

# Color preference in red–green dichromats

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Edited by Dale Purves, Duke University, Durham, NC, and approved June 12, 2015 (received for review February 2, 2015)

**Around 2% of males have red–green dichromacy, which is a genetic disorder of color vision where one type of cone photoreceptor is missing. Here we investigate the color preferences of dichromats. We aim (i) to establish whether the systematic and reliable color preferences of normal trichromatic observers (e.g., preference maximum at blue, minimum at yellow–green) are affected by dichromacy and (ii) to test theories of color preference with a dichromatic sample. Dichromat and normal trichromat observers named and rated how much they liked saturated, light, dark, and focal colors twice. Trichromats had the expected pattern of preference. Dichromats had a reliable pattern of preference that was different to trichromats, with a preference maximum rather than minimum at yellow and a much weaker preference for blue than trichromats. Color preference was more affected in observers who lacked the cone type sensitive to long wavelengths (protanopes) than in those who lacked the cone type sensitive to medium wavelengths (deutanopes). Trichromats' preferences were summarized effectively in terms of cone-contrast between color and background, and yellow–blue cone-contrast could account for dichromats' pattern of preference, with some evidence for residual red–green activity in deutanopes' preference. Dichromats' color naming also could account for their color preferences, with colors named more accurately and quickly being more preferred. This relationship between color naming and preference also was present for trichromat males but not females. Overall, the findings provide novel evidence on how dichromats experience color, advance the understanding of why humans like some colors more than others, and have implications for general theories of aesthetics.**

dichromacy | aesthetic preference | color vision | color naming

Individuals vary in their perceptual experience of the world, and sometimes this variation is caused by genetic differences (1–4). Dichromacy is a form of color-vision deficiency affecting about 2% of human males in which only two of the three types of retinal cone photoreceptors are functional because of genetic factors (1, 2). Protanopes, deutanopes, and tritanopes lack cone photoreceptors sensitive to long (L), medium (M), and short (S) wavelengths, respectively. Accordingly, dichromats' color discrimination is poorer, and their spectral sensitivity is slightly shifted to longer wavelengths (deutanopes) or is moderately shifted to shorter wavelengths (protanopes) compared with that of normal trichromats (common observers; see table 3.6 in ref. 5).

In normal trichromats, cone responses are the input signals for two chromatic cone opponent mechanisms, red–green and yellow–blue, based on L–M and S–(L+M) cone responses, respectively, and one achromatic mechanism, mainly based on L+M responses (1). Traditionally it has been considered that protanopes and deutanopes lack functionality in the red–green mechanism, because this opponent mechanism is based on the comparison of L and M cone responses, and one of those cone types is affected. (Thus such observers are called “red–green dichromats.”) However, research also has shown that a large proportion of red–green dichromats have residual activity in this mechanism with increasing stimulus size (over 3°; see refs. 6, 7), resulting in surprisingly good color naming (8–11). The origin of such red–green residual activity remains unknown and is open to several explanations (7, 10, 12, 13). Other research has shown that protanopes and deutanopes also exhibit minor alterations in the performance of the achromatic and yellow–blue mechanisms (see figures 4 and 5 in ref. 14). These functional

alterations in red–green dichromacy also affect color naming: Moreira et al. (15) have developed a model that explains 94% of the color-naming variance in protanopes and 96% of that in deutanopes. The color naming of dichromats suggests that, at least in some circumstances, dichromat color perception is supported by red–green residual activity ( $R-G_{res}$ ), in addition to yellow–blue and achromatic mechanisms (modeled as  $s'$  and  $L^*_T$  in ref. 15). These mechanisms also might be relevant for other aspects of dichromats' color perception, such as color preference.

Although there has been much research on dichromats, their affective response to color has not been systematically investigated previously. Some visual simulations of how different stimuli appear to dichromats (16) have been demonstrated to work reasonably well (17). For example, these simulations suggest that some hues that appear reddish to common observers would appear desaturated and brownish for dichromats—a hue that normal trichromats typically dislike (18). Do dichromats also dislike a brownish appearance? Alternatively, if dichromats perceive a brownish appearance more commonly than trichromats, does this increased perception alter their preference for that appearance relative to other hues? Could dichromats' and trichromats' color preferences, like naming, be surprisingly similar if a residual red–green mechanism feeds into dichromats' color preference?

