this color vision polymorphism is maintained only by a trichromat advantage. However, studies concerning this hypothesis have ambiguous or unsupportive results (DePasquale et. al., 2021; Vogel et. al., 2007; Fedigan et. al., 2014), showing a need to explore other hypotheses.

Capuchin monkeys are a New World monkey species that forage for both fruit and cryptic prey. For this reason, they serve as an ideal subject to test two leading hypotheses concerning both fruit and cryptic prey. Capuchin monkey color vision, like most other New World monkeys, is characterized by a sex-linked polymorphism. Trichromats, individuals with full and presumably human-like color vision, must be heterozygous for these alleles on each of two X chromosomes, and therefore only female capuchin monkeys can be trichromatic (Pessoa et. al., 1997; Hiramatsu et.al., 2005). Homozygous females and all males are dichromatic, meaning that they are red-green colorblind (Goulart et. al., 2013). The overall proportion of female capuchins that are heterozygous or homozygous is currently unknown. There are three different types of trichromacy and dichromacy, a total of six distinct genotypes. There are phenotypic differences within these trichromatic or dichromatic genotypes, but behavioral studies have found that despite this, there is a significant difference between red-green color discrimination abilities in trichromats versus dichromats regardless of which genotype they belong to (Pessoa et. al., 1997; Saito et. al., 2005a).

Sex-linked polymorphic traits cannot be predicted through phenotype alone, thus complicating the mechanisms by which they are influenced by natural selection. However, capuchin color vision is controlled by a single gene on the X chromosome, a system that has persisted for a long time and exists in most New World monkeys. This persistence indicates that this system is adaptive and maintained by natural selection (DePasquale, 2021). The mechanisms that maintain this polymorphism are not yet understood. One possibility is the niche differentiation hypothesis, which posits that trichromats and dichromats may occupy distinct foraging niches, meaning reduced intragroup feeding competition and higher fitness for both phenotypes (DePasquale, 2021). This would mean both a trichromat advantage and a dichromat advantage.

Prior research provides behavioral evidence for two leading hypotheses that would explain the co-occurrence of both advantages: that there is a trichromat advantage in fruit foraging and a dichromat advantage in hunting cryptic prey. Specifically, the trichromat advantage in red fruit foraging is based on the assumption that the red-green contrast of some ripe fruits against green leaves may be important for detecting ripe fruit from a distance (Sumner and Mollon, 2000). Indeed, there is observational and experimental evidence of trichromatic primates displaying greater efficiency in foraging for red fruits, relative to dichromatic primates (Smith et. al., 2003; Riba-Hernandez et. al., 2004; but see Hiramatsu et. al., 2008). In a manual color discrimination task, tamarins searched for differently colored boxes, corresponding to unripe, mid-ripe, and ripe fruits. Trichromats required fewer training trials than dichromats and picked more ripe fruits within the first six fruits taken (Smith et. al., 2003). In another study, field observations of fruit consumed by spider monkeys found that trichromats were able to detect all species of red fruits analyzed, slightly more than dichromats (Riba-Hernandez et. al., 2004). However, this advantage may not be as apparent in close-range foraging, as field observations following fruit foraging efficiency at grasping distance in spider monkeys found no difference between dichromats and trichromats, and suggested that luminance contrast was the main determination of foraging efficiency (Hiramatsu et. al., 2008).

The second hypothesis focuses on dichromat advantage in hunting cryptic prey. This hypothesis proposes that the limited color vision of dichromic primates may assist them in seeing ‘through’ the camouflage utilized by many invertebrates by reducing additional color ‘noise’ that distracts from differences in pattern and texture between the prey and its background (Saito et al., 2005). One study found that dichromatic monkeys were able to distinguish geometric shapes when the images were camouflaged with a green/red mosaic overlay. Trichromats were unable to differentiate the images above chance (Saito et al., 2005).

For the niche differentiation hypothesis to be correct, it is likely that trichromats and dichromats have different foraging behaviors that may stem from different abilities related to their respective niches. Indeed, prior field observations have shown that dichromatic capuchins (both male and female) were more efficient at capturing visually exposed insects than trichromatic females. Trichromats captured more insects that were embedded in substrates, meaning that they captured their prey without visual cues using extracting foraging (Melin et. al., 2010). A possible explanation for this may be that dichromats are better at visually finding insects, and so trichromats found a separate niche in extractive foraging when hunting for cryptic prey. Recent work comparing conspicuous fruit and cryptic invertebrate consumption directly found that color vision did not predict the proportion of time spent foraging for either fruit or invertebrates. These results reject the hypothesis that color vision differences result in divergent activity budgets (DePasquale et. al., 2021). However, they do not reject the possibility of differences in foraging efficiency, as intake rate and net food intake were not observed.

The majority of research has mostly been conducted in the field or using manual apparatuses. This makes other possible factors that influence foraging behavior difficult to control. In particular, capuchins are highly social, and choices made by conspecifics can influence individual's foraging activity, so results obtained from field observations may be influenced by social information (Dindo et al., 2009). Experiments using manual apparatuses can control for social influences when used in isolation, but other sensory information, like smell, may influence decisions when searching for food. Because there is a strong possibility of other sensory or social information influencing behavior, a controlled experiment that can isolate color as much as possible is necessary.

This study continues direct evaluations of 'red fruit foraging' and 'cryptic prey hunting' hypotheses in the same subjects, but focused on detection ability instead of activity budget. This study was done using computerized tasks in order to control for scent, luminosity, and social influences. While subjects were tested with visual access to each other, they were without physical contact or ability to move around or follow each other, as they might in natural foraging contexts. Computer tasks are at close-range, but this task uses two-dimensional images with solid colors, likely eliminating luminance that comes from 3-dimensional objects as a potential cue. The tasks that test each hypothesis were nearly identical in procedure and stimuli, with only hypothesis-relevant changes made, so the results of both tasks could be directly compared. This way, in addition to testing ecological abilities in a controlled environment, we intended to determine if the ability to identify red objects on green backgrounds and 'see through' color camouflage are inversely related in the same individual. Unfortunately, due to subject constraints, we were unable to compare results in the same individuals. While we hypothesized that color vision would be a predictive factor in task choice, we were unable to conduct genetic testing with our subjects and do not have information regarding the identities of dichromats and trichromats (this is in progress but was unavailable for this thesis). Therefore, we predicted that males (who are all dichromatic) would show less variation in task choice than females (who are very likely to consist of both dichromats and trichromats). We also predicted that all males and some females would have more success in the color camouflage task and be near chance in the color contrast task, while the remaining females would have more success in the color contrast task and be near chance in the color camouflage task. However, we were only able to collect data from one male for each task and cannot apply results from one individual to all males.

