

Naturalistic color discriminations in polymorphic platyrrhine monkeys: Effects of stimulus luminance and duration examined with functional substitution

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Abstract

X-linked photopigment polymorphism produces six different color vision phenotypes in most species of New World monkey. In the subfamily Callitrichinae, the three M/L alleles underlying these different phenotypes are present at unequal frequencies suggesting that selective pressures other than heterozygous-advantage operate on these alleles. Earlier we investigated this hypothesis with functional substitution, a technique using a computer monitor to simulate colors as they would appear to humans with monkey visual pigments (*Visual Neuroscience* 21:217–222, 2004). The stimuli were derived from measurements of ecologically relevant fruit and foliage. We found that discrimination performance depended on the relative spectral positioning of the substituted M and L pigment pair. Here we have undertaken a systematic examination of two simulation parameters—test field luminance and stimulus duration. Discriminability of the fruit colors depended on which phenotype was simulated but only at short stimulus durations and/or low luminances. Under such conditions, phenotypes with the larger pigment peak separations performed better. At longer durations and higher luminances, differences in performance across different substitutions tended to disappear. The stimuli used in this experiment were analyzed with several color discrimination models. There was limited agreement among the predictions made by these models regarding the capabilities of animals with different pigment pairs and none predicted the dependence of discrimination on changes in luminance and stimulus duration.

Keywords: New World monkeys, Opsin genes, Color vision, Cone pigments, Fruit discrimination

Introduction

Visual ecologists have long been interested in the diversity of visual pigments across animal species. It is generally assumed that this diversity is adaptive, that animals produce visual pigments optimized for tasks that are either performed often or are otherwise important in the struggle for survival (Osorio et al., 2004; Marshall et al., 2003; Geisler & Diehl, 2002; Regan et al., 2001; Chiao et al., 2000; Nagle & Osorio, 1993; Lythgoe & Partridge, 1991; Lythgoe & Partridge, 1989). New World monkeys provide an excellent model group for testing this assumption because sex-linked polymorphisms produce visual pigment diversity within populations of most species (Jacobs, 1998). Individuals within a population presumably share the same ecological goals, so the relative frequencies of different photopigment genes should reflect the relative adaptive values of the photopigments.

Two broad types of investigation have been used to assess photopigment optimality, direct observations of animal behavior in either natural or semi-natural situations (e.g., Saito et al., 2005;

Leal & Fleishman, 2004; Caine et al., 2003; Dominy et al., 2003; Smith et al., 2003; Caine & Mundy, 2000), and computational modeling of visual performance (e.g., Osorio et al., 2004; Lucas et al., 2003; Sumner & Mollon, 2003; Dominy & Lucas, 2001; Regan et al., 2001; Sumner & Mollon, 2000; Vorobyev & Osorio, 1998; Osorio & Vorobyev, 1996). Some recent studies have employed both approaches (e.g., Stoner et al., 2005; Riba-Hernandez et al., 2005). We have developed a third type of approach, functional substitution (Rowe & Jacobs, 2004; Rowe et al., 2006). The idea behind functional substitution is that when provided with appropriate stimuli, human observers can act as surrogates for animals with different photopigments. In this way, individual humans can perform the same experiment several times, each time simulating observation through a different pigment set. This makes it possible to assess the extent to which one set of pigments is better than another in the performance of an ecologically relevant task. Because the experiment is performed repeatedly by the same subject, the approach maintains one of the principal benefits of computational models of color discrimination—the ability to modify photopigment spectral sensitivities while keeping everything else constant. At the same time, functional substitution also maintains a benefit of behavioral studies in that results are mediated by the performance of living subjects who may be able to exploit

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stimulus information in ways that are not yet incorporated in the models. As employed here, functional substitution assumes that the most important difference between animals with different photopigment complements is the difference in relative quantal catch rates of photoreceptors from different spectral classes. It is not assumed that post-receptor processing is necessarily the same in humans and monkeys; rather, the question addressed is how human discrimination performance depends on cone spectral sensitivities when all else is equal. Barring direct evidence to the contrary we do assume that differences in performance mediated by different pigment sets will be qualitatively similar across species.