Investigating color preference in dichromats may provide insight into how they perceive color and also may shed light on the origins of color preference and inform ways to test further theories and models of color preference. Decades of color research have indicated a systematic pattern of preference in trichromats: Blue hues are commonly preferred, and yellow–green hues are commonly disliked (18–20). This pattern has been so systematic across studies that some have claimed it is universal, although others have pointed out that cross-cultural differences in color preference can be found also (21). Patterns of color preference have been explained in terms of the emotional response to color (22) and in terms of the valence of objects associated with colors (18).

Another theory is that color preferences can be summarized in terms of the cone contrast between a color and its background

## Significance

**Around 2% of males have red–green dichromacy, which is a genetic disorder of color vision that affects how well certain colors can be seen and discriminated. Humans with normal color vision are known to have systematic and reliable preferences for some colors over others (e.g., blue is liked and yellow–green is disliked). We show that red–green dichromats have a different reliable pattern of color preference in which, for example, yellow is the most, not the least, preferred color. We test current theories of color preference and provide novel evidence that how easily a color can be named is related to how much it is liked. The findings further understanding of dichromacy, color preference, and aesthetics in general.**

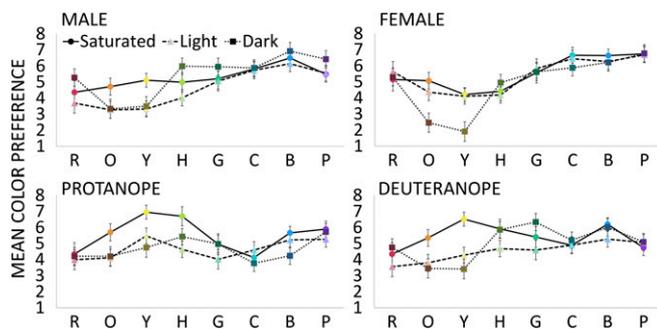
Author contributions: L.Á., H.M., J.L., and A.F. designed research; L.Á. and J.L. performed research; L.Á. and H.M. analyzed data; and L.Á., H.M., J.L., and A.F. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1502104112/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1502104112/-DCSupplemental).



**Fig. 1.** Mean preference ratings ( $\pm$  SEM) for 24 colors from the saturated, light, and dark sets, averaged for trichromatic males and females and dichromatic protanopes and deuteranopes. The  $x$  axis gives the hue: red (R), orange (O), yellow (Y), chartreuse (H), green (G), cyan (C), blue (B), and purple (P). Marker colors are only an approximation of those in the experiment.

(19). Supporting this theory, around 70% of the variance in preference across a set of hues could be explained by L–M and S–(L+M) cone contrasts for British and Chinese trichromats (19). However, other studies have failed to account for this much of the variance with cone contrasts alone (18, 21). Palmer and Schloss (18) extended the model, adding achromatic contrast and saturation as predictors, but accounted for only 37% of the variance. If the cone-contrast model works, we should find altered patterns of color preference in dichromats that reflect their altered color vision. If so, we should be able to model dichromat color preference, as Moreira et al. (15) did for color naming, using a model tailored for dichromats’ altered cone-opponent mechanisms.

The current study investigates color preference in male dichromat (protanopes and deuteranopes) and trichromat observers (males and females). Color preference was measured for a set of 24 colors from the Berkeley Color Project (BCP) (18), comprising saturated, light, and dark versions of eight hues used in prior studies of trichromat color preference (18, 20, 21) and also the focal colors of the basic color categories (Fig. S1). The type of dichromacy was confirmed through the use of a set of color-vision tests including the Nagel anomaloscope. Observers rated their preference for the colors twice and also named the colors. Color preferences were compared across groups. To test the cone-contrast model, trichromat color preferences were modeled with trichromat cone contrasts as in Hurlbert and Ling (19). Dichromat color preferences then were modeled with cone contrasts that take into account dichromats’ altered cone responses. In addition, we explore the relationship between color naming and color preference in dichromats and trichromats, investigating whether color categorization, accuracy, speed, and consistency of naming predict how much a color is preferred.