Methods

Participants

We began training a total of 23 brown tufted capuchin monkeys (15 females and 7 males, age: M±SD= 19.64 ± 8.31, range: 9 to 47 years) at the Language Research Center (LRC) of Georgia State University and were able to collect testing data from 9 capuchins (7 females and 2 males, age: M±SD= 18.11± 6.94, range: 9 to 30 years). Capuchins at the LRC are socially housed in stable mixed-sex groups in which they have long-term, often life-long, relationships, as is the case in wild populations. Each group has their own large indoor/outdoor enclosure and are regularly provided a variety of physical and food-based enrichment items. The capuchins were previously trained to voluntarily separate into testing boxes attached to their indoor enclosures for cognitive and behavioral studies; subjects are never restricted from food, water, treats, or outdoor or social contact to encourage participation. All subjects are given a daily diet of fruits, vegetables, nuts, and biscuits. All monkeys had access to water at all times, including during testing. This study, like all research at the LRC, was non-invasive and was carried out in accordance with all applicable international, national, and institutional ethical guidelines and requirements. The Language Research Center is fully accredited by the Association for Assessment and Accreditation of Laboratory Animal Care. This research was approved by the GSU IACUC (A20018 to Sarah Brosnan) and met the recommendations of the Animal Behavioral Society and the American Society of Primatology.

Procedure

Monkeys were tested in their individual boxes using computer systems in which they were able to make choices among stimuli by using a joystick to move an onscreen cursor. All stimuli were created using Procreate by SE and tasks were coded using Python. Subjects participated in two tasks. Both tasks were dichotomous choice tasks, in which the capuchins initiated a trial by selecting a start button and then chose one of the stimuli on a computer screen using a joystick. The side on which stimuli appeared was randomized. Both tasks involved 3 training levels that were designed to ensure that subjects were completing trials with the correct objective: to choose the image containing a drawing of an apple (see Figures 1a-1c and Figures 2a-2c). This allowed us to manipulate testing trials to determine what type of image subjects were drawn to. Task 1 tested whether capuchins would pick an image of a red apple on a green background or a green apple on a green background (see Figure 1d). Task 2 tested whether capuchins would pick an apple that was hidden by red-green camouflage or blue-yellow camouflage (see Figure 2d).

The capuchins were first trained to pick the image that contained an apple versus an identical image without an apple (see Figures 1a and 2a). Apples were identical in appearance and their location on the images was randomized between 9 possible positions on the image using a 3x3 grid. As they progressed through training, the backgrounds incorporated line-drawn trees, bushes, and plants, to create a more ecologically-accurate image, as a natural background typically consists of complex lines and shapes (see Figures 1b and 2c). Line-drawn backgrounds were identical across all stimuli. On test trials, both images contained apples (red or green for the Color Contrast task and on a red-green or blue-yellow background for the Color Camouflage task). The goal of these test trials is to discover which apple they see first. A tendency to choose red over green apples and red-green images over blue-yellow images indicates an advantage in identifying the target object.

Training blocks were nine trials long with a ten second inter-trial interval and subjects participated in unlimited blocks per day. To move up a level in training, and ultimately begin testing, capuchins had to perform with at least 77% accuracy (seven out of nine trials correct) in two blocks in a row. Once they passed the third training level and moved on to testing, blocks had 12 trials in order to ensure randomization in apple placement. Testing sessions were limited to ten blocks per day in order to limit any boredom or frustration towards the tasks for the capuchins.

For testing, we utilized a probe structure, in which the trials that test our hypothesis (the probes) are dispersed among training trials. Because we are looking at the attraction to a particular stimulus, there is no correct answer, and all probes are rewarded; this non-differential reinforcement also avoids inadvertent training. The purpose of dispersing probes among different trials is so subjects do not 'catch on' and associate the reward in testing trials to the stimulus they chose. Probes occurred in 25% of trials in each testing block. In both tasks, the remaining 75% of testing trials were identical to their final training level (see Figures 1c and 2c). Testing was coded so that one probe trial occurred at a random location within every four trials. In probes, like training, the location of the apple and the side that the apple appeared on was randomized. Each capuchin was targeted to complete a total of 40 testing blocks for each task, equating to 120 probe trials for each task. For the Color Contrast task, 4 subjects reached at least 120 probes (120, 120, 124, 157), 2 subjects reached at least 100 probes (103, 112), and 2 subjects reached 30 probes. For the Color Camouflage task, 3 subjects reached at least 120 probes (120, 120, 136) and 1 subject reached 116 probes. Low probe count for some subjects was typically due to subjects passing training late in our timeline of data collection or subject refusal to continue testing. Some subjects completed more than the target number of probes because testing was limited to 120 trials per day (30 probes), so if a subject completed less than 120 trials in a day, they needed to test more than 4 days and as a result, may go over the 480 trial (120 probe) target.

Color Contrast Task

Training proceeded through a series of steps designed to teach the capuchins to select images with an apple so that we could test their ability to discern red objects on green backgrounds. In Training 1, capuchins had to select the image out of the pair containing an apple to receive a reward. Both stimuli were solid green backgrounds, only one of which contained a white apple (see Figure 1a). They were presented side-by-side, each approximately five inches tall. In Training 2, we increased the complexity of the stimuli by adding the background line drawings, with slight variation in green on each object, to both sides (see Figure 1b). Capuchins were still rewarded for selecting the image with the apple. In Training 3, we changed from an easy-to-discern white target to a target that represents a red-green color contrast. In this condition, the apple became red at a similar luminosity to the green background (see Figure 1c). Capuchins continued to be rewarded for selecting the image with the apple.

Testing consisted of probe trials inserted among Training 3 trials. To assess if the color of the apple aided detection, probe trials used the same stimuli as Training 3, but with an apple on both images (see Figure 1d). One apple was the same shade of red as used in training and the other was a shade of green that was as close of a value to the red apple as we could given our equipment. Brightness equivalence was determined by turning images to greyscale and adjusting the color until they were indistinguishable to the human eye. We predicted that trichromats would be drawn to the red apple and choose images with red apples more often than images with green apples. Because dichromats see little to no variation between red and green, we predicted that they would choose between the red and green apples at chance.