Earlier, we applied functional substitution to determine whether some tamarin (Callitrichidae) color vision phenotypes have advantages over others (Rowe & Jacobs, 2004). Tamarins have three M/L photopigments with absorption maxima at about 543 nm, 556 nm, and 562 nm (Jacobs et al., 1987). Females that are heterozygous at the single M/L gene locus express any pair of pigments drawn from these three. Human surrogates standing in for the three trichromatic phenotypes of female tamarins were tested for their abilities to distinguish the colors of ripe *versus* partially ripe fruit against a leafy background. We found that under several viewing conditions the 556 nm/562 nm pairing is disadvantaged relative to either of the other two possible pairs (Rowe & Jacobs, 2004).

In subsequent experiments, we discovered that the performance of subjects with different substituted pigment sets depended on specific features of the stimuli. Accordingly, we have now systematically manipulated two such features, stimulus luminance and duration, to determine their effects on discrimination performance. We have also tested the results of these experiments against predictions made by a variety of models.

Materials and methods

Psychophysics

The basic methods were identical to those of the previous report (Rowe & Jacobs, 2004). In brief, data from Smith et al. (2003) were used to determine the relative quantal catch rates of the four tamarin cone types (1 S and 3 M/L) as the animals viewed the fruit and leaves of *Abuta fluminum*, the fruit being a common food source for tamarins (Smith et al., 2003). A calibrated computer monitor produced in the cones of human subjects relative quantal catch rates that were the same as the computed relative quantal catch rates of the cones of tamarins viewing these objects. The equipment used in these experiments was the same as that used before except for the monitor (a P95f+; ViewSonic Corp., Walnut, CA) and the graphics card (a Radeon 9200; ATI Technologies Inc., Markham, Ontario) that drove it. For some of the experiments the monitor was viewed through glass filters (GG475 and neutral density, Schott North America, Inc., Elmsford, NY) to allow an extension of the dynamic range over which luminances could be modulated.

Computations based on environmental illumination, object reflectance, and the spectral absorption functions of tamarin cones constrained the chromaticities of all stimuli, but luminance was treated as a free parameter. Variation in illumination and orientation of surfaces renders luminance an unreliable cue for primates foraging for fruit (Mollon, 1989). Such foraging has been argued to be one of the primary selection forces driving the evolution of primate color vision, so we elected to examine our subjects' abilities to distinguish fruit colors in the absence of luminance cues. Thus, except for slight variation in the "leaves" as described

later, all stimuli presented during any given trial were nominally isoluminant, similar to the task described as "isoluminant fruit and leaves" in Rowe and Jacobs (2004). The background consisted of 2000 rectangles of random size, position, and luminance. Background chromaticities matched the relative quantal catch rates of human cones to the relative quantal catch rates of tamarin cones viewing *A. fluminum* leaves. The luminances of the background rectangles during a block of trials were centered on the luminance of the fruit colors used as targets for that block, and ranged 10% above and below that luminance level. Each of the monitor's three phosphor types could be controlled with 10-bit precision, but software limitations constrained the output to 256 unique r, g, and b combinations during the presentation of any single video frame. One of these combinations was set to the monitor's black level (for the fixation point), and two were set for the fruit colors (one partially ripe and one fully ripe). The remaining 253 combinations were available for the background, but the constraints of chromaticity, range, and spatial randomness of intended luminances limited any given background to a smaller number of physically distinct colors.

The properties of the background are important; pilot studies indicated that spatial chromatic contrast effects can affect subject performance. In natural settings objects will appear against a variety of backgrounds. To gauge an animal's capabilities, discrimination performance should be tested over a similar variety of backgrounds. However, changing backgrounds between pigment-set substitutions would have confounded differences mediated by the changes in pigment sets. Consequently, for any given subject, the background was fixed (aside from slight differences in chromaticity associated with viewing the leaves through different pigment sets) over the course of an experimental session.

