Food search through the eyes of a monkey: A functional substitution approach for assessing the ecology of primate color vision

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A B S T R A C T

Efficient detection and selection of reddish fruits against green foliage has long been thought to be a major selective pressure favoring the evolution of primate trichromatic color vision. This has recently been questioned by studies of free-ranging primates that fail to show predicted differences in foraging efficiency between dichromats and trichromats. In the present study, we use a unique approach to evaluate the adaptive significance of trichromacy for fruit detection by undertaking a functional substitution model. The color vision phenotypes of neotropical monkeys are simulated for human observers, who use a touch-sensitive computer interface to search for monkey food items in digital images taken under natural conditions. We find an advantage to trichromatic phenotypes – especially the variant with the most spectrally separated visual pigments – for red, yellow and greenish fruits, but not for dark (purple or black) fruits. These results indicate that trichromat advantage is task-specific, and that shape, size and achromatic contrast variation between ripe and unripe fruits cannot completely mitigate the advantage of color vision. Similarities in fruit foraging performance between primates with different phenotypes in the wild likely reflect the behavioral flexibility of dichromats in overcoming a chromatic disadvantage.

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1. Introduction

The color discrimination ability of most humans and many other primates exceeds that of other mammals and is believed to be an adaptation for finding reddish food items, such as ripe fruit. Yet surprisingly, neotropical monkeys possess remarkably variable color vision due to the persistence of a widespread, stable genetic polymorphism (Boissinot et al., 1998; Hiramatsu et al., 2005; Hiwatashi et al., 2010; Jacobs & Deegan, 2001, 2003, 2005; Mollon, Bowmaker, & Jacobs, 1984; Surridge and Mundy 2002; Talebi et al., 2006). This presents a unique puzzle to evolutionary geneticists, behavioral ecologists, and anthropologists that remains open to extensive debate (see Jacobs, 2010; Kawamura et al., 2012; Lucas et al., 2007 for recent reviews). Studies on the functional consequences of this color vision variation are hindered by the methodological obstacles inherent with observations of non-human primates. Here, we introduce a novel method for investigating primate visual ecology – human functional substitution. This approach simulates, for color-normal human primates, the appearance of real-world targets (fruit) to monkeys with different color vision phenotypes and generates unique insights into the

consequences of differing trichromatic and dichromatic visual phenotypes for the speed and accuracy of food detection.

1.1. Primate color vision

Primates are the most visually-oriented mammalian order (e.g. Heesy, 2009) and the derived characteristics of their visual system include trichromatic color vision. Whereas the majority of diurnal mammals have dichromacy via two retinal cone pigments, one short-wavelength sensitive (S) and the other sensitive to long-to-middle wavelengths (L/M), most primates possess an additional L/M photopigment. This reflects the duplication and divergence of the ancestral L/M opsin gene and results in an improved capacity to distinguish among red, orange, yellow and green hues (Dulai et al., 1999). Primate trichromacy is widely believed to be a foraging adaptation wherein enhanced color vision is hypothesized to facilitate the discrimination of reddish ripe fruit (Mollon, 1991; Mollon, Bowmaker, & Jacobs, 1984; Osorio et al., 2004; Regan et al., 2001; Smith et al., 2003b; Sumner & Mollon, 2000) or young leaves (Dominy & Lucas, 2001; Lucas et al., 2003) from mature green foliage. Because color vision provides luminance-independent chromatic contrast, it is especially useful for object detection in environments with variable illumination, such as tropical forests where down-welling light is dappled by the trees (Mollon, 1989).

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Intriguingly, primate color vision is highly variable both between and within species. The L/M opsin polymorphism of most neotropical monkeys is X-linked, such that only heterozygous females possess trichromatic color vision. In the tri-allelic system characterizing many species, the photopigments have peak sensitivities (λ_{max}) that range from relatively green-shifted (~530 nm) to red-shifted (~560 nm) (Jacobs & Blakeslee, 1984; Mollon, Bowmaker, & Jacobs, 1984; Saito et al., 2005a). Among the possible trichromatic phenotypes, the variant with the most spectrally separated L/M photopigments (530 nm and 560 nm) is believed to be most favorable, as it allows the widest range of chromatic discriminations (Osorio et al., 2004; Rowe & Jacobs, 2004). By the same reasoning, among dichromats (males and homozygous females) the red allele is suggested to be the most favorable variant as it is the most spectrally separated from the S photopigment (420 nm) common to all individuals. Compellingly, the red-shifted allele is often found at the highest frequency in wild populations (Hiramatsu et al., 2005; Surridge & Mundy, 2002; Surridge et al., 2005), but see (Cropp, Boinski, & Li, 2002).

