Color vision test for dichromatic and trichromatic macaque monkeys

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Dichromacy is a color vision defect in which one of the three cone photoreceptors is absent. Individuals with dichromacy are called dichromats (or sometimes "color-blind"), and their color discrimination performance has contributed significantly to our understanding of color vision. Macaque monkeys, which normally have trichromatic color vision that is nearly identical to humans, have been used extensively in neurophysiological studies of color vision. In the present study we employed two tests, a pseudoisochromatic color discrimination test and a monochromatic light detection test, to compare the color vision of genetically identified dichromatic macaques (*Macaca fascicularis*) with that of normal trichromatic macaques. In the color discrimination test, dichromats could not discriminate colors along the protanopic confusion line, though trichromats could. In the light detection test, the relative thresholds for longer wavelength light were higher in the dichromats than the trichromats, indicating dichromats to be less sensitive to longer wavelength light. Because the dichromatic macaque is very rare, the present study provides valuable new information on the color vision behavior of dichromatic macaques, which may be a useful animal model of human dichromacy. The

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behavioral tests used in the present study have been previously used to characterize the color behaviors of trichromatic as well as dichromatic new world monkeys. The present results show that comparative studies of color vision employing similar tests may be feasible to examine the difference in color behaviors between trichromatic and dichromatic individuals, although the genetic mechanisms of trichromacy/dichromacy is quite different between new world monkeys and macaques.

Introduction

Color vision has been studied in a wide range of animal species. These studies have established the presence or absence of color vision as well as the dimensionality and sharpness of color vision in different species (Jacobs, 2009, 2012; Jacobs & Nathans, 2009; Mancuso, Neitz, & Neitz, 2006). They have also provided fundamental knowledge that has increased our understanding of the function of color vision and its biological basis. Among the various species studied, monkeys are in close lineage to humans, so an understanding of color vision in monkeys is of particular relevance for the understanding of color vision in humans.

Color vision of primates have been studied using various behavioral tests including measurement of increment-threshold spectral sensitivity (Blakeslee & Jacobs, 1982; Jacobs, 1972, 1977, 1983, 1984; Jacobs & Blakeslee, 1984; Sidley & Sperling, 1967), wavelength discrimination (Blakeslee & Jacobs, 1982; De Valois & Morgan, 1974; Jacobs, 1984; Mollon, Bowmaker, & Jacobs, 1984), Rayleigh match (Blakeslee & Jacobs, 1982; Jacobs, 1984; Mollon et al., 1984; Blakeslee & Jacobs, 1985), or a pseudoisochromatic test (Mancuso, Hauswirth et al., 2009; Mancuso, Neitz et al., 2006; Saito, Kawamura et al., 2005; Saito, Mikami et al., 2003), and these studies have characterized the properties of color vision of various primate species. These behavioral studies have shown the presence of polymorphisms in color vision within a number of species in new world monkeys, and color vision behaviors were compared between trichromatic and dichromatic individuals (Blakeslee & Jacobs, 1982; Jacobs, 1977, 1983, 1984, 1990; Jacobs & Blakeslee, 1984; Jacobs, Neitz, & Crognale, 1987; Mollon et al., 1984). These observations and the estimated underlying mechanisms were consistent with the results from genetic analysis or the analyses based on physiological methods such as microspectro-photometric measurement or electroretinogram (Bowmaker, Jacobs, & Mollon, 1987; Jacobs, Bowmaker, & Mollon, 1981; Jacobs et al., 1987). However, no study has yet compared color vision behaviors between trichromatic and dichromatic macaques, although macaque monkeys are widely used to study the neural mechanisms of color vision (Gegenfurtner, 2003; Komatsu, 1998; Solomon & Lennie, 2007).

Macaque monkeys have trichromatic color vision homologous to that in humans (De Valois, Morgan, Polson, Mead, & Hull, 1974; Oyama, Furusaka, & Kito, 1986; Stoughton et al., 2012). However, through molecular genetic analysis we demonstrated the existence of a dichromatic genotype among the crab-eating macaques (Onishi et al., 1999). Using polymerase chain reaction (PCR) to specify genotype, we identified male dichromats and female heterozygotes spread among some troops in Pangandaran National Park, Indonesia. Moreover, absorbance spectrum analysis of their photoreceptors (Onishi et al., 1999) and spectral sensitivity measurements using electroretinogram flicker photometry (Hanazawa et al., 2001) revealed that those animals lack the L photopigment (protanopic dichromats).

In the present study, we examined the color vision of dichromatic and trichromatic macaques using two behavioral tests related to the two symptoms of human protanopic dichromats. We first conducted a pseudoisochromatic test to examine the ability of macaques to discriminate a colored target from achromatic distracters. In the second test, the spectral sensitivities to two monochromatic lights were compared to assess the sensitivity to long wavelength light. Both of these methods have been used previously to examine the color vision of monkeys. Spectral sensitivities have been measured for a long time (Jacobs, 1972; Sidley & Sperling, 1967), and pseudoisochromatic tests have been more recently applied to cathode ray tube (CRT) display (Reffin, Astell, & Mollon, 1991; Regan, Reffin, & Mollon, 1994), and they were used to characterize the color discrimination abilities of squirrel monkeys whose color vision was genetically identified (Mancuso, Hauswirth et al., 2009; Mancuso, Neitz et al., 2006). Our present study will contribute in two aspects to that body of knowledge. First, although it is known that both trichromatic and dichromatic individuals exist among various new world monkey species, their genetic mechanisms of trichromacy/dichromacy are very different from those in old world primates, including macaques and humans (Jacobs, 1998, 2008; Jacobs & Nathans, 2009; Nathans, 1999). Therefore, the dichromatic macaque may be a more appropriate animal model with which to conduct studies to investigate the neural mechanisms underlying human color vision, and the present study is the first attempt to examine the color discrimination behavior of dichromatic macaques. Second, the frequency of dichromacy in macaques is very low: Dichromatic macaques have been found in only one place so far.

Consequently, this strain could be very useful for studying the development and neurophysiology of neural circuits for color vision in macaques. It is therefore of importance to characterize the color vision behavior of these animals.

Materials and methods

Animals

Two genetically identified dichromatic (males 4.5–5.0 kg; Didi, Dito) and two normal trichromatic (one female and one male 2.7–5.8 kg; Nofy, Noby) crab-eating macaques (*Macaca fascicularis*) participated in the experiments.