Subjects were given a "same/different" task: during a trial they were presented with two squares and were forced to indicate whether the two squares were the same or different. The squares subtended one degree of visual angle on a side, and were centered on the perimeter of an imaginary circle with a radius of two degrees. The stimulus geometry is depicted in Fig. 1. Trials were balanced such that on half of the presentations in a given block the two squares were the same. Among trials where the two squares

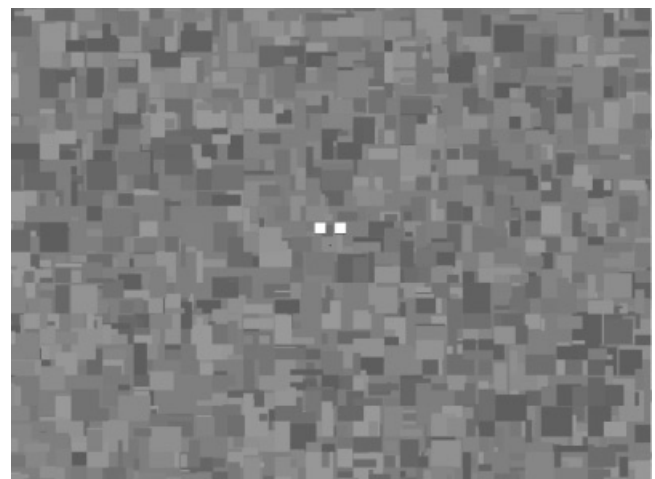


Fig. 1. Representative stimulus geometry. The two light squares are located at positions that fruit colors might appear during a single trial. The remaining rectangles have chromaticities derived from leaf colors.

were different, presentations were farther balanced by having the color simulating ripe fruit appear on the left side during exactly one half of the trials.

The method of constant stimuli was used to generate psychometric curves as a function of duration with luminance fixed, and as a function of luminance at fixed duration. When stimulus duration was varied, luminance was fixed at the highest attainable value, approximately 150 cd/m². The monitor was refreshed at 120 Hz, and the squares were held visible for anywhere from 1–15 frames (8–125 ms). When luminance was varied, stimulus duration was fixed at 12 frames (100 ms). Luminances ranged from approximately 5–150 cd/m², the lowest of which were achieved by using a 0.8 Neutral Density filter. In this way, the number and scaling of distinct background luminances was kept essentially the same across all experiments.

A total of four subjects participated. All had normal color vision. One subject was tested only at variable luminances, and another only at variable stimulus durations. The remaining two subjects were used in both experiments. Two of the four subjects were experienced from having participated in the earlier study (Rowe & Jacobs, 2004).

Data analysis

The data were analyzed using a Bayesian analysis incorporating software developed specifically for modeling psychophysical data (Kuss et al., 2005). The software performs a Markov chain Monte Carlo (MCMC) simulation designed to estimate the probability density functions for the parameters of the model given the data. We ran each of the simulations for 2000 steps. From the MCMC analyses, confidence intervals were derived for the parameters of fits to the data. The confidence intervals around parameters determined for different pigment substitutions were compared to indicate the likelihood that overall performance depended on pigment substitution. Luminances were log transformed prior to analysis.

Fig. 2 illustrates the three parameters of the basic model used to fit the data: lapse probability, threshold, and width. The lapse probability is the likelihood that a subject will make a response that is independent of the stimulus (i.e., that the subject's attention lapses) during any given trial. Threshold is arbitrarily defined as the stimulus level at which performance is 75% (ignoring lapses). Width is defined as the difference in stimulus levels at which performance rises from 55% to 95% (i.e., between 10% and 90% of the way from the lower to the upper limits of performance, again ignoring lapses). Threshold and width are defined only for the purposes of describing the fits; they have no intended perceptual meanings beyond characterization of the underlying data.