Color Camouflage Task

Training again proceeded through a series of steps designed to teach the capuchins to select images containing an apple. However, this task was designed to determine the ability to discern objects in red-green camouflage, where dichromats are predicted to have an advantage. In Training 1, capuchins again had to select the image containing a white apple to receive a reward. Of the two images in each pair, one had a red-green camouflage background, and one had a blue-yellow camouflage background (see Figures 2a-d). Of the two camouflage colors, the one on which the white apple appeared was randomized across trials. In Training 2, we extinguished the possibility of subjects only looking for white objects. In this condition, we replaced the white apple with a black outline. Capuchins were still rewarded for selecting the image with the outlined apple. In Training 3, we added background line drawings, identical to those used in the Color Contrast Task. Capuchins continued to be rewarded for selecting the image with the outlined apple.

Like the Color Contrast task, testing consisted of probe trials (with an apple on both sides) inserted among Training 3 trials (see Figures 2c and 2d). Trichromats, seeing the full spectrum of both red-green and blue-yellow color camouflages, should find them equally difficult in finding the apple. However, dichromats, seeing the variation in the blue-yellow but not in the red-green, should find the red-green camouflage less difficult. We predicted that trichromats would have no preference for camouflage color, while dichromats would tend to choose the side in which finding the apple was easier, the red-green camouflage background.

Stimuli Adjustments

Because many of the subjects were unable to pass training with the original stimuli, we made some adjustments two months into training (2/22/21). Adjustments were made to any subject not testing at that moment and not at level 3 of their respective training (15 out of 22 monkeys involved in this study), though only three subjects later passed and tested with the new stimuli (Liam, male, task 1; Lily, female, task 1; Wren, female, task 2). The apple objects were transformed to 1.5x their original size in case they were not large enough to be obvious to subjects. The images were made slightly smaller and farther apart to reduce the possibility of the images being confused with each other or unintentionally selected. The joystick was reprogramed to only go up before touching the start button to avoid the possibility that subjects were moving the cursor at an angle and accidentally touching an image after going through the start button. The red color of the apple in the Color Contrast task was also found to have been marginally lightened in the processing of the image, so it was made slightly darker to match the lightness of the green apple more effectively.

Scoring and Data Reduction

We measured the rate that each capuchin chose each option type (Contrast Task: red apple or green apple; Camouflage Task: red-green camouflage or blue-yellow camouflage). We also measured the latency to choose (time between touching the start button and making a choice for each task). We intended to compare variation in males with variation in females and searched for a possible bimodal split in females. We also tracked the time and number of trials it took for each capuchin to pass all training levels to discern if behavior differed based on difficulty learning the task.

Analysis

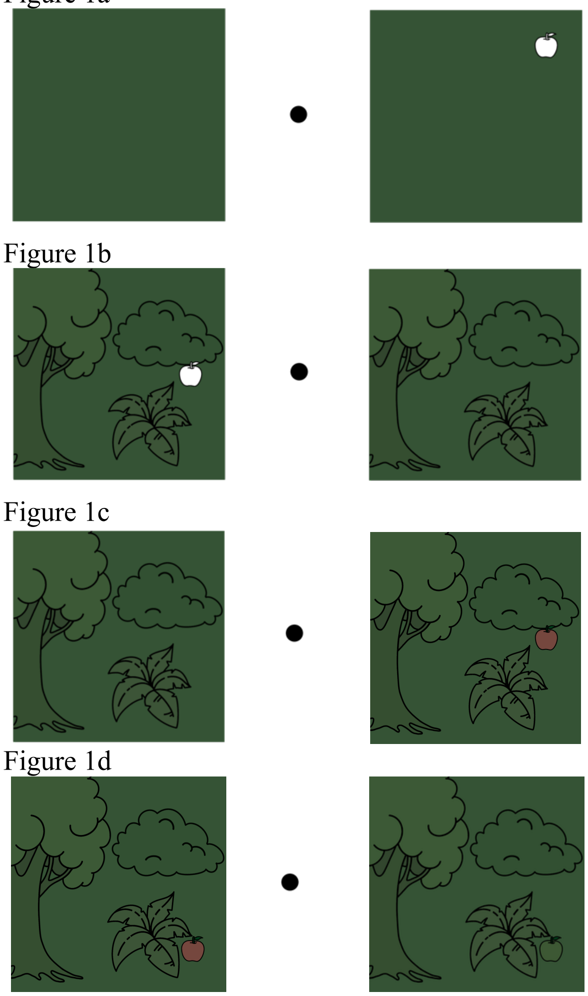
To identify any significant color preferences, we conducted a one sample T-Test on overall female performance for the Color Contrast task as well as Exact Binomial Tests for each subject individually. We also assessed side biases by comparing the counts of both type of stimuli chosen and assessed filler performance by measuring the percentage of filler trials answered correctly. To determine if sex was a predictive factor of performance, we intended to conduct logistic regression tests for both choice frequency and choice delay, using a Wald Chi-Square test to find explanatory variables such as apple location, background type, and stimulus side. We were unable to conduct this predictive test due to subject and sample size limitations.

Figure 1a

Figure 1b

Figure 1c

Figure 1d



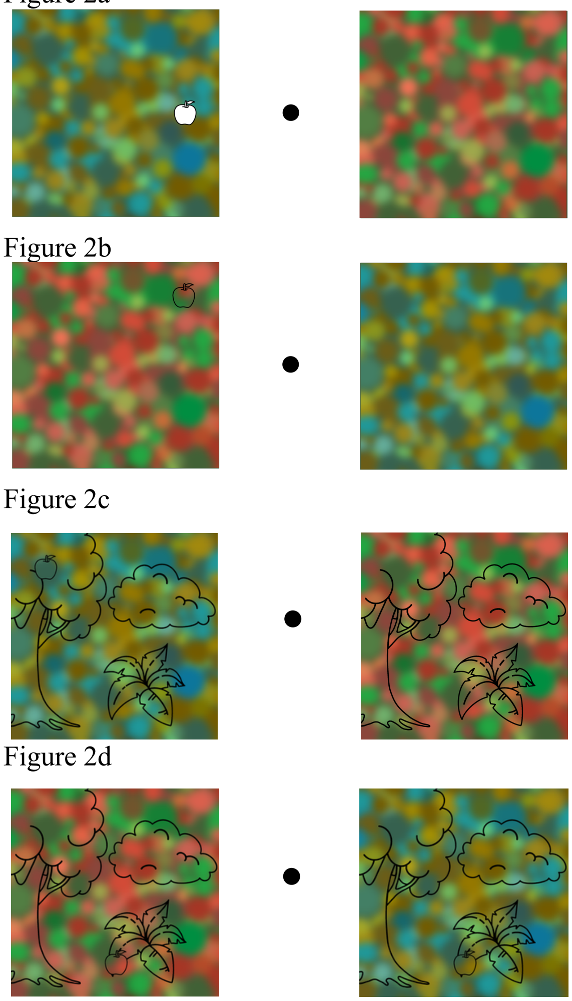
Figures 1a-d. Examples of choice stimuli for each training level and testing in the color contrast task.
1a. Level 1: Green background vs. white apple on green background. **1b**. Level 2: Full background vs. white apple on full background. **1c**. Level 3/Filler Trials: Full background vs. red apple on full background. **1d**. Probe Trials: Red apple on full background vs green apple on full background.