Originally found in Pangandaran National Park, Indonesia, dichromatic macaques were bred in the Bogor Agricultural University, Bogor, Indonesia. Two females of the second generation (one homozygous dichromat and one heterozygous career) were transferred to the Primate Research Institute of the Kyoto University, Inuyama, Japan. There, these females were bred with trichromatic males, and we obtained monkeys of the third generation, which included dichromatic male monkeys. Two of these dichromats from the third generation participated in the present experiments.

In each daily experimental session, the monkey was moved from its home cage to the experimental cage, which was then carried to the experimental room. The monkey was not fed before the experiment. After the experiment, the monkey was returned to its home cage, where it was given chow ad libitum. No water deprivation was done.

Stimuli and task

Calculation of stimulus intensity and chromaticity was based on the standard human trichromatic observer (CIE 1931). Stockman's cone fundamentals were used to compute cone responses (Stockman, MacLeod, & Johnson, 1993). Stimulus color was calibrated using a color meter (CS-200, Konica-Minolta, Osaka, Japan) and a spectrometer (PR-650, Photo Research, Chatsworth, CA).

Experiment 1: Pseudoisochromatic color discrimination test

In the first experiment, monkeys performed three alternative forced choice tasks to detect colored targets. Each monkey was placed in a dimly illuminated experimental cage (W50 × D40 × H70 cm), after which the experimenter started the task control program. Three images, one target, and two distractors (4.5 cm × 4.5 cm each, Figure 1a), were then presented on a computer screen (FlexScan EV2335W, NANAO, Epson, Matsumoto, Japan) located on a wall of the experiment cage (Figure 1b). The pixel size on the screen was 0.265 mm, and size of each image was 170 × 170 pixels. Both the target and the distractors appeared on a black background. Below each image, there was a button, and the monkey was rewarded with a small piece of sweet potato or apple if it pressed the button below the target image. The animal was allowed to press the button while the stimuli were presented (2.0–2.6 s), and after a button was pressed all three images were turned off. The intertrial interval (ITI) was typically 3.3 s (range 2.6–3.7 s). Rewards were given using the same rule for all animals; thus if the target was undetectable, the reward frequency would correspond to chance (33%).

Both the target and distractor stimuli were composed of numerous small circular dots of various sizes, but whereas the distractor stimuli were filled entirely with gray dots, the target stimuli contained a ring of colored dots (Figure 1a). The diameters of both the gray and colored dots ranged from 1.3–2.9 mm, and they were randomly distributed without overlap at a dot density of 56.1%–56.4%. Dots were generated and filled sequentially from largest to smallest until the smallest dots filled all possible spaces in the image. The luminance of each dot varied according to a Gaussian distribution with a mean of 30 cd/m^2 and *SD* of 10 cd/m^2. The chromaticity of the gray dots varied on the CIE-u′v′ coordinate system as a two dimensional (2-D) Gaussian distribution whose center coordinate was D65 (u′ = 0.2949, v′ = 0.3198) and *SD* was 0.0040. The random distribution of the luminance and color of the gray dots was intended to prevent target detection based on artifacts. Target color was selected from 16 hues and four saturation levels (Figure 1c, d). In each trial, 1 of 16 hues was randomly selected as the target color, but only one saturation level was employed in each experimental block. The hue-angle and saturation level of the target were defined using CIE-u′v′ metrics, with 0° denoting the u′ positive angle (red hue), 90° denoting the v′ positive angle (yellow hue), and so on (Figure 1d). The hue angles were placed at equal 22.5° intervals, and saturation was distributed from 0.02 to 0.05 at equal intervals of 0.01. The chromaticity of the colored dots making up the targets varied on the CIE-u′v′ coordinate system as a 2-D Gaussian distribution with an SD of 0.0040, and their luminance had the same distribution as the gray dots ($M = 30$ cd/m^2, $SD = 10$ cd/m^2).

Each experimental block was composed of 48 response trials, including 16 hues and three target