Model comparisons

Numerous models of color vision have been proposed that attempt to map physical stimuli to behavioral responses. There are two basic ways that such maps have been constructed: (1) Empirical models are derived essentially by curve fitting; the biological mechanisms mediating the transformation between stimulus and response are treated as a black box, (2) Theoretical models are derived by computationally mimicking the processing performed in nervous systems. The theoretical models can farther be broken down into two broad classes, those that map the linkage between stimuli and performance through limitations set by receptors and

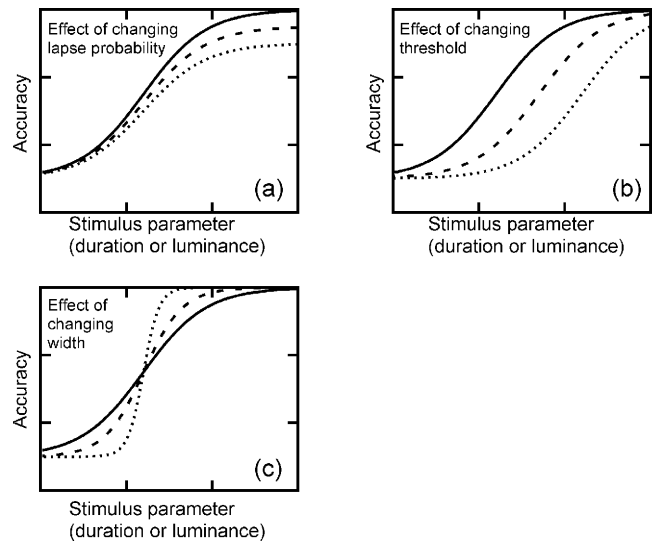


Fig. 2. Fit parameters. The curves in (a) differ by having three different values of the lapse rate, in (b) the three curves have a lapse rate of zero, but they have three different thresholds. In (c), the three curves have different widths.

those that assume performance limits are established by post-receptoral processing events.

We compared and contrasted the data to predictions made by several models of color processing (Sumner & Mollon, 2000; Vorobyev & Osorio, 1998; Vorobyev et al., 2001 as implemented in Appendix B of Osorio et al., 2004; Maxwell triangle with cone quantal catch rates as cardinal axes as described in Kelber et al., 2003; CIELAB and CIELUV, Wyszecki & Stiles, 1982). As indicated in Table 1, these include representatives of each of the approaches noted above. Beyond that, we chose these models for a variety of reasons. Two of them (Sumner & Mollon, 2000; Osorio et al., 2004) have been applied to primates foraging for fruit and are thus of obvious relevance. One of the remaining models (Vorobyev & Osorio, 1998) is an earlier version of the model used by Osorio et al. (2004). It has been used to characterize color vision in a variety of animals (e.g., birds: Håstad et al., 2005; lizards: Stuart-Fox et al., 2004; frogs: Siddiqi et al., 2004; hymenopteran insects: Vorobyev et al., 2001), so there seems to be a consensus that it is applicable to many color vision systems. The Maxwell triangle was originally developed for humans (Wyszecki & Stiles, 1982), but it has also been generalized for use in studying other trichromatic animals (e.g., Neumeyer, 1981). The CIELAB and CIELUV color difference formulae are derived from empirical measurements of human abilities to discriminate colors (Wyszecki & Stiles, 1982), and thus would seem most likely to predict accurately the performance of our subjects.

Two of the models (Vorobyev & Osorio, 1998; Osorio et al., 2004) assume that noise in the receptors establish the limits of color vision performance. One of the models (Sumner & Mollon, 2000) assumed performance depends on the magnitude of color opponent signals with the nature of the opponency, believed to be common among primates. The remaining models make no assumptions about the coding of color signals, only that larger differences in the responses of receptors lead to larger differences in perceptions.