Figure 2a

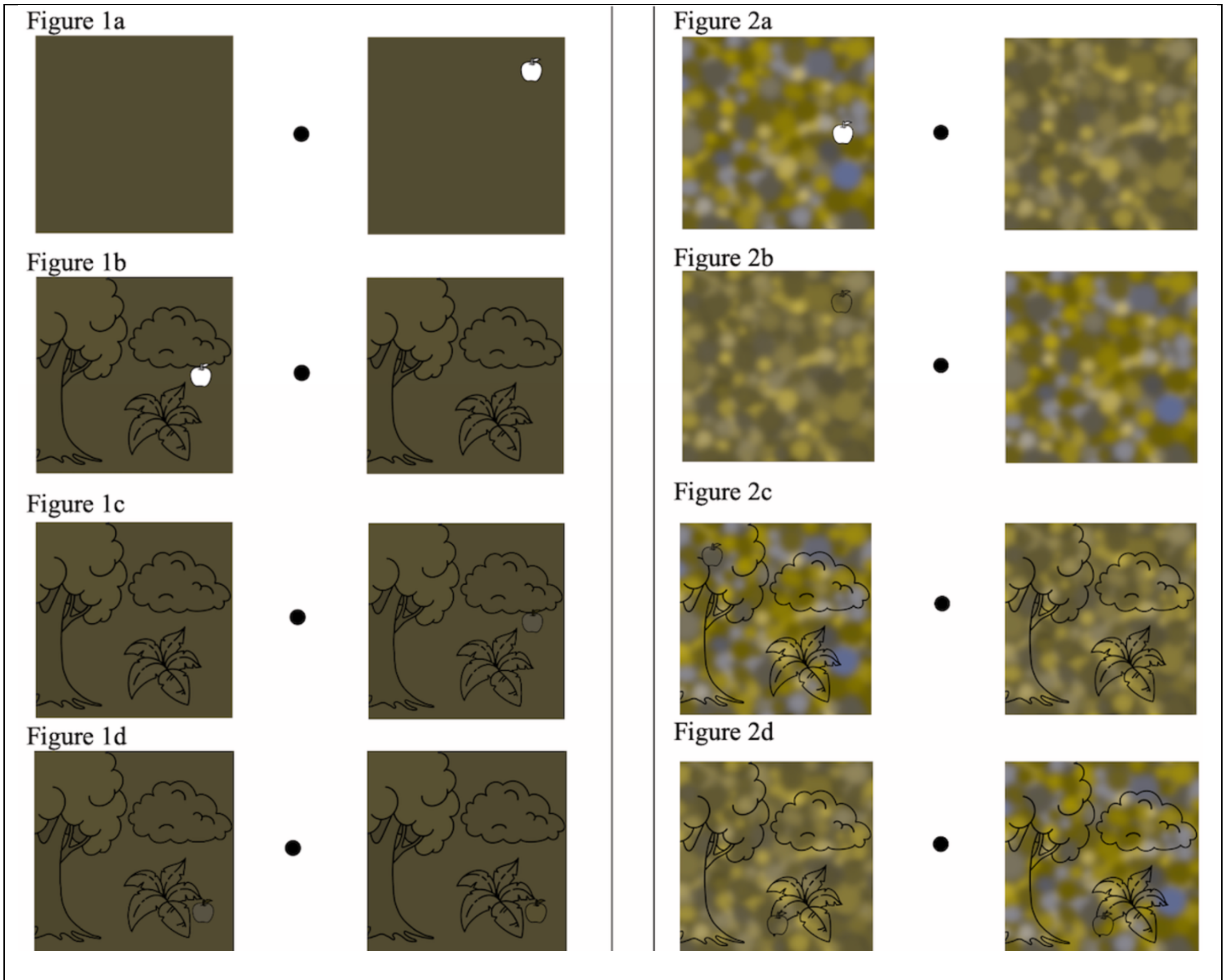
Figure 2b

Figure 2c

Figure 2d



Figures 2a-d. Examples of choice stimuli for each training level and testing in the color camouflage task.
2a. Level 1: Red-green camouflage background vs. white apple on blue-yellow camouflage background. **2b**. Level 2: Apple outline on red-green camouflage background vs. blue-yellow camouflage background. **2c**. Level 3/Filler Trials: Full red-green camouflage background vs. apple outline on full blue-yellow camouflage background. **2d**. Probe Trials: Apple outline on full RG background vs apple outline on full BY background.



Figures 3 and 4: Simulated versions of what the stimuli might look like to a protanope (red-green color-blind person). These images were created using Colblindor, and are not necessarily an accurate representation of what colorblind capuchins see, only an estimate of how a colorblind person might see these stimuli, https://www.color-blindness.com/coblis-color-blindness-simulator/

Results

Color Contrast Task

Only 1 male out of 7 was able to pass the training phase of this task, and because he did so late in training, we were only able to collect 30 probe trials for him. Because of this, we do not have a large enough sample size to perform a logistic regression test but can still compare t-test results between sexes. In contrast, 8 out of 13 females were able to pass training, though we were only able to test seven. Testing at the LRC is voluntary, and one of the females that passed training did not volunteer to test during the time we were collecting data.

We predicted that some females -presumably those that are trichromats- would be able to identify the red apple on the green background more easily than the green apple on the green background and should choose the red apple more frequently. For other females -presumably dichromats- and all males, predicted no preference. Liam, the one male in our sample, did not significantly prefer red or green apples ($M = 0.43$, $p = 0.82$). We found that on a group level, when given the option between the red and green apples, females significantly preferred the red apple ($M = 0.71$, $SD = 0.126$, $t(5) = 4.065$, $p = 0.005$). However, not all females performed similarly. Of the 7 female capuchins tested, 5 showed a significant preference for the red apple ($M = 0.67$, $p < 0.0001$; $M = 0.73$, $p = 0.008$; $M = 0.81$, $p < 0.0001$; $M = 0.73$, $p < 0.0001$; $M = 0.86$, $p < 0.0001$) while 2 showed no significant difference between apple colors ($M = 0.54$, $p =0.189$; $M = 0.57$, $p =0.08$). These two subjects (Bias and Nala) had side biases, choosing one side of the screen over the other most times, resulting in a near 50% split between red and green apples. Both individuals has a bias for the left side; Bias chose the left side in 291 trials and the right side on 120 trials, while Nala chose the left side on 355 trials and the right side on 92 trials. They also performed near chance on all filler trials in the Contrast task (52.8% and 55.2% correct, respectively). One other subject, Lychee, also performed near chance on filler trials (51.1% correct). Due to a coding error, we were unable to tell if our male subject showed a side bias, but, like the females that performed similarly to him on probes, he also performed near chance on filler trials (44.4% correct). It is important to note that both Liam and Lychee only ran 30 probe trials, compared to the target 120 and their results may not be as accurate as other subjects' results.