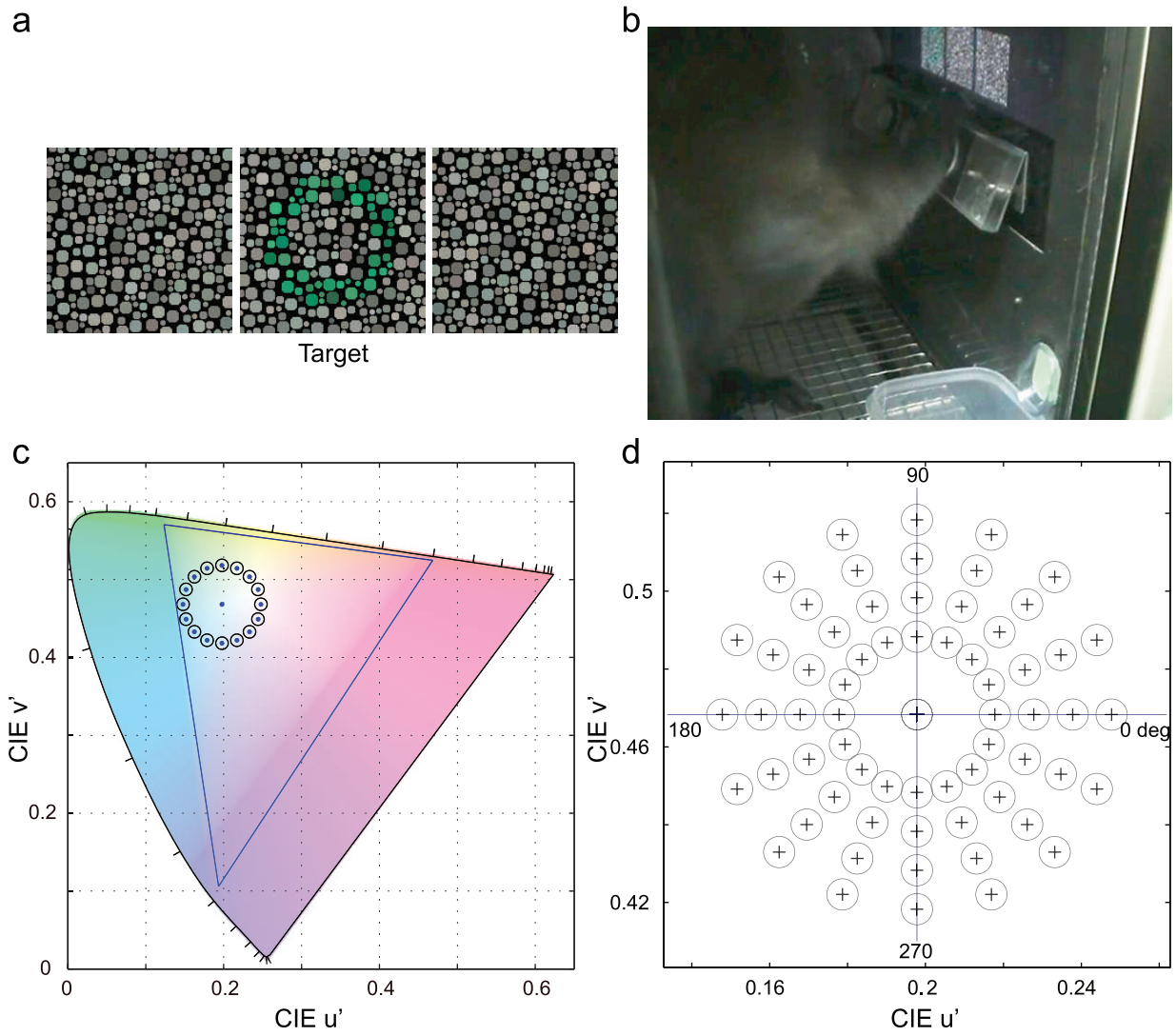

Figure 1. Stimuli used in Experiment 1 (pseudoisochromatic test). (a) Example of a stimulus used for Experiment 1. Each stimulus consisted of three images, one target (center image in this example), and two distractors. Both the target and the distractors were composed of small circular gray dots with varying luminance, but only the target contained a colored ring. (b) Photograph showing the inside of the experiment cage. Stimuli were presented on a computer screen located on one wall, with three response buttons located just below the images. A piece of sweet potato or apple was presented in a tray at the bottom when the monkey made a correct response. (c) The color of the target ring was determined from the CIE u′v′ chromaticity diagram. Sixteen evenly distributed hues were used (open circles with dots). Here only the most saturated colors are shown. A dot at the center denotes the neutral background color. A blue triangle indicates the color gamut of the display. (d) Chromaticity coordinates for all 64 target colors, which consisted of 16 hues and four saturation levels (crosses). Circles indicate the standard deviation of the color jittering of the target.

positions, and the number of target positions was balanced across three possible locations in each block. If the monkey made an incorrect response, a trial with the same target was repeated once, but the response in the repeated trial was not included in the subsequent analysis. The animals freely watched the screen, so the visual distance was not fixed, but it was usually between 10 and 30 cm. The number of trials the animals performed in a daily session ranged from 50 to 600. The number of trial repetitions for each stimulus ranged from 9 to 56, and the median for each monkey was 19 (Didi), 29 (Dito), 28 (Nofy), and 33 (Noby).

Experiment 2: Detection test for monochromatic lights

In the second experiment, monkeys performed a light detection task (Figure 2a). The stimulus was a single circular light with a diameter of 8 mm. The stimulus light was produced by either an orange light

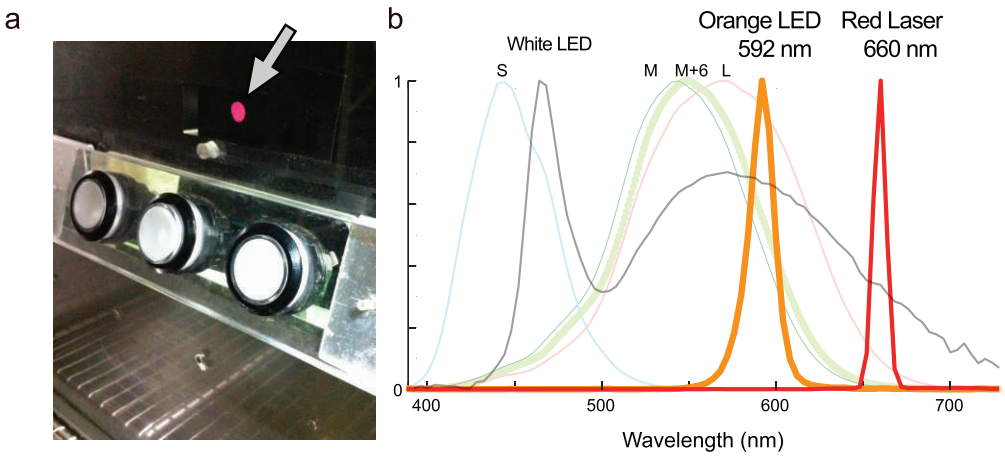

Figure 2. Stimuli used in Experiment 2 (light detection task). (a) The target color was displayed through the aperture of an integrating sphere. Red (660 nm) light is presented in this example (arrow). (b) Spectra of the two monochromatic lights used in Experiment 2. Peaks were at 660 nm (red) and 592 nm (orange). Spectrum of white background LED light is also shown (gray line) that was installed in the integrating sphere and was turned on throughout the experiment. In addition, cone fundamentals in humans (red [L], green [M], and blue [S] thin lines) and estimated spectrum of the hybrid M cone of dichromats (M + 6), in which the peak is shifted 6 nm toward longer wavelengths (Onishi et al., 1999) are shown.