## Results

**Reliability.** To check that participants have reliable color preferences, the individuals’ preference ratings were averaged within each group and were correlated for the two times that colors were rated. Preferences showed high and significant correlations for the four groups (male,  $r = 0.98$ ; female,  $r = 0.97$ ; protanope,  $r = 0.94$ ; deuteranope,  $r = 0.95$ , all  $P < 0.01$ ). Preference also was reliable at the individual level (SI Text).

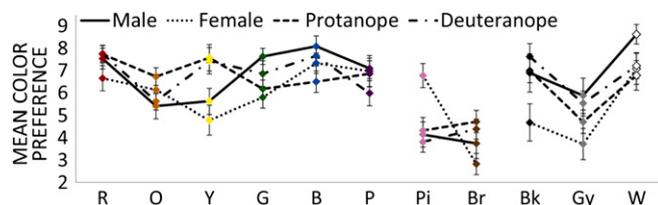
**Normal Trichromat and Dichromat Color-Preference Curves.** Fig. 1 shows color-preference curves (preference plotted as a function of hue). The pattern of preferences for native Spanish normal trichromats in the current study is highly similar to those of normal trichromats from the United States (18) and the United Kingdom (20): Trichromats have the lowest preference for some yellowish-greenish hues, and preference rises steadily with increasing greenness, with a maximum around blue (Fig. 1 *male* and *female*). In contrast, dichromats have a distinctly different color-preference pattern (Fig. 1 *protanope* and *deuteranope*). For

protanopes, preference is fairly flat across dark and light sets, but there is clear variation for saturated colors, for which preference peaks at yellow, with a minimum at cyan and red. Deuteranopes appear more similar than protanopes to male trichromats in their preference, particularly for light and dark sets. However, deuteranopes’ preference curve for saturated colors, like that for protanopes, has a peak at saturated yellow rather than at saturated blue, as seen for trichromatic males (see SI Text for analyses of the similarity in color-preference curves).

The pattern of color preference for focal colors (Fig. 2) is similar to that of the saturated set (Fig. 1) for all four groups. As seen for the BCP stimulus set, preference for focal yellow was elevated for dichromats relative to trichromats. For the desaturated focal color categories (Fig. 2, *Center*), only females had a high preference for focal pink, and all four groups had a low preference for focal brown. For the achromatic categories, male trichromats appear to like white more than the other groups.

To specify group differences in preference for specific hues, two sets of ANOVAs were conducted, one on the BCP stimulus set (Fig. 1) and another on the focal stimulus set (Fig. 2). For the BCP stimuli, a mixed-model ANOVA with set (saturated, light, and dark), color [red (R), orange (O), yellow (Y), chartreuse (H), green (G), cyan (C), blue (B), and purple (P)], and group (trichromat males, trichromat females, protanopes, and deuteranopes) was conducted on preference ratings, with the Greenhouse–Geisser correction applied when appropriate. This analysis revealed significant main effects of set [ $F(1.82,60) = 6.49, P < 0.01$ ] and color [ $F(4.30,60) = 16.62, P < 0.001$ ] and interactions of set and color [ $F(9.32,60) = 13.39, P < 0.001$ ] and color and group [ $F(12.88,60) = 5.19, P < 0.001$ ]. To unpack the interaction relevant to our hypotheses, post hoc one-way ANOVAs on the mean preference for each color (mean for saturated, light, and dark sets) were conducted with group as a factor. These analyses revealed group differences for yellow [ $F(3,60) = 9.07, P < 0.001$ ], cyan [ $F(3,60) = 6.23, P < 0.01$ ], and purple [ $F(3,60) = 3.11, P < 0.05$ ]. Bonferroni-corrected pairwise comparisons revealed that protanopes preferred yellow more than trichromat males ( $P < 0.01$ ), and protanopes preferred cyan less than trichromat males ( $P < 0.05$ ). Comparisons with females are provided in SI Text.