Color Contrast Task: Number of Trials Per Training Level

Monkey	Sex	Age	Level 1	Level 2	Level 3	Total Trials	Pass Task Training
Albert	Male	10	40	41	229	310	No
Liam	Male	18	242	124	312	678	Yes
Atilla	Male	9	1333	120	-	1453	No
Gabe	Male	23	72	700	574	1346	No
Griffin	Male	24	466	-	-	466	No
Nkima	Male	14	396	225	35	656	No
Logan	Male	16	22	-	-	22	No
Gambit	Female	25	392	-	-	392	No
Gretel	Female	18	451	797	328	1576	No
Lily	Female	24	117	66	285	468	Yes
Nala	Female	19	63	185	66	314	Yes
Paddy	Female	12	72	72	103	247	No
Widget	Female	13	99	63	162	324	Yes
Wren	Female	19	36	126	27	189	Yes
Bailey	Female	22	10	-	-	10	No
Bias	Female	30	189	81	289	559	Yes
Gonzo	Female	15	54	45	36	135	Yes
Lychee	Female	22	72	811	725	1608	Yes
Star	Female	47	360	45	182	587	No
Ingrid	Female	9	18	36	18	72	Yes
Ivory	Female	23	290	-	-	290	No

Table 1: Total number of trials on each Color Contrast training level per subject; Most subjects with more than 54 total training trials (the minimum number of trials needed to pass training) reached level 3 (15/18). Most males ran hundreds of trials yet were unable to pass training (5/6).

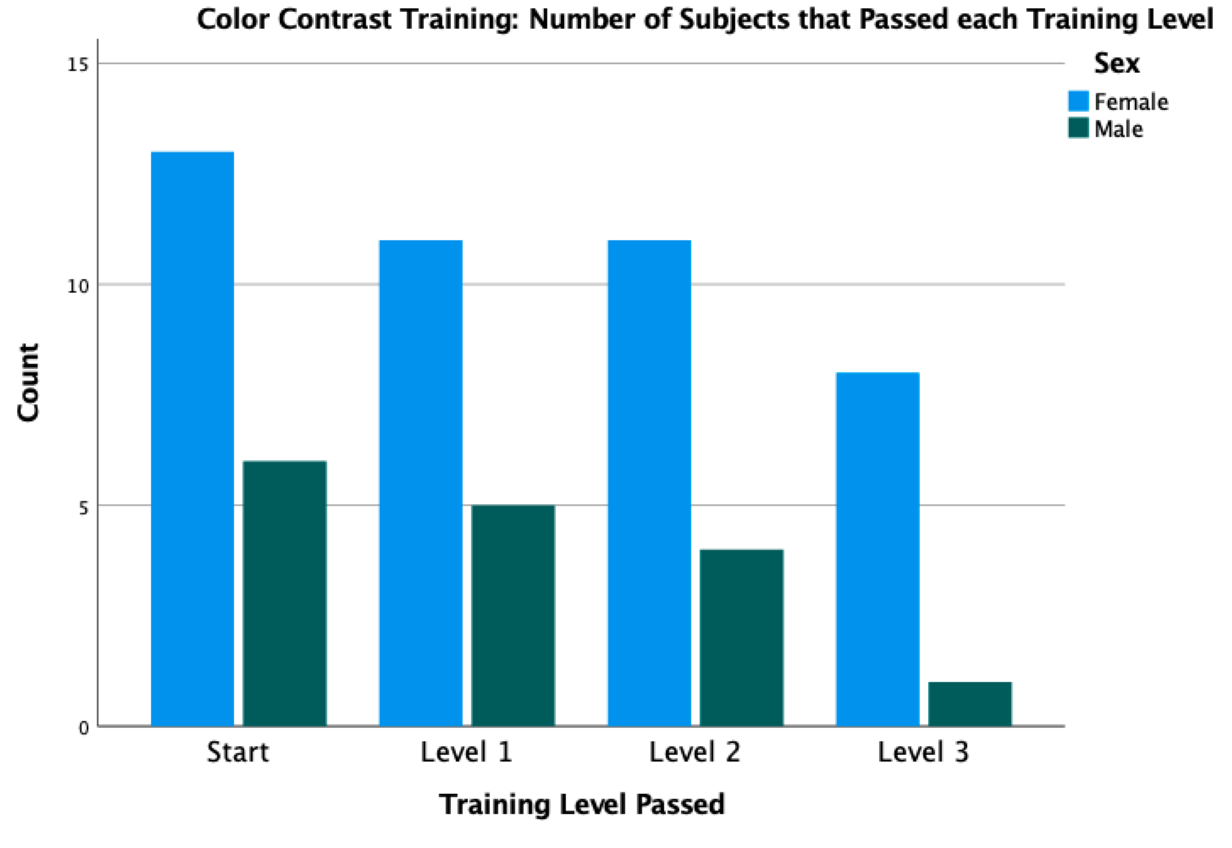


Figure 6: Highest Color Contrast training level reached by sex; 2 subjects with less than 54 total training trials (the minimum number of trials needed to pass training) were excluded (1 male and 1 female); Only 2 female and 2 males were unable to pass levels 1 and 2, combined, while 3 females and 3 males were unable to pass level 3. A greater percentage of males (72.7%) were stuck on level 3 than females (30%). This supports the possibility that dichromats (all males and some females) had greater difficulty with level 3 than trichromats (some females), resulting in many dichromats not qualifying for testing.