emitting diode (LED, 592 nm, HWHM 8 nm) or a red solid-state laser (660 nm, HWHM 4 nm, Figure 2b), which were situated within an integrating sphere. To improve uniformity, a white diffuser was placed at the aperture of the integrating sphere, which also contained a white LED (CIE $x = 0.3611$, $y = 0.3814$) with a broad spectrum (Figure 2b) that was always on, making the background luminance of the diffuser 2.0 cd/m^2. The inside of the experiment cage was very dimly illuminated, and the animals could easily recognize the location of the stimulus from the white background. The orange or red light, flickering at 10 Hz, was added to the white background light and was presented for 1000 ms. The flickering was added to facilitate detection. The monkey was rewarded when it pressed the button below the stimulus while the orange or red flickering light was on. The ITI was typically 3.3 s (range, 2.7–3.9 s). If the monkey made no response, the ITI was shortened and the subsequent stimulus was displayed with an average ITI of 1.2 s. The animal's behavior was carefully monitored, and when the animal did not look at the screen for several seconds, the experimenter suspended the experiment-control program to reduce the unintended miss responses. The effect of this suspension was not dependent on the specific stimuli because the suspension was made solely based on the monkey's behavior and not on the stimulus presented. Furthermore, the next stimulus was randomly selected by the computer, and the experimenter could not know the stimulus that would be presented when the task is restarted. Both the intensity and the wavelength of the target stimulus were randomly selected from five levels of orange light (0.12, 0.50, 2.0, 8.0, 32.0 mW/sr/m^2 in radiance, or 0.06, 0.25, 1.0, 4.0, 16.0 cd/m^2 in luminance) and four levels of red light (0.75, 3.0, 12.0, 48.0 mW/sr/m^2 in radiance, or 0.03, 0.13, 0.50, 2.0 cd/m^2 in luminance). The intensity of the stimulus light was controlled by the electrical current. Rod photoreceptors may have made some contribution to the stimulus detection, because the luminances of the stimulus and background were relatively low. However, this would not affect our main conclusion, if the difference in the sensitivities is observed between trichromats and dichromats. It should be explained only by the presence or absence of L cones. The animals performed between 50 and 300 trials daily. The number of trial repetitions for each stimulus ranged from 13 and 50, and the median for each monkey was 30 (Didi), 40 (Dito), 26 (Nofy) and 49 (Noby).

Training

The animals were initially trained to associate a button press with a reward. Subsequent training for each experiment was as follows.

For the color discrimination task (Experiment 1), the colored ring of the target stimulus initially had a large luminance contrast and highly saturated colors. The colors of the targets were yellow, green, blue, and purple, which do not overlap with any dichromatic confusion lines. Gradually, the luminance

contrast was reduced, while the color was kept the same, and jittering of the color and the luminance of each circular dot was added. Thereafter, the color contrast was gradually reduced from a CIE-u′v′ distance of 0.07 to a distance of 0.02. The final color contrast (0.02) was the same as the most desaturated stimuli used in the main experiment. Training took one week.

For the detection task (Experiment 2), a bright orange (>10 cd/m^2, or 20 mW/sr/m^2) or red (>2 cd/m^2, or 48 mW/sr/m^2) target light was used initially, and then the luminance was gradually reduced to estimate the detection threshold. This took about eight days. The animals were then trained for 2 days to perform the detection task using the method of constant stimuli with the same set of stimuli used in the main experiment. Following this training, the main experiment was conducted.

All the experiments were approved by the ethics committee of the Primate Research Institute of Kyoto University, where all of the experiments were performed. All procedures for animal care and experimentation were in accordance with the U.S. National Institutes of Health *Guide for the Care and Use of Laboratory Animals* (1996) and adhere to *the ARVO Statement for the Use of Animals in Ophthalmic and Visual Research*.

Results

Experiment 1: Pseudoisochromatic color discrimination test

Color discrimination performance was compared between dichromatic and trichromatic monkeys. For each target color, the error rate is shown as the diameter of a circle in Figure 3. We expected that the dichromats would make errors more frequently and consistently along the color confusion line, while the trichromats would not. We first focused on the hue dependency of the errors. For both dichromats tested, numerous errors were observed in the horizontal direction on the CIE-u′v′ chromaticity diagram (red and cyan hues) (Figure 3a, b). Even for highly saturated colors, corresponding to outer positions in the diagram, their performance was at the chance level (67% error, filled symbols; $p > 0.05$, Fisher's exact test). The center of the error distribution was displaced slightly downward from the 0° to 180° line, and errors were more frequently observed in the lower half of the diagram. Comparing the rightward (red hue) and leftward (cyan hue) directions, errors were observed more frequently in the leftward direction. This asymmetry will be considered in the Discussion. Very small numbers of errors were observed in directions other than horizontal (e.g., 45° to 135°, orange-green hue, or 225° to 315°, blue-purple hue). For these other hue directions, even colors with low saturation, corresponding to inner positions in the diagram, yielded only small numbers of errors, which were significantly lower than chance (open symbols; $p < 0.05$, Fisher's exact test). When we compared the monkeys' discrimination performances along the color confusion lines with those of the two major types of dichromatic humans, namely protanope and deuteranope, it was clear that the direction where the animals made frequent errors was more consistent with the human protanopic confusion line than the deuteranopic one (Figure 3; Smith & Pokorny, 1975).

The results obtained with the trichromatic monkeys differed considerably from those of the dichromats. For trichromats, error responses were observed over a broad range of hue directions, with the highest error rates reaching the chance level for low-saturation colors (Figure 3c, d): 112.5° and 135° (green hue) for monkey Nofy (Figure 3c) and 225° and 270° (blue hue) for monkey Noby (Figure 3d). These directions were not consistent between the two animals and did not correspond to any color confusion lines in dichromatic humans. In both trichromats, better performance was consistently observed for reddish hues (right side of the diagram) than for cyanish hues (left side of diagram). Potential causes of this bias will be considered in the Discussion.

To quantitatively evaluate the difference in the monkeys' performance, we computed and compared the discrimination threshold across different hues, which is an effective way to highlight the difference between dichromats and trichromats (Mancuso, Hauswirth et al., 2009; Mancuso, Neitz et al., 2006). To compute discrimination thresholds, we first calculated the psychometric function for each hue using the least squares fit of the cumulative Gaussian function for the data, after which the discrimination threshold was determined as the saturation level where the performance corresponded to 67% correct responses (Figure 3e). Fitting and threshold calculations were made on the log CIE-u′v′ distance. When the monkey did not make an error at any saturation level (e.g., yellow hue for monkey Didi, Figure 3a), the fitting failed, and we instead assigned the minimum threshold observed for other hues. Comparison of the threshold between dichromats and trichromats showed clear dissociation (Figure 3f). The dichromats exhibited noticeable threshold elevation in two hue directions, whereas the trichromats did not. The hue angles where elevated thresholds were observed were 0° and 180° (red and cyan hue, respectively) that seem to better correspond to the

protanopic confusion line (4.1° and 184.1°) than with the deuteranopic confusion line (170.6° and 350.6°).

We quantitatively estimated the confusion angle from the color discrimination thresholds for all tested hue directions through least square fitting using the n-th power of the cosine function with four free parameters: phase, multiplier, amplitude, and offset. The phases of the best-fitted function for the dichromats were −1.78° for Didi and −0.88° for Dito. These values are more similar to the angle of the protanopic confusion line (4.1°) than to the deuteranopic line (−9.4°), which confirms the aforementioned observations.