Where appropriate, we applied the models over ranges of their underlying parameters. In particular, the Osorio et al. (2004) model

Table 1. Comparison of psychophysics and computational predictions for three different trichromatic phenotypes. Number of greater than symbols indicate relative sizes of differences in the rank ordering (best to worst) of performance predictions within a given model. Derivation refers to the type of model (see text for details).

Model	Performance Prediction	Derivation
Psychophysics—current experiment	543/562 = 543/556 > 556/562	direct empirical result
Vorobyev and Osorio (1998)	543/556 ≈ 543/562 > 556/562	receptor noise
Osorio et al. (2004)	543/562 > 556/562 ≫ 543/556	receptor noise
Sumner and Mollon (2000)	543/562 > 543/556 > 556/562	opponent processing
Maxwell's Triangle	543/562 > 543/556 > 556/562	receptor signals
Maxwell's Triangle (von Kries scaling)	543/562 ≈ 556/562 > 543/556	adapted receptor signals
CIELAB	543/562 > 543/556 > 556/562	empirical
CIELUV	543/562 > 543/556 > 556/562	empirical

predicts that discrimination performance depends on intensity because quantal fluctuations are relatively more important at lower light levels. Because there is an unknown scale factor relating quantal flux at the cornea to the predictions of this model, we performed computations over a wide range of scalings to determine if any range predicted the psychophysical results. The earlier version of the model (Vorobyev & Osorio, 1998) requires information about the relative numbers of cones of each type in the retina. To evaluate that model, calculations were performed over a range of assumptions likely to characterize the relative proportions of the cone types in human subjects (L:M varies from 1:1 to 4:1—Carroll et al., 2002; 7% of total cones are S cones—Curcio et al., 1991) and in marmosets (L:M is 1:1 and S cones represent 8% of the total cone complement—Wilder et al., 1996). The coordinates in CIELAB and CIELUV color spaces depend on the tristimulus values of a nominally white stimulus, so we performed the computations under a variety of assumptions about the nature of this stimulus.

We implemented the Maxwell triangle model in two different ways. Photoreceptors rapidly adapt (Fain et al., 2001) and this process is frequently modeled by dividing the computed quantal catch rates of photoreceptors by their quantal catch rates when stimulated by the background. This division, called von Kries scaling, changes the coordinates of the stimuli and can thereby lead to different predictions. We determined the coordinates of our stimuli in Maxwell triangles with and without von Kries scaling.

Except for the CIELAB and CIELUV computations, all of the models begin with computations of the rate of quantal absorption of each of the cone classes. For the two CIE models, we computed tristimulus values based on measurements of the spectra of the monitor's phosphors, and the 1-nm version of the CIE 1931 two-degree color-matching functions (Wyszecki & Stiles, 1982 from the CVRL database, www.cvrl.org).

The outputs of all of the models are quantities presumably related to quantities computed by the nervous system as it compares two different spectral power distributions. Because none of the models include time as a parameter and, because most of the models predict no differences in performance when all intensities for a given trial are scaled up or down, it was not possible to compare quantitatively the results of these computations to those of the psychophysical experiment. However, each model does make predictions about the relative facility each pigment pair provides for distinguishing colors, so qualitative comparisons could be made between the model predictions and our results.

Results

Fig. 3 depicts the data from one representative subject in both experiments. All of the data could be fit with a variety of sigmoidal functions. The qualitative results of such fitting were the same in each case, so we report only the results using the logistic equation. Fig. 3 includes curves computed with the means of the parameters