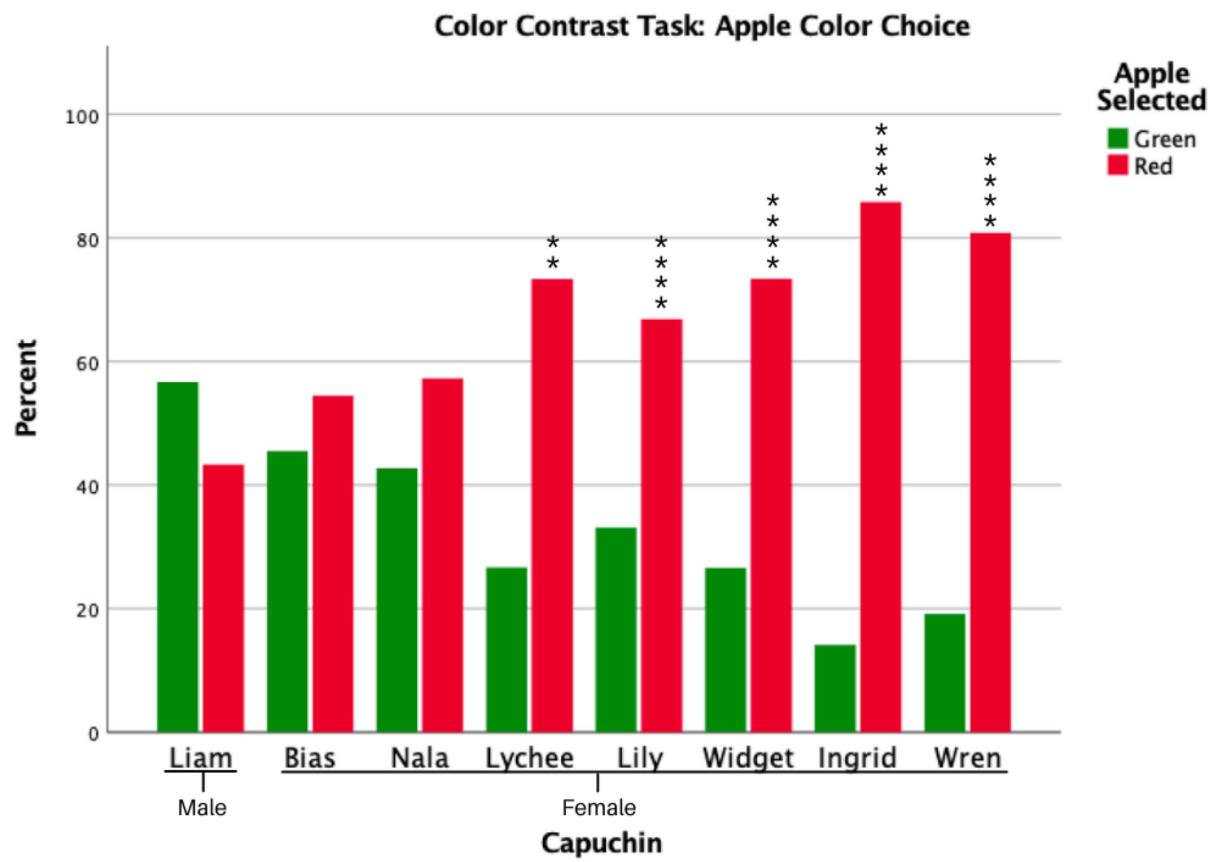


Figure 7: The results for the Color Contrast task; percentage of images with red or green apples chosen during probe trials. Liam (male), Bias (female), and Nala (female) showed no preference, while Lychee (female). Lily (female), Widget (female), Ingrid (female), and Wren (female) all showed a significant preference for red apples. We speculate that Bias and Nala may be dichromats, while the remaining females may be trichromats.

Color Camouflage Task

Four subjects were able to pass all training levels in the Camouflage task, one male and three females. Trichromats were expected to have no preference as the difficulty of each camouflaged background should be equal. Dichromats were predicted to prefer the red/green background because it should be easier to 'see through'.

Atilla, the male, had no significant preference between the red/green or blue/yellow backgrounds (M = 0.55, p = 0.15). Atilla also performed at chance in the filler trials (54%), which indicates a low grasp of the task. The three females showed no combined significant preference ($M = 0.53$, $SD = 0.124$, $t(2) = 0.372$, $p = 0.373$), but this can be explained by the differences between individuals. One female, Ingrid, had a significant preference for red/green ($M = 0.67$, $p < 0.001$). The other two females, Widget and Wren, had no significant preference ($M = 0.46$, $p = 0.87$; $M = 0.45$, $p = 0.88$). Wren's results can again be explained by her side bias (chose left in 364 trials and right in 116 trials) and both Wren and Widget performed near chance on filler tasks (49.2% and 57.5% correct, respectively).

Given that 3 out of 4 subjects tested performed at chance, we investigated whether the number of training blocks ran matched the number of training blocks theoretically required to pass by chance. The threshold to pass one training level was 77% for two 9-trial blocks in a row, which should happen by chance 0.8% of the time, equating to 1 out of every 125 blocks. Wren got to training level 3 after 5 blocks, so she likely passed levels 1 and 2 by understanding the task and not by chance. However, she then ran 227 blocks (2,043 trials) on level 3 before passing training. Widget, however, passed all three training levels within 19 blocks (10 of which were on level 3).