Experiment 2: Detection test for monochromatic lights

Detection performance was measured as a function of luminance range from 0.12 to 48.0 mW/sr/m^2 (Figure 4a through d). To examine the difference in the response quantitatively, we performed a generalized multiregression analysis, and determined the detection threshold for each light. Maximum likelihood fitting of the logistic equation as a function of the log luminance was performed using the glmfit command in MATLAB. Fitting was performed separately for each target color; thus both the intercept and slope coefficients were estimated independently. For better fitting, the upper and lower limits of the function were not assigned 0 and 1; instead minimum and maximum observed response rates for each animal were used as asymptotes, taking into account the floor and ceiling of the response. The same asymptotes were settled for both the red and orange lights. Although three monkeys mostly missed targets with low luminance, one monkey responded to many (about 40%) of the low luminance targets, and detection performance for low luminances did not reach zero (Dito, Figure 4b). This monkey also made many responses before stimulus onset. After the fitting, the threshold was determined as the luminance corresponding to the response level at the midpoint between the upper and lower extremes, and the observed thresholds were distributed from 0.5 to 25 mW/sr/m^2 (Figure 4e). The absolute values of these thresholds differed among the animals and stimuli. Inferring from a protanopic human observer, one might expect that loss of sensitivity to long wavelength light might result in a higher threshold for both the orange and red lights in dichromats, as compared to trichromats. However no consistent elevation in absolute threshold was observed with dichromatic macaques. This is likely due to the fact that the absolute threshold depends on the criteria or behavioral strategy of each monkey. We therefore focused on the relative threshold between the orange and red lights, because the red target would induce a larger elevation in detection threshold than the orange light. The relative threshold between stimuli showed clear segregation between groups.

To illustrate the relative threshold for each animal, the threshold for the red light was normalized to that for the orange light (Figure 4f). Both dichromats showed a higher relative threshold than the trichromats. To assess the significance of the difference between the two groups, the thresholds were estimated separately for different experiment sessions (small symbols in Figure 4f), which revealed a significant difference between the two groups ($p < 0.01$, t test).

Discussion

In the present study, we compared the color vision of dichromatic and trichromatic macaque monkeys using two behavioral tests. These tests have been used previously to characterize the color vision behavior of normal macaques as well as trichromatic and dichromatic new world monkeys, but this is the first attempt to characterize the color vision behavior of dichromatic macaques. The present results show that comparative studies of color vision employing similar tests may be feasible to examine the difference in color behaviors between trichromatic and dichromatic individuals, although the genetic mechanisms of trichromacy/dichromacy is quite different between new world monkeys and macaques. In addition, the dichromatic macaque is very rare, with only one strain being confirmed so far. Thus the present study provides valuable information on the color vision behavior of dichromatic macaques, which has the potential to be a useful animal model of human dichromacy.

We compared color discrimination performance between trichromatic and dichromatic (protanopic) genotypes in macaque monkeys and found clear segregation between two groups. The dichromats showed color confusion along the protanopic confusion line in a pseudoisochromatic color discrimination test, while the trichromats did not (Experiment 1). In addition, when we compared the animals' sensitivity to two monochromatic lights, the dichromats showed lower relative sensitivity to long-wavelength light than did the trichromats. These results are consistent with the two major difficulties reported in human protanopes (Ruddock, 1991; Sharpe, Stockman, Jagle, & Nathans, 1999; Wyszecki & Stiles, 1982). In the context of our earlier genetic