Another mixed-model ANOVA with color [R, O, Y, G, B, P, pink (Pi), brown (Br), black (Bk), gray (Gy), and white, (W)] and group on focal preference ratings revealed significant main effects of color [ $F(7.04,60) = 20.64, P < 0.001$ ] and an interaction of color and group [ $F(21.11,60) = 3.22, P < 0.001$ ]. To investigate this interaction, one-way ANOVAs with group as a factor were conducted on the preference ratings for 11 focal stimuli. These analyses revealed significant group differences for green [ $F(3,60) = 3.41, P < 0.05$ ], yellow [ $F(3,60) = 5.23, P < 0.01$ ], pink [ $F(3,60) = 6.90, P < 0.001$ ], and black [ $F(3,60) = 3.12, P < 0.05$ ]. Bonferroni-corrected pairwise comparisons did not show significant differences between dichromat and trichromat males for any color. For several colors, however, dichromat and male color preferences differed from those of females (SI Text).



**Fig. 2.** Mean preference ratings ( $\pm$  SEM) for 11 colors from the focal set, averaged for trichromatic males (solid line) and females (dotted line), dichromatic protanopes (dashed line), and deuteranopes (dotted and dashed line). The  $x$  axis gives the basic color term for the focal saturated color categories (*Left*), the desaturated color categories of pink and brown (*Center*), and the achromatic categories (*Right*): red (R), orange (O), yellow (Y), green (G), blue (B), purple (P), pink (Pi), brown (Br), black (Bk), gray (Gy), and white (W). Marker colors are only an approximation of those in the experiment.

**Predictors of Color Preference: Cone Contrast, Lightness, and Saturation.**

As in Hurlbert and Ling (19), we analyzed color-preference data (excluding foci) in terms of the two dimensions of opponent cone-contrast space (23). [The focal set has been excluded from these analyses to provide analyses that are comparable to previous research (19, 21), which did not include focal colors. In addition L–M and S–(L+M) will fail to account for the preference of the three achromatic foci.] L–M and S–(L+M) cone contrasts between stimulus and background were calculated (SI Text) and entered as predictors in linear regressions with average color-preference ratings as the outcome variable. We conducted separate regressions for each group of observers. The cone-contrast model significantly accounted for just under half of the variance in the average pattern of color preference for the BCP color set for normal trichromats (Table 1), but for dichromats this model accounted for less variance and was not significant (and therefore is not included in Table 1). S–(L+M) was the only significant predictor for trichromat males [ $t = 2.65, P < 0.05$ ] and females [ $t = 3.90, P < 0.001$ ]; over a third of the variance was explained by S–(L+M) in a univariate model (Table 1), but L–M was not a significant predictor for any group (all  $P > 0.05$ ). Equivalent regressions with predictors drawn from a multistage model that rotates the standard axes into RG, YB (Fig. S2) (24) produced a highly similar pattern of results (SI Text). Additional regressions indicated that lightness ( $L^*$ ) and saturation ( $s_m$ ) were not significant predictors of trichromats' preferences (SI Text).

Hurlbert and Ling (19) applied the cone-contrast model to preference ratings for colors that varied only in hue and accounted for much more variance than seen in subsequent research, which, as here, used BCP stimuli that vary in lightness, saturation, and hue (18, 21). Both Taylor et al. (21) and Palmer and Schloss (18) suggested that this discrepancy could be caused by the cone-contrast model capturing preference better when the stimuli entered into the regression mainly vary in hue. To explore this possibility, we performed separate regressions for each set (saturated, light, and dark) so that the variation in the lightness and the saturation of the stimuli was minimized. Fig. 3 provides the cone contrasts for the three sets (Fig. 3 A–C) and the regression weights when these cone contrasts are entered as predictors of preference for those colors. If cone contrast strongly predicted preference, then the color-preference curves in Fig. 1 should resemble the cone-contrast curves in Fig. 3, and the regression weights should be strong and significant. The cone-contrast model accounted for 75% to almost 100% the variance, depending on color set, for trichromats. S–(L+M) was a significant predictor in these regressions (all  $P < 0.05$ ) (Fig. 3D) except for trichromat males for the saturated set ( $P = 0.06$ ; see Fig. 3D). L–M was a significant predictor only for the trichromat males' preferences in the light set ( $t = -1.45, P < 0.001$ ) (Fig. 3E).