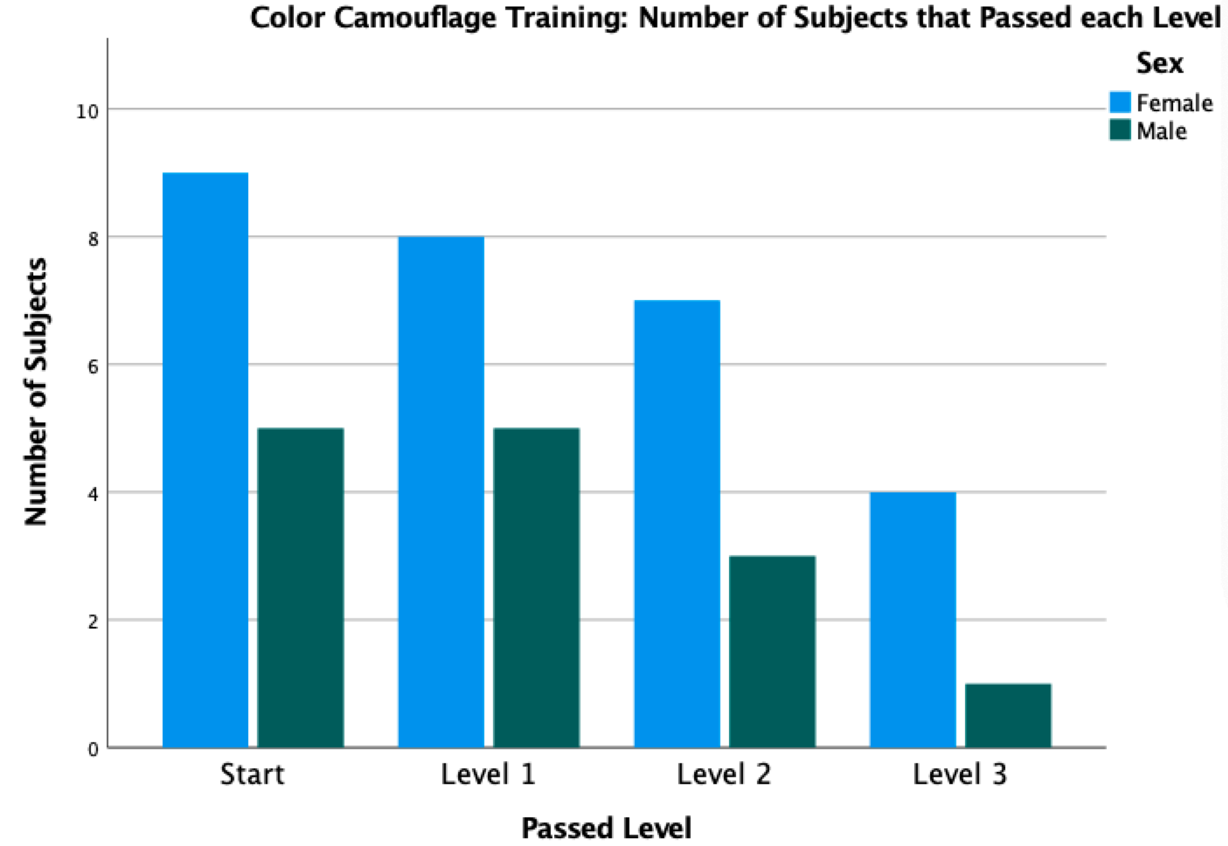


Figure 8: In contrast with figure 6, which showed a steady decrease from Start to Level 2 and a drop in subjects that passed Level 3, Male Color Camouflage Training showed no difference between Start and Level 1, then a steady decrease from Level 1 to Level 3. This contextualizes our findings from the Color Contrast Training analysis; that male (and some female) subjects have more difficulty on level 3 of the Color Contrast Task. Female training progression followed a similar pattern to the Color Contrast Task, which likely reflects an increase in general difficulty for Level 3 in both tasks.

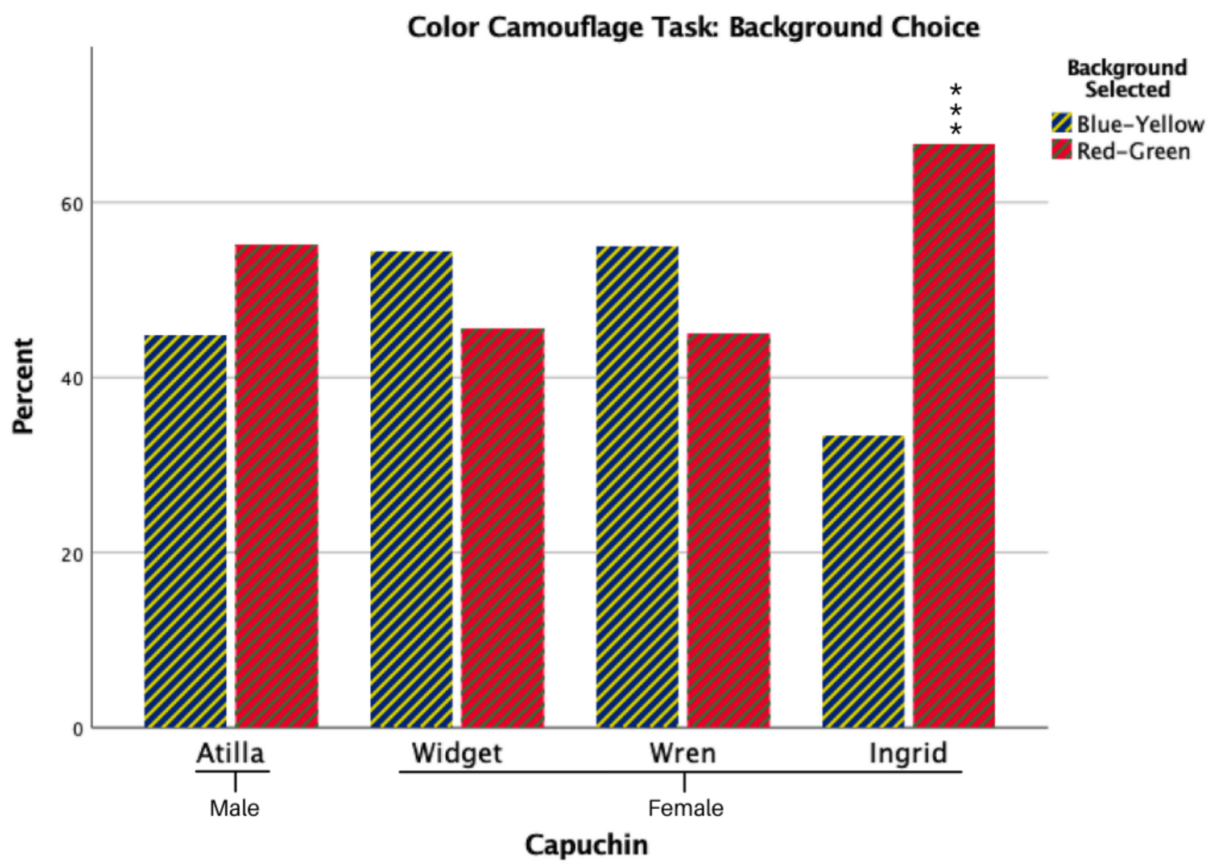


Figure 9: The results for the Color Camouflage task; percentage of images with red-green or blue-yellow backgrounds chosen during probe trials. Atilla (male), Widget (female), and Wren (female) showed no significant preference, while Ingrid (female) significantly preferred the red-green background. Due to side biases and poor filler trial performance, we conclude that the results of this task are likely not explained by color vision.

Discussion

Color Contrast Task

In terms of training, we predicted that because trichromat females would likely be able to easily identify the white apples in training levels 1 and 2 and the red apples in training level 3, they should move through training relatively smoothly. By contrast, training level 3 should be much more difficult for dichromatic females and males, as the red apple likely blends into the background for them. We assumed that passing level 3 would take longer for dichromats, but that they would eventually pass regardless of genotype. On the contrary, 14.3% of males and 61.5% of females were able to pass the training phase of this task.