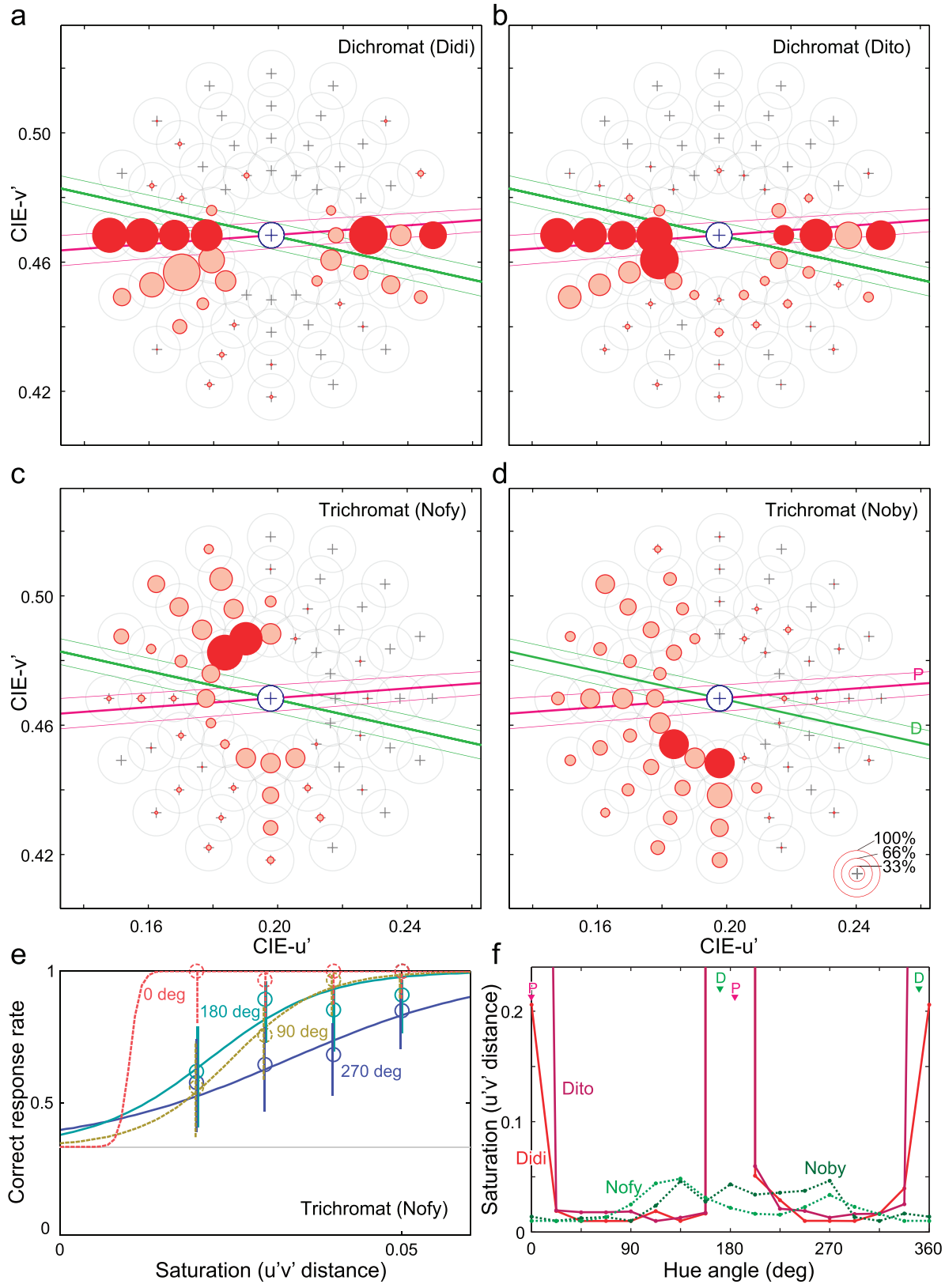

Figure 3. Color discrimination performance of two dichromats (a, b) and two normal trichromats (c, d) in Experiment 1. Error response rates are indicated by the size of the red circles at the point corresponding to the chromaticity coordinates of the target color. Significant deviation from chance (0.67) is shown by an open circle ($p < 0.05$, Fisher's exact test); otherwise the circle is filled. Magenta lines denote the protanopic color confusion lines in humans. One line (middle one) passes through the neutral point.

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Green lines denote the deuteranopic color confusion lines. Protanopic confusion lines gradually converge as they move to the right; ultimately, they will converge into a point, the protanopic confusion point, beyond the boundary of this Figure. Deuteranopic confusion lines converge gradually as they move to the left. (e) Relationship between the saturation level and the rate of correct responses by monkey Nofy for four hue angles (red: 0°, yellow: 90°, cyan: 180°, violet: 270°). Shown are rates of correct responses with error bars of the 95% confidence interval plotted in relation to the saturation level and fitted psychometric functions. The saturation level was determined as the CIE- u′v′ distance from the neutral point. A horizontal gray line indicates chance level (0.33). (f) Color discrimination threshold for each hue angle. Arrowheads indicate the angle of the confusion lines for protanopes (P) and deuteranopes (D).

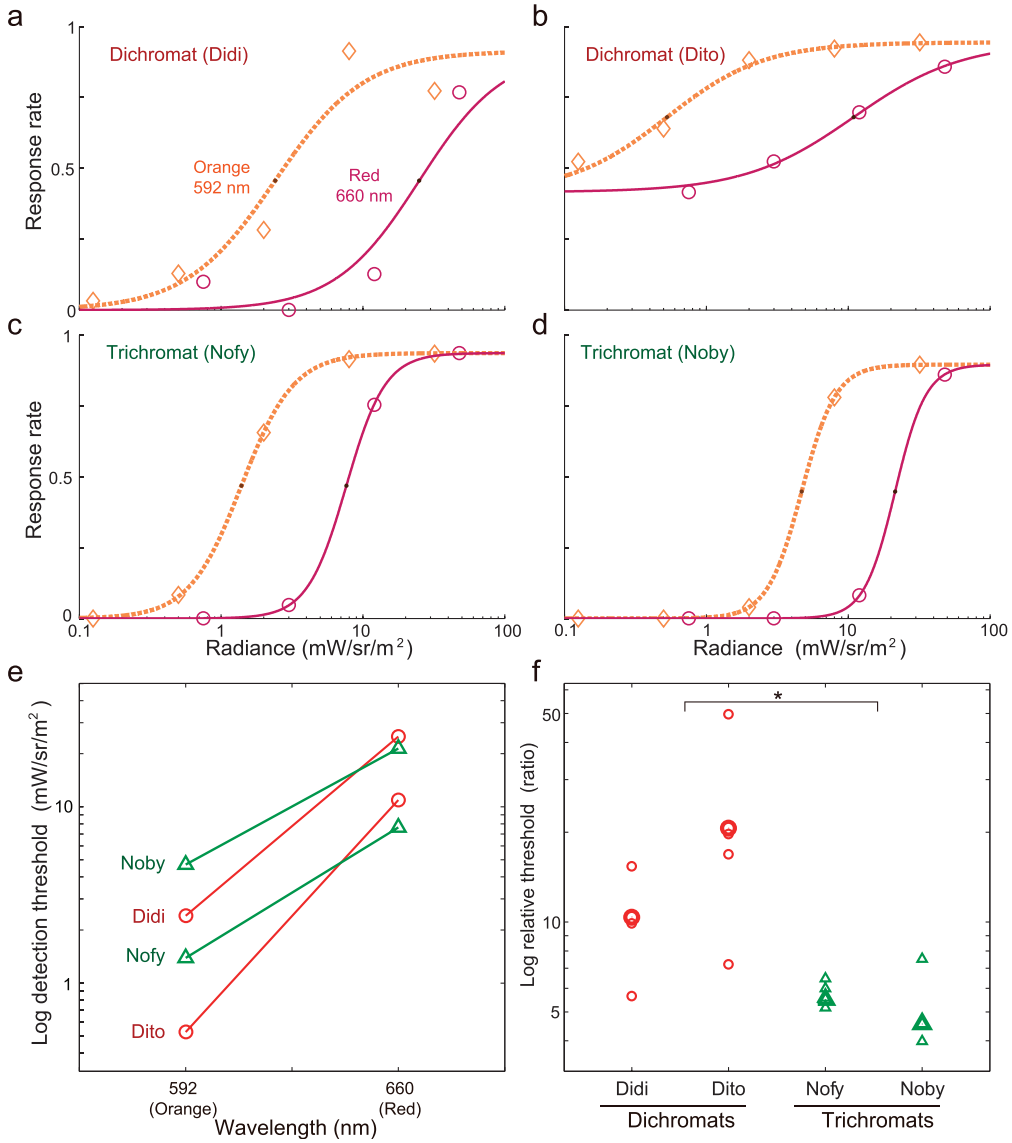

Figure 4. Detection of two monochromatic lights by two dichromats (a, b) and two normal trichromats (c, d) in Experiment 2. The relationship between the radiance and the response rates, together with the fitted logistic functions for the red (circles and solid line) and orange (diamonds and dotted line) targets are shown. (e) Detection thresholds for orange and red stimuli for two dichromats (circles) and two normal trichromats (triangles) were determined using the midpoint of the fitted functions. (f) Relative thresholds of the orange and red lights for each monkey. Small symbols indicate the relative thresholds estimated separately from the different experimental sessions. An asterisk indicates significant difference ($p < 0.05$, t test).

analysis (Onishi et al., 1999) and electroretinogram measurements (Hanazawa et al., 2001), the present results add behavioral evidence indicating that genotypically identified protanopic macaques do indeed manifest protanopic phenotypes. In the following sections, however, we will consider several factors that may have affected the monkeys' behavior and obscured the results.