The above regressions based on a trichromatic cone-contrast model were repeated for dichromats and, surprisingly, accounted for a significant amount of the variance (78%) for deuteranopes'

preference of the light set, with L–M being a significant predictor ( $t = -0.97, P < 0.05$ ) (Fig. 3G). Regressions were conducted to investigate whether corrected variables that take into account dichromats' cone responses (15) for lightness ( $L^*_{\tau}$ ) and saturation ( $s'$ ) (SI Text) could predict dichromat color preferences. Transformed lightness ( $L^*_{\tau}$ ) could not account for color preference in dichromats (SI Text). Because dichromats' preference curves peaked both at yellow and blue (Fig. 1 *protanope* and *deutanope*) and  $s'$  takes positive values for yellowish colors and negative values for bluish colors (SI Text), we thought that absolute  $s'$  (mechanism activation) was more appropriate for saturation estimations for protanope and deutanope observers. We found  $|s'|$  was a significant predictor for protanopes and explained more than 25% of the variance (Table 1). Because  $s'$  is related to yellow–blue mechanism activity, we repeated the cone-contrast regressions but with absolute S–(L+M). As expected, similar to  $|s'|$ , the variance explained by  $|S-(L+M)|$  was significant and explained almost two thirds of the variance in protanopes' preference for the full color set and more than three quarters of the preference for saturated and light colors (Fig. 3F). For deuteranopes,  $|S-(L+M)|$  was a significant predictor of preference only for saturated colors (Fig. 3F).

**Relationship of Color Preference and Color Naming.** The naming data were used to group the stimuli according to the 11 terms used (red, green, yellow, blue, orange, pink, purple, brown, black, gray, and white; see *Methods* for corresponding terms in Spanish). For each observer, each category was composed of stimuli consistently named with the appropriate term. One-way ANOVA analyses of preference ratings when stimuli were classified according to each participant's naming showed group differences for yellow [ $F(3,216) = 13.38, P < 0.001$ ], blue [ $F(3,403) = 8.93, P < 0.001$ ], brown [ $F(3,109) = 3.31, P < 0.05$ ], black [ $F(3,60) = 3.32, P < 0.05$ ], and pink [ $F(3,219) = 8.97, P < 0.001$ ] categories. Bonferroni-corrected comparisons revealed that both groups of dichromats preferred colors named as yellow more than trichromat males ( $P < 0.05$ ), and protanopes preferred blues less than deuteranopes and trichromat males ( $P < 0.05$ ). Female comparisons are given in SI Text.

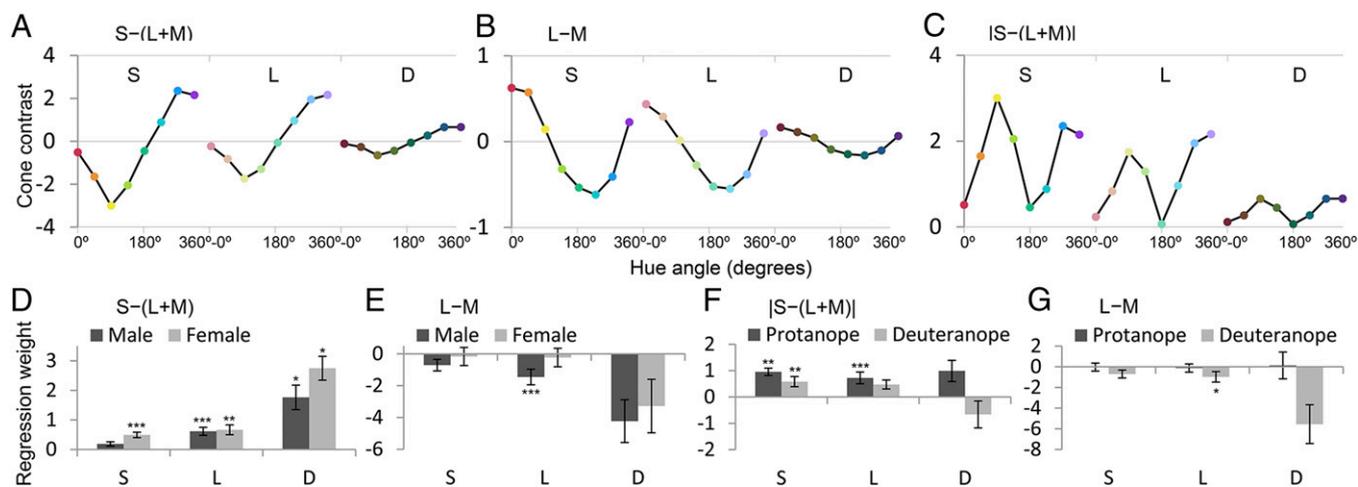
Table S1 gives the frequencies of color names provided by each group. The naming-error rate (a name was considered an error if it was not the modal response of normal trichromats) (11) was significantly larger ( $t = 4.49, P < 0.001$ ) in protanopes (39.14%) than in deuteranopes (27.56%). Additional analyses are given in SI Text.