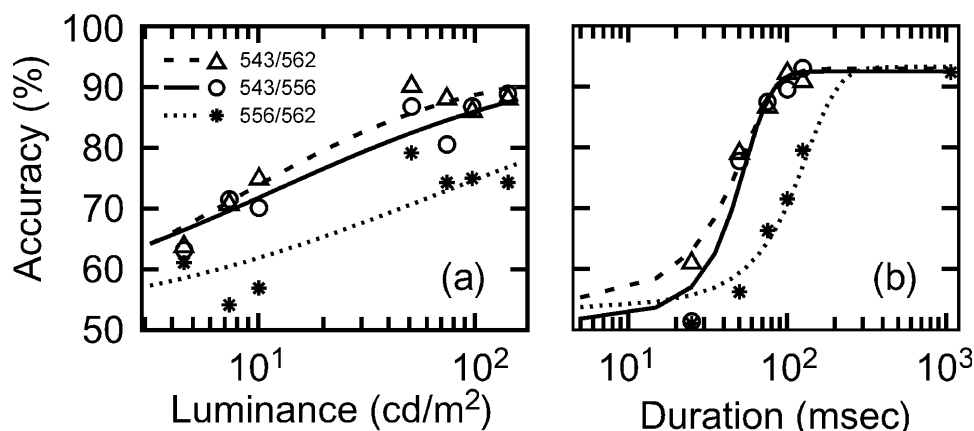


Fig. 3. Data and fits for one subject. The data and curves correspond to the three different pigment set substitutions as indicated in the legend. These are data from Subject 1. Curves indicate the best fits according to the Bayesian analysis.

estimated by Bayesian analysis of the illustrated data. The results were similar for all subjects. As shown in Fig. 4, the estimated thresholds in both experiments were reliably higher for the 556 nm/562 nm pigment combination than for either of the other two substitutions. The estimated widths of the psychometric functions were also larger in the case of the 556 nm/562 nm combination for all subjects in both experiments. However, in most cases, the 95% confidence intervals around these width estimates had at least some overlap with the confidence intervals around the estimates of the widths for the other pigment combinations. Estimated lapse probabilities showed no relation with subject or pigment substitution in either experiment.