Advantages of dichromacy and disadvantages of trichromacy

One confounding result was that trichromats made numerous errors in the color discrimination task (Experiment 1). In fact, the average performance of the trichromats was not better than that of the dichromats; the mean accuracy of the two groups across all color sets was the same (82% and 82% for dichromats, 81% and 84% for dichromats). Since it is inevitable that errors would be made by dichromats around the confusion hues, our finding that their average performance is the same as that of the trichromats seems curious.

The observed performance similarity cannot be explained by a difference in training because the number of training days and time course of training was the same for all animals. Assuming that color discrimination along the confusion line is very difficult for the dichromats, these animals may be motivated to discriminate other hues, even at low saturation levels, to compensate for the inevitable loss of reward around the confusion line. This compensatory effect might have balanced the mean performance between the dichromats and trichromats. Consistent with that idea, we observed that the dichromats exhibited excellent discrimination among yellow and blue hues (top and bottom directions in Figure 3a, b), even at the very beginning of the experiment, whereas the performance of the trichromats gradually improved as the experiment progressed (see Appendix).

One might be concerned that in Experiment 1, some animals would learn to use the spatial distribution of individual phosphors on the screen as the cue if the animals were allowed to get very close to the screen and dichromatic monkeys may have used such cue. We think it is highly unlikely that the animals have used the information of the spatial distribution of individual phosphors to perform the task. First, the size of a single pixel was 0.265 mm (96 dots per inch [dpi]), and each phosphor (red, green, and blue) has three times finer resolution (288 dpi), too fine to be recognized. Second, even if each phosphor were recognizable, this would result in only a very slight positional shift of the colored pixels relative to the gray pixels. Such a positional shift in the phosphors would provide no information toward solving the task because each dot is randomly positioned within each image.

One possible explanation for the performance similarity is the lack of color masking in dichromats. In the present study, color jittering in the stimulus and gray background dots would work as noise and should deteriorate discrimination performance. However, no masking effect due to color jittering along the L-M cone axis was detectable in dichromats, which would benefit the performance of those animals. This is similar to results obtained from human dichromats, who exhibit an advantage with control Ishihara plates (plates 18–21 in the 10th Edition, London: Kanehara Shuppan). In these plates, the figural element is easily seen by dichromats through activation of S cones, but is not readily seen by most trichromats due to masking by strong L/M signals.

Finally, the excellent color discrimination by dichromats of yellow and blue hues may be an ordinary characteristic of dichromats, attributable to processing in the central nervous system. To solve the color discrimination task in the present study, some spatial grouping or integration of color signals and comparison between the target and distractors is required, and this likely involves color processing at the cortical level. Although this is speculation, the dichromats may devote more resources to processing the residual color signal, namely the yellow-blue signal, assuming that both trichromats and dichromats have the same neuronal resources for color information processing in the cortex. As a result, the dichromats may acquire superior color discrimination for yellow and blue hues.

There are reports showing advantages of dichromacy over trichromacy for some behaviors (Morgan, Adam, & Mollon, 1992; Saito, Mikami et al., 2005; Sharpe, de Luca, Hansen, Jagle, & Gegenfurtner, 2006). In those experiments, the advantage was observed when subjects were detecting targets defined by luminance and were breaking color-camouflage (Morgan et al., 1992; Saito, Mikami et al., 2005), and it was explained by the greater capacity of protanopes to use luminance cues (Sharpe et al., 2006). However, the task and stimuli in those studies were very different from those in our present experiments. The advantage of dichromatism for color discrimination will be an important topic of future research, and the dichromatic macaque strain may be a useful resource for conducting such studies.

Applicability of humans' color-matching function

Another confounding result in trichromats is the nonuniformity of the color discrimination threshold,

as shown in Experiment 1. Given that the CIE-u′v′ color space reflected the metrics of human color discrimination performance (Wyszecki & Stiles, 1982), color discrimination thresholds for different hues were expected to be uniform. However, we observed a consistent tendency for the threshold around reddish hues to be lower than around other hues. The stimuli used in the present study were determined based on their chromaticity and luminance, which are based on human standard observers. Although macaque monkeys have photoreceptors homologous to humans, and much primate research has adopted the color space determined for humans, some differences have also been reported. In macaques, for example, the L : M cone ratio and the equiluminance point along the red-green line is different from those in humans (typical $M = 1.8$ in *Macaca fascicularis* vs. $M = 2.0$ in humans, ranging from 0.3 to 19.0; Albrecht, Jagle, Hood, & Sharpe, 2002; Bowmaker & Dartnall, 1980; Brainard, Calderone, Nugent, & Jacobs, 1999; Carroll, McMahon, Neitz, & Neitz, 2000; Carroll, Neitz, & Neitz, 2002; Cicerone & Nerger, 1989; Dartnall, Bowmaker, & Mollon, 1983; de Vries, 1949; Hagstrom, Neitz, & Neitz, 1998; Hofer, Carroll, Neitz, Neitz, & Williams, 2005; Kremers, Scholl, Knau, Berendschot, Usui, & Sharpe, 2000; Kremers, Usui, Scholl, & Sharpe, 1999; Rushton & Baker, 1964; Yamaguchi, Motulsky, & Deeb, 1997). In addition, the relative sensitivity to long wavelength light is weaker in macaques (Deeb, Diller, Williams, & Dacey, 2000; Dobkins, Thiele, & Albright, 2000). However, it is unlikely such species differences are the cause of the observed nonuniformity in discrimination thresholds. Even if the L : M cone ratios did significantly differ across species, this would only affect the discrimination threshold along the L-M axis, which would result in nonuniform thresholds elliptically elongated or contracted along the L-M axis. Contrary to this expectation, however, the observed color discrimination threshold did not elongate along a particular axis, but asymmetrically rose at specific angles (Figure 3c, d). It has also been reported that the retinal densities of S cones differ between macaques and humans (Calkins, 2001). This would predict shifts in the discrimination threshold along the S-cone axis, but again the observed thresholds did not show this tendency. It is therefore unlikely that the present results can be explained based on retinal architecture.