In addition, for each stimulus and for each group, naming consistency (the percentage of observers using the same color name in both stimulus presentations) and naming consensus (how much observers within a group agree on the name, the percentage frequency of the most frequent term for that group) were computed. We obtained significant correlations between preference and naming response time (negative), naming-error rate (negative), consistency (positive), and consensus (positive) for all groups except females (Table 2 and Fig. S3).

**Table 1. Results for multivariate [L–M and S–(L+M) as predictors (Model)] and univariate [S–(L+M),  $|s'|$ , L–M, or  $|S-(L+M)|$  as predictors] regressions conducted on trichromat or dichromat preference ratings for various stimulus sets**

Trichromat preference ratings							Dichromat preference ratings						
Predictor	Set	df	Male		Female		Predictor	Set	df	Protanope		Deutanope	
			F	R <sup>2</sup>	F	R <sup>2</sup>				F	R <sup>2</sup>	F	R <sup>2</sup>
Model	BCP	2,21	<b>6.8</b>	<b>0.393*</b>	<b>9.0</b>	<b>0.462**</b>	Model	L	2,5	0.2	0.074	<b>9.0</b>	<b>0.782*</b>
	S	2,5	<b>7.0</b>	<b>0.738*</b>	<b>34.9</b>	<b>0.933**</b>	$ s' $	BCP	1,22	<b>8.4</b>	<b>0.276**</b>	1.9	0.079
	L	2,5	<b>531.7</b>	<b>0.995***</b>	<b>15.9</b>	<b>0.864**</b>	L–M	L	1,6	0.1	0.019	<b>7.0</b>	<b>0.537*</b>
	D	2,5	<b>5.9</b>	<b>0.703*</b>	<b>6.0</b>	<b>0.707*</b>	$ S-(L+M) $	BCP	1,22	<b>34.3</b>	<b>0.609***</b>	3.8	0.146
S–(L+M)	BCP	1,22	<b>9.6</b>	<b>0.305**</b>	<b>18.3</b>	<b>0.454***</b>		S	1,6	<b>19.1</b>	<b>0.761**</b>	<b>6.6</b>	<b>0.524*</b>
	S	1,6	5.5	0.479	<b>76.6</b>	<b>0.927***</b>		L	1,6	<b>42.7</b>	<b>0.877***</b>	3.6	0.375
	L	1,6	<b>22.3</b>	<b>0.788**</b>	<b>36.2</b>	<b>0.858***</b>							
	D	1,6	<b>7.3</b>	<b>0.548*</b>	<b>11.4</b>	<b>0.655*</b>							

Only regressions that are significant (bold) for at least one normal trichromat or dichromat group are reported. BCP, Berkeley Color Project; D, dark; L, light; S, saturated; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .



**Fig. 3.** Values for regression predictors (A–C) and resulting regression weights (D–G). (A–C)  $S-(L+M)$  (A),  $L-M$  (B), and  $|S-(L+M)|$  (C) stimulus–background cone-contrast values for saturated (S), light (L), and dark (D) colors. (D–G) Mean ( $\pm$  SEM) individual regression weights when  $S-(L+M)$  and  $L-M$  are entered as predictors of trichromat preference of saturated, light, and dark colors (D and E) or  $|S-(L+M)|$  or  $L-M$  is entered as the predictor of dichromat preference (F and G).

An analysis was conducted to investigate whether dichromats preferred colors more if they gave them the same name as trichromats than if they made naming errors. Unpaired *t* tests revealed that dichromats preferred colors that they named the same as trichromats (preference for hits,  $P_h$ ) more than those to which they gave different names on at least one of the two naming trials (preference for errors,  $P_e$ ), and this effect was significant for both protanopes (mean  $P_h = 5.41$ , mean  $P_e = 4.98$ ,  $t = 2.33$   $P < 0.05$ ) and deuteranopes (mean  $P_h = 5.59$ , mean  $P_e = 4.64$ ,  $t = 5.37$   $P < 0.001$ ). Additional analyses of error-naming rate are given in *SI Text*.