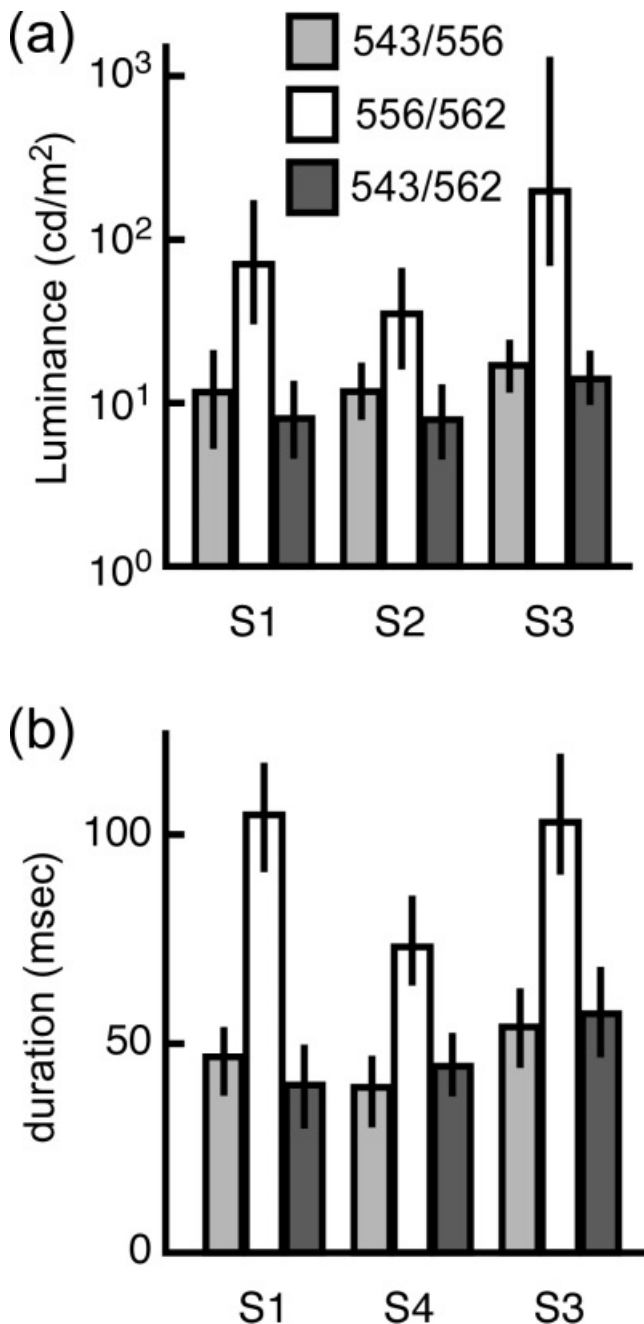


Fig. 4. Mean threshold estimates and 95% confidence intervals for all subjects in both experiments. Subjects 3 and 4 participated in the previous work (Rowe & Jacobs, 2004).

Table 1 shows that over the limited degree to which they can be compared, there is little agreement among the predictions from the models or between the model predictions and the current results. At variance with the data, most of the models predict that performance should be different for all three pigment combinations. There is broad agreement on one point; nearly all approaches predict that the 543 nm/562 nm pigment combination will outperform the 556 nm/562 nm combination, but there is no such consensus about the capabilities provided by the 543 nm/556 nm combination relative to either of the other two. Of the several models, only that of Vorobyev and Osorio (1998) correctly predicts the full ordering indicated by the data. The predictions made by this model did not appreciably vary with respect to different assumptions about the relative numbers of cones of each type. Similarly, the CIELAB and CIELUV models gave essentially the same predictions whether we assumed that a nominally white object reflected the spectrum of D65 (simulated daylight), Illuminant A (incandescent bulb), or the spectrum of a “white” patch of the monitor used for stimulus presentation.

Four of the models (Vorobyev & Osorio, 1998; Sumner & Mollon, 2000; both Maxwell triangle models) predict that color discriminations are invariant with respect to a scale factor multiplying the intensities of all stimuli. Therefore, subject performances should not depend upon luminance when the relative quantal flux rates are fixed as they were within any given pigment set substitution in our experiments. As such, these models predict that the curves of Fig. 3a should be flat. If the nominal white spectrum was not scaled across blocks with differing luminance (to simulate a change in illuminant intensity), the two CIE models do correctly predict that performance improves as intensity increases.

The Osorio et al. (2004) model assumes that performance is limited by photon shot noise at low intensities, but that Weber’s law behavior characterizes performance at higher intensities. This model also correctly predicts that performance will improve at higher luminance levels. However, even though we believe the scale factors that were used (see Methods) modeled a luminance range much larger than that in our experiments, the relative capabilities predicted by this model never matched the psychophysical data.

Discussion

The data reported here confirm and extend the results of the previous report (Rowe & Jacobs, 2004), but they also raise new questions. It is frequently assumed that the photopigments of an animal are optimized for its visual ecology, yet it may not be generally true that selective pressures are sufficiently strong to adapt photopigment spectral sensitivities. Chittka and Briscoe (2001) suggest that the fitness advantages of one color vision phenotype compared to another may be inconsequential. Indeed, the current work suggests that animals could use behavioral strategies to offset or neutralize genetic disadvantages. For instance, the data show that discriminations are more difficult for all tested phenotypes at lower luminance levels, but animals with the 556 nm/562 nm pigment pairing are relatively more impaired. Such animals could compensate for this disadvantage by foraging at higher luminance levels. Similarly, all phenotypes perform more poorly as stimulus duration is shortened. Again, 556 nm/562 nm animals are affected more strongly. However, under the conditions of the test, this difference in performance disappears at long stimulus durations. For our human subjects, the difference disappears somewhere around 200 msec. During a visual search task, Rhesus macaques normally make three to four saccades per second

(Schiller et al., 1980). If New World monkeys have similar saccade frequencies and processing times similar to humans, there may not be a significant difference in the animals' abilities to discriminate fruit when luminance isn't also limiting.