If dichromacy explains this sex difference in training performance, then males should 'get stuck' on level 3 much more than levels 1 and 2. Females should show a similar pattern, but at a lower rate than males, as a smaller proportion of females are dichromatic. An independent samples proportion test found a significant difference between sexes in passing level 3 (Males: 1/4, Females: 8/11, $p = 0.048$) as well as a significant difference between sexes in passing all of training (Males: 1/7, Females: 8/14, $p = 0.031$).

Given that most females that were unable to pass training performed similarly to the males in training, it is possible that their inability to pass may be due to dichromacy. If so, we must also consider why one male and possibly other dichromatic females were able to initially pass training. There are multiple types of dichromacy, each with slightly varied levels of ability to distinguish between red and green. Because of this, different dichromats can see and perform in different ways. Therefore, the dichromats that passed training may be able to see some difference between red and green or may have simply put forward more effort in training. In short, our training data suggests that dichromacy makes passing level 3 of training very difficult, but not impossible.

Though we were unable to run genetic testing to determine which female monkeys were dichromatic or trichromatic, we plan to send samples to Dr. Amanda Melin at the University of Calgary for genetic testing this year. Until then, we can draw conclusions based on the behavioral data collected. It is possible that the four females with a preference for red and a high performance on filler trials are trichromats, while the two with no color preference and chance performance on fillers are dichromats. If this is the case, their side biases- which frequently arise when a subject becomes frustrated with a task or doesn't understand it- and poor filler trial performance could be a result of increased difficulty of the task as it relates to color vision. Like level 3 training trials, fillers should still be difficult for dichromats. They may have been able to initially pass testing with effort but stopped trying as hard when given an extensive amount of the difficult filler trials. The overall performance of Liam, Bias, and Nala suggests that, though they initially passed all training levels, they did not completely understand or were unable to accurately complete the task. Future plans to genotype the capuchins will be able to answer these questions and provide a more concrete explanation for these results.

Females overall preferred the images with red apples, which aligns with our hypothesis and supports the existing literature that identify a female ability to differentiate red objects on a green background, extended to red fruit on a green, leafy background. Furthermore, the one male who reached the testing phase did not show a preference, and while we cannot generalize one male's results to all males, there is a female advantage over this male in distinguishing red objects on green backgrounds.

We may not have generalizable male testing data, but training data indicates that females were better at passing level 3 of training than males. This supports the argument that trichromats can more easily identify red objects on green backgrounds than dichromats, based on existing literature that shows trichromat individuals finding and eating red fruits at higher frequencies than dichromats. Our results were gathered in controlled conditions, with no luminance, smell, or social information interfering with choice, so it is likely that field results are also reliably due to color vision ability and not other confounding factors.

Color Camouflage Task

Atilla's results do not support the hypothesis, as we predicted that dichromats would significantly prefer the red/green background. Ingrid's performance was one that we expected from a dichromat, though we predict Ingrid to be a trichromat based on her testing data in the Color Contrast task. This also does not support the hypothesis and may be because 1) there is no dichromat advantage in seeing through color camouflage, 2) color vision does not explain the results of the task, or 3) our monitors weren't adequate and that the task wasn't appropriate.

It is likely that Wren passed level 3 by chance, and because the filler trials are equal to level 3 training trials, it is not surprising that she performed at chance on fillers and developed a side bias. Widget likely passed all training levels because she understood the task, and not due to chance. Her poor performance on filler trials may be due to a drop in motivation when moved to testing. Unfortunately, Atilla's training data for this task was accidentally deleted while replacing stimuli on his computer, so we are unable to fully explain his poor filler trial performance. However, he did pass all three levels within 3 days of training. It is unlikely that he ran 125 blocks within those 3 days, so his poor performance on filler trials, like Widget, may also be due to a drop in motivation.

The individuals with no preference showed evidence for a lack of effort or understanding of the task. In addition, Wren, Widget, and Ingrid were speculated to be trichromats on the basis of the Contrast task, and if this is true, the fact that their results differ wildly indicates that trichromacy may not influence their results. For these reasons, we conclude that color vision does not explain the results of this task.

It is possible that Ingrid's probe trial results could be a product of associative learning, in which a monkey pays selective attention to one type of image background and associates it –

instead of the apples - to the rewards. Ingrid performed well in both training and filler trials and had no side bias or color bias, indicating that she understood the task. One possible strategy she may have used, to search for the apple in the red/green background first before looking in the blue/yellow background, was ruled out, as her average response time for choosing both red/green and blue/yellow images was nearly equal (1.51 seconds and 1.57 seconds, respectively). She may have instead developed an arbitrary preference for the red/green background, which she relied on when there were apples in both images.

Because the results of the Color Camouflage task indicate a failure in the task to assess differences due to color vision, we cannot directly compare results between tasks. As indicated by data from Atilla, Wren, and Widget, the Color Camouflage task may also be too difficult for some subjects to consistently identify an apple outline on either background. The background camouflages utilize variation in both lightness/darkness and color, which, combined, increases camouflage effectiveness for both trichromats and dichromats. It is likely that the variation in lightness was unnecessary and detrimental to the task.

Future Directions

The possible explanations for the Color Camouflage Task results give us a few possible directions in improving this task's methodology. To reduce difficulty, a simpler color camouflage background could vary only in color while keeping the same lightness across the image. In addition, the difference between red/green and blue/yellow may be so stark that monkeys may pay more attention to that difference over the difference between apple/no apple. Future tasks could only use the colors green and red, replacing the blue/yellow background with a camouflage background consisting of mostly red and only a few green splotches (or vice versa). In this way, trichromats would likely have an easier time 'seeing through' this new condition while dichromats, who see less variation between colors, might have less of a preference. In addition, the stimuli in both tasks could be made simpler by removing the line drawing backgrounds that were originally designed to add composition complexity to the images. The hypothesis would change to predict that dichromats would have no preference on both tasks and the stimuli would be easier and only use the colors red and green.

In addition, future studies will benefit from the use of equipment designed for color assessment. In this study, we had to use equipment already on hand, which did not include a color spectrophotometer or monitors that can control for color appearance. A future study with simpler stimuli and color assessment technology may allow us to accurately compare results between tasks and more clearly assess the possibility of a foraging-related trichromat advantage as it relates to a hunting-related dichromat advantage.

Future genotype data to may allow us to directly compare dichromat and trichromat Color Contrast performance without the need for additional male data. If the genotypes match what we speculate, our results would support a trichromat advantage in foraging for red fruits in green forest environments, providing color-controlled evidence that supports existing literature from the field.

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