Tests of the trichromatic advantage hypothesis, which predicts the highest foraging efficiency and implicitly the highest fitness to trichromatic primates, include theoretical models of primate visual perception (Osorio et al., 2004; Regan et al., 2001; Smith et al., 2003b; Sumner & Mollon, 2000; Vorobyev, 2004). These studies have demonstrated that primate cone photopigment sensitivities are optimized for discriminating ripe fruits from leaves. Behavioral experiments with captive New World monkeys provide an additional line of supportive evidence. Caine and Mundy (2000) and Smith et al. (2003b) have found that trichromatic callitrichid monkeys (*Callithrix*, *Saguinus*) located yellowish or reddish food targets against a green background more quickly than their dichromatic cohorts. However, while some studies on free ranging primates hint at foraging advantages of trichromacy (Bunce et al., 2011; Melin et al., 2009; Smith et al., 2003a) convincing accounts are lacking, and other studies find no effect of color vision phenotype on fruit feeding rates (Hiramatsu et al., 2008; Vogel, Neitz, & Dominy, 2007). This has led researchers to question the practical utility of color vision for foraging among wild primates and suggest that non-chromatic visual differences between target and background, including size, shape and luminance contrast, are generally sufficient for food detection and evaluation.

Yet before an adaptive explanation for trichromacy during fruit foraging is discarded, it is important to consider the limitations of behavioral studies, especially those in the field where many variables cannot be controlled. For example, researchers cannot actually know when a monkey has seen an object; visual detection must be inferred by observing the monkey's gaze and subsequent actions, such as food handling. As a result, decisions to pass over a potential food item after a quick visual assessment may be missed. Furthermore, if burdened by deficient color vision, dichromatic primates are expected to have adopted successful coping strategies. Among humans, luminance contrast is important to all observers for discrimination of form, depth and movement (Livingston, 2002; Logothetis et al., 1990), but even more so for color deficient observers. For example, people with color vision deficiencies rely more heavily on achromatic cues to identify objects (Ramaswamy & Hovis†, 2011), a tactic that allows them to break color camouflage more efficiently (Morgan, Adam, & Mollon, 1992). Similar results have also been obtained for non-human primates (Saito et al., 2005b). Thus, trichromatic advantage could be hidden by observational limitations or successful counter-adaptation by dichromats. To overcome the difficulties associated with primatological field studies while maintaining biological relevance, we developed a new human functional substitution approach and testing paradigm to evaluate the effect of visual phenotype on foraging search tasks experienced by wild monkeys.

1.2. The human functional substitution model

Humans are readily able to complete computer-based trials under controlled conditions and ideal subjects for investigator-guided psychophysical studies of visual detection. Humans also make excellent monkey surrogates because they share the derived characteristics of anthropoid visual systems, including a cone-dense fovea with a macula lutea, a large binocular visual field, high acuity, and strong cortical representation of central vision (Ross and Kay, 2004; Ross and Kirk, 2007). Using a custom-developed computer program, "Color Vision Simulator" (CVS), we adjusted the chromaticity of digital images to accord with the known photopic color sensitivities of the six different capuchin monkey phenotypes. This is based on the presumption that our method represents a reasonable first-order approximation of how food targets would appear to monkeys with differing color vision abilities. Participants located the target food items in these images using a touch-sensitive graphic tablet interface. This approach is similar to that adopted by others (Ramaswamy & Hovis†, 2011; Rowe & Jacobs, 2004, 2007), however we used digital images of naturally situated fruit scenes rather than geometric shapes to capture their real-world visual cues, including shape, size and orientation, in addition to chroma, as closely as possible. We based our simulations on a tri-allelic L/M opsin polymorphism, generating three possible dichromatic and three possible trichromatic phenotypes. For comparative purposes, we also simulated cone monochromacy (i.e., complete colorblindness) and recruited a small sample of naturally color-deficient humans.

Our aim was to assess how color vision phenotype impacts detection speed and accuracy of locating the food targets that monkeys search for in the wild. We expected that simulated trichromats would be faster and more accurate than simulated dichromats for detection tasks where the targets differ from background leaves in long wavelength hues (i.e. reddish or yellowish fruits), but not for targets that are of similar hue to the background foliage (greenish) or those that differ strongly in achromatic contrast from leaves (dark fruits). We further hypothesized that the trichromatic phenotype with the widest spectral separation between cone pigments would be the most advantageous. Among the dichromats, we predicted that those with the most red-shifted photopigment would be the fastest and the most accurate for food item search. Finally, we anticipated that simulated dichromacy would be more beneficial than simulated monochromacy.

2. Methods

2.1. Study design

We chose to model the visual phenotypes and foraging tasks of capuchin monkeys (*Cebus capucinus*) in the tropical dry forests of the northwestern Costa Rica because their color vision (Hiramatsu et al., 2005; Melin et al., 2007; Vogel, Neitz, & Dominy, 2007) and frugivorous diet (McCabe & Fedigan, 2007, Melin et al., 2008, in press, Parr, Melin & Fedigan, 2011) are well documented. The images used in all trials were digital photographs of fruits taken *in situ* in the Área de Conservación Guanacaste (ACG), Costa Rica using a Nikon D-90 10.0 megapixel digital SLR camera. The utility of such color-calibrated images to investigate color vision has previously been demonstrated (e.g. Parraga, Troscianko, & Tolhurst, 2002). To standardize the camera's color rendering we followed the recommendations of Stevens et al. (2007) and Stevens, Stoddard, and Higham (2009). White balance was set at the start of each photography session under natural illumination using the GretagMacbeth ColourChecker White Balance Card®. We used the standard 24 square GretagMacbeth Colour Chart® and PictoColour