At what light level might luminance become limiting? One must be cautious in trying to answer such questions with a functional substitution experiment because an animal's performance limitations may be influenced by various factors beyond their cone spectral sensitivities; for example, the dioptric apparatus and post-receptoral processing. Because many of these factors will differ between animals and human surrogates, functional substitution cannot provide precise quantitative predictions of any other species' capabilities. However, such concerns are somewhat muted when the study subjects are as closely related to humans as are Callitrichids.

The range of luminances achievable with the psychophysical setup is at the low end of the ranges of daytime environmental luminances. Even the highest luminance, 150 cd/m², would likely be found only in the shade, under a heavy overcast layer, or at twilight (c.f. luminances reflected from white surface in the field at the Cambridge database of natural spectra, <http://vision.psychol.cam.ac.uk/spectra/guiana/illums.txt>). However, at this luminance and a stimulus duration of 100 ms, all three subjects in the luminance-varying experiment still performed more poorly with the 556 nm/562 nm pigment combination than with either of the other two. The fits to the data suggest that such differences will persist up to light levels 10 to 100 times higher, suggesting applicability to a wide range of natural daylight conditions.

To our knowledge, there are no data directly addressing how callitrichids with different forms of trichromacy vary in saccade frequency or light level preference. It is perhaps noteworthy that Yamashita et al. (2005) found that populations of allelic trichromats generally utilize a smaller range of luminance levels than do populations of routine trichromats. In that study, females chose to feed at higher light levels than males when foraging for "non-green" food. Being hemizygous for M/L pigments, these males are all dichromats. The females presumably included various dichromatic and trichromatic phenotypes. Do these animals choose to feed at light levels high enough to minimize or eliminate differences in discrimination abilities? Our results suggest that animals with identified phenotypes should be observed in an effort to address this question.

According to this analysis, current color models would not be of great value in aiding that effort. Our data reveal no differences between performance mediated by the 543 nm/556 nm combination and the 543 nm/562 nm combination, but with some viewing conditions these simulated phenotypes do reliably differ from the performances supported by the 556 nm/562 nm combination. One might consider a model to be relatively successful if it indicated that humans simulating monkeys with the 556 nm/562 nm combination should perform more poorly than when simulating either of the other two, and if that performance difference was considerably larger than the difference predicted between the other two simulations. By those criteria, only the Vorobyev and Osorio (1998) model performed well, and we note in passing that this model does not depend on any mechanisms peculiar to humans. However, this model assumes that scaling all stimuli would result in no difference in performance, and this assumption seems to be invalid over the range of light levels explored here. None of the models that would predict improvements in performance at higher light levels correctly predicted the relative capabilities of our subjects compared across different photopigment substitutions.

Similarly, none of the models allow one to predict the dependence of performance on stimulus duration. Although Vorobyev et al. (2001) suggest that temporal summation can improve color discriminations, none of the models considered here meaningfully encompass any temporal parameters. That is, in no case does changing viewing times lead to specific predictions about changes in performance.

Although in the current work we did not systematically manipulate the precise spatial structure of the background, such structure also influences performance. Chromatic contrast effects have been well studied in human psychophysics but rarely considered in discussions of visual ecology. The task described here is considerably easier when the background is spatially uniform (unpublished observations). In designing the stimulus for this effort, one goal was to provide a spatial structure that captured some of the features of natural scenes. Just as it may not be advisable to try to model color independent of timing and intensity, it may not be prudent to assume that ecologically relevant color discriminations can be modeled independent of stimulus geometry (Dyer & Neumeyer, 2005).

We emphasize that the inability of the models to capture our results does not necessarily mean that the models characterize human (or other animal) performance poorly. To be fair, models must be evaluated in the contexts for which they were designed. The conditions of this experiment involved manipulations of luminance and viewing time that are typically not factors inherent in models of color discrimination. Determining how much the accuracy of any color model depends on matching its assumptions to the conditions under which it is applied will require additional behavioral experiments. Functional substitution represents a relatively new form of behavioral experiment that may prove useful in evaluating such models and in bridging the gap between laboratory and field studies of visual discrimination.

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