A final series of multiple regression analyses was performed to evaluate whether adding naming response times to the cone-contrast regressions accounted for more variance in preference. Naming response time was a significant predictor that increased the explained variance for the three male groups ( $t = -5.39$ , explained variance increased from 39.9 to 75.2%,  $P < 0.001$ , in trichromat males;  $t = -2.19$ , explained variance increased from 60.9 to 68.2%,  $P < 0.05$ , in protanopes;  $t = -3.89$ , explained variance increased from 14.6 to 50.3%,  $P < 0.001$ , in deuteranopes) but not for females ( $P > 0.05$ ; the increase in explained variance from 46.2 to 51.8% was not significant).

### Discussion

Research on dichromacy has covered various topics such as genetics (2), psychophysics (5), color naming (11, 15), and even color-appearance models (7, 16, 25). Here we provide a novel report of the color preference of red–green dichromats and compare their color preference with the color preference and its explicative mechanisms of normal trichromats, including suitable transformations of such mechanisms for dichromats ( $L^*_T$  and  $s'$ ). In addition, we investigated the relationship between color naming and color preference. We find that dichromats reliably prefer some colors over others, but these preferences do not fit the systematic pattern found in normal trichromats, who commonly prefer blue hues and commonly dislike yellow-green hues (18–20). Instead, saturated yellow was the most preferred color for dichromats, and protanopes' preference for cyan was muted compared with normal trichromats. The patterns of dichromat and trichromat color preference were more similar across the focal colors than for a set of colors that included less typical examples.

Color-preference patterns were summarized in terms of the cone contrasts between stimulus and background, as in Hurlbert and Ling (19), explaining almost half of the variance in trichromat male and female color preference for all colors, with  $S-(L+M)$  being the most significant predictor. As in Palmer and Schloss (18) and Taylor and Franklin (20), less variance was explained than

reported in Hurlbert and Ling (19). However, when we modeled preference for colors that varied mainly in hue (as in ref. 19), the explained variance increased substantially, by more than two thirds, depending on the color set, with  $S-(L+M)$  remaining the main predictor.  $L-M$  also was a significant predictor for trichromat males, but only for lighter colors. Hurlbert and Ling (19) also found that  $L-M$  contributed to the male preference for colors that were similar to ours in lightness (our mean  $L^*$  was  $\sim 80$ ; Hurlbert and Ling's mean  $L^*$  was  $\sim 77$ ).

As expected, the cone-contrast model could not explain dichromat color preference: Dichromats supposedly lack  $L-M$  cone opponency, and  $S-(L+M)$  cone contrast cannot explain high preferences both for blue and yellow hues simultaneously. However,  $|S-(L+M)|$ , which ignores the contrast sign but captures its intensity, accounted for almost two thirds of the variance in protanope preference. When colors varied mainly in hue,  $|S-(L+M)|$  predicted more than three quarters of the variance in protanope preference. For deuteranopes, neither  $|S-(L+M)|$  or  $|s'|$  was a significant predictor of preference when colors varied in hue, saturation, and lightness, but  $|S-(L+M)|$  was a significant predictor for deuteranope preference of saturated colors that varied mainly in hue. Surprisingly, given the lack of M cones for deuteranopes,  $L-M$  significantly predicted more than half of the variance in deuteranope preference for light colors, as it did for the trichromat males in this study and in Hurlbert and Ling (19).

As in prior studies (18–20), we modeled color preference using a cone-contrast model [ $S-(L+M)$ ;  $L-M$ ] developed from psychophysical experiments (i.e., threshold detection; see ref. 23). Some have argued that this kind of model does not fully account for hue perception (*SI Text*). Alternative models that combine the responses from the three cone types in a different way (e.g., a multistage model described in ref. 24, in which there is an

**Table 2.** Correlation coefficients (*r*) between preference and naming response time, naming-error rate, naming consistency, and consensus

Group	Response time	Naming-error		
		rate	Consistency	Consensus
Male	-0.68**	-0.44**	0.35*	0.44**
Female	-0.20	-0.20	0.30	0.20
Protanope	-0.74**	-0.36*	0.51**	0.54**
Deuteranope	-0.68**	-0.44**	0.50**	0.51**

*n* = 35 stimuli; \* $P < 0.05$ ; \*\* $P < 0.01$  (one-tailed).

important contribution of S-cone signals for both red–green and yellow–blue axes) have been shown to be more consistent with perceptual experience (26). When we repeated analyses using the multistage model, we found that the two kinds of model equally accounted for the color preference of normal trichromats (*SI Text*).