A discrepancy between the results expected from the standard luminous function and the trichromat's performance was also observed in Experiment 2. If detection performance reflects luminous efficiency, their relative threshold would be 12.0. However, observed thresholds in the trichromats significantly differed from the prediction. One possibility is that the better performance with the red light might reflect the characteristics of the incremental threshold. In the present experiment, white light (2.0 cd/m^2) was added as a pedestal for the target; thus the incremental detection threshold was measured in the detection task. The spectral sensitivity determined by the incremental threshold is known to differ from the standard luminous function, which is derived from flicker photometry (King-Smith & Carden, 1976). In the experiment measuring the incremental threshold on a white background, the amount of added color signal will help the detection of the target, even if the luminance contrast is insufficient for the detection. In addition, the color signal will change the saturation of the stimulus color, which may in turn affect the perceived brightness of the stimulus, regardless of the luminance change. Such extra brightness is related to the Helmholtz-Kohlraush effect (Wyszecki & Stiles, 1982) and may result in deviation of the stimulus detectability from what would be expected based on the standard luminous function.

Another potential problem with using the human color-matching function is that the density of the macular pigment differs between macaques and humans. In humans, it is distributed from 0 to 1.2 density units at a peak absorbance wavelength of 460 nm (Wyszecki & Stiles, 1982), and 0.35 density units was assumed for the standard observer when the color matching function was derived (Stockman et al., 1993). On average, the density of the macular pigment in macaques appears to be slightly higher than in humans: It ranged from 0.42 to 1.0, and three out of four monkeys had densities between 0.42 and 0.46 (Snodderly, Auran, & Delori, 1984). If we assume that the pigment density in macaque is two times greater than in humans, the consequence would be a 1-nm increase in the confusion spectrum calculated by modulating the cone fundamental (Stockman et al., 1993). This would result in a 5° clockwise rotation of the confusion line in the chromaticity diagram, which would give better agreement to the performance of the dichromats in Experiment 1 than the original confusion angle (4.1°). The effect of macular density on Experiment 2 was negligible, as the stimuli were long wavelength lights in which no macular absorption was made. These considerations also indicate that the human color-matching function is a reasonable approximation with which to describe the color vision behavior of macaque monkeys.

Asymmetry in color confusion

In the dichromats, we found an asymmetry of color confusion in Experiment 1 (Figure 3a, b), such that the

distribution of errors was slightly wider and the error rates were higher around cyan hues (180°) than around the red hues (0°). Because the chromaticity of the cyan and red target hues is symmetrically located with respect to the neutral point, the asymmetry of the error distribution between cyan and red cannot be simply ascribed to a difference in color signals between two opposite directions. One might argue that the asymmetry is related to the convergence of the confusion lines. It is known that the confusion lines are distributed radially from their convergence points. For protanopes, the convergence point is located in the far red chromaticity (Smith & Pokorny, 1975); consequently, the confusion lines would be more spread for cyan hues than red hues. But although this radial effect might be a potential cause of asymmetry, the convergence of the confusion lines is negligible within our stimulus range (Figure 3a through d), and the spread of the color confusion lines is nearly symmetrical with respect to the neutral point. Another potential cause of the observed asymmetry between the red and cyan directions is the polarity of the luminance contrast for the dichromats. Because the luminance cue received by protanopic observers depends solely on M-cone outputs, red targets will become darker than the gray background, whereas cyan targets will become brighter than the gray background. This is because the luminance of the target and background were matched to the luminous function of a standard trichromatic observer in whom both L and M cones are present. Such asymmetry in the luminance contrast could potentially be related to the asymmetry of the color discrimination performance in the dichromats. The luminance contrast determined by the Michelson contrast between the most saturated cyan target and the background, or the most saturated red target and background, were 0.055 and 0.062, respectively. The larger contrast for red targets may have enabled better color discrimination performance in that direction in the dichromats.

Keywords: dichromacy, color vision, macaque monkey, behavioral experiment

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Appendix

Time course of color discrimination performance

Color discrimination performance in Experiment 1 was analyzed separately for the first and second half of the trials for each stimulus. The results are shown in Figure 5, which is formatted as in Figure 3. It should be noted that saturated stimuli were frequently tested at the beginning of the experiment. Consequently, the border session separating the two halves differs across stimuli. The difference in the performance between the two halves was obvious for the trichromats but was not as clear for the dichromats. Nevertheless, the hue dependencies of the errors were consistent between the two halves. The relatively stable performance of the dichromats indicates that the color discrimination performance for hues remote from the color confusion line was not the result of the training in the current experiments.

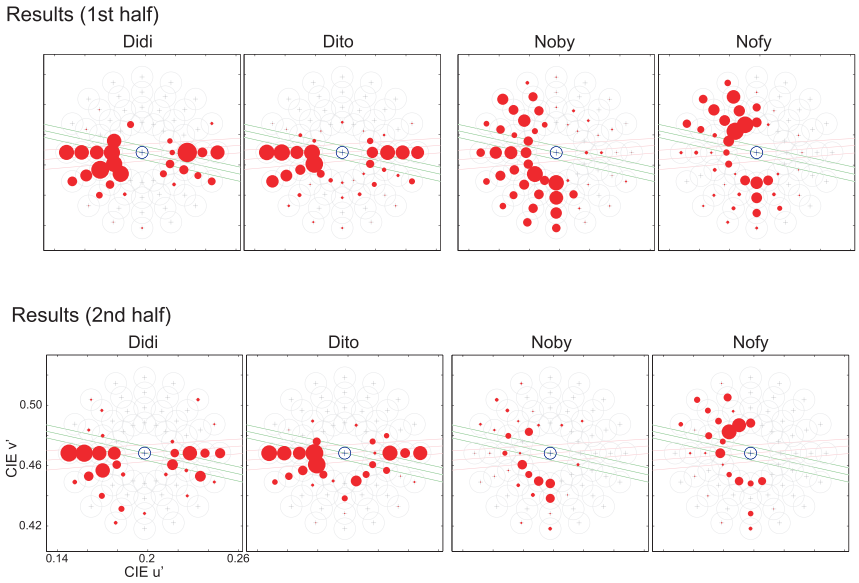

Figure 5. Color discrimination performance of first (top) and second (bottom) half of the trials. Format is same as in Figure 3.