Dichromats named colors differently than trichromats about one third of the time. As previously found (11), there were significantly more naming errors by protanopes than by deuteranopes. The difference probably is related to (i) the greater alteration of the achromatic mechanism in protanopes than in deuteranopes (see, for example, the luminous efficiency curves in figure 4 in ref. 14) and (ii) the greater importance of the achromatic mechanism in dichromat than in trichromat naming (see figure 3 in ref. 11). When color preferences were analyzed according to naming, dichromats preferred colors named as yellow more than trichromats, and protanopes preferred blues less than trichromats. Colors that were named more quickly and with less error, consistently, and according to group consensus were most preferred for all groups except females. In addition, dichromats preferred colors that they named the same as trichromats more than colors that they named differently from trichromats.

Combined, the findings have implications for our understanding of (i) how red–green dichromacy affects color perception; (ii) the mechanisms of color preference; and (iii) general principles of aesthetics and perception. We discuss each in turn.

First, the findings suggest that dichromacy affects color perception more in protanopes than in deuteranopes. For both naming and preference, the similarity between dichromats and trichromats was less for protanopes than for deuteranopes. This result supports prior research, which has found that protanopes make more naming errors than deuteranopes (9, 11), and shows for the first time, to our knowledge, that this effect extends to color preference. For deuteranopes, there also was evidence of a residual red–green mechanism affecting color preference, because L–M significantly predicted deuteranope preference for light colors, as it did for male trichromats. Prior research has argued for a residual red–green mechanism influencing dichromat color naming for stimuli over 3° (8–11). Here, we show that such a mechanism is likely at play when deuteranopes decide how much they like light colors and provides evidence of residual red–green discrimination in an aesthetic aspect of color perception. Various explanations have been proposed for this residual red–green mechanism, such as rod intrusion (10), gains and nonlinearities applied to the receptor signals (7), or the influence of chromatic aberrations (12). Further research is needed to understand this mechanism and why it appears to influence deuteranope but not protanope preference.

Second, the findings have implications for color-preference models. We show that cone contrast can be amazingly effective in capturing color preference when colors vary mainly in hue (explaining almost 100% of the variance in the male preference in light colors) but is less effective for colors that vary in hue and vary strongly in saturation and lightness. Therefore, the model can provide a useful way of comparing the mechanisms of hue preference across groups even if it does not capture preference in a 3D color space. The fact that dichromat color preferences could be modeled using modified variables that consider their altered cone response provides further corroboration that hue preferences can be modeled by the underlying subsystems of color vision. The current findings also suggest that the yellow–blue mechanism is much more important for human color preference than the red–green one, perhaps explaining why the red and green preferences of dichromats with a residual red–green mechanism were so similar to those of trichromats.

Color preference has been explained in terms of the emotional response to color (22) and the valence of objects associated with colors (18). Here, we also show that the degree to which males (but not females) like a color is related to how easy it is to name the color. Response time explained up to half the variance in color preference for trichromat males and for dichromats.

Although this variance is less than that explained by the relationship between color preference and the valence of color-associated objects (80%) (18) or emotional response (67%) (22), the relationship between naming speed and preference is still substantial. Furthermore, when we used both the most relevant cone-opponent mechanism and naming response time as predictors, the explained variance increased significantly (by more than 50% for all male groups). Cone contrast and color naming do not account for all the variance in preference. Given that past research has revealed other predictors which also partially explain color preference, future research should aim at understanding the relationships between the various predictors, including those identified in the current study, and should investigate the extent to which each predictor is weighted by different groups. Some combination of predictors may provide a more complete model, although accounting for 100% of the variance in a human judgment such as preference is, of course, a challenge. Future research also should consider whether non-linear models account for more of the variance, because only linear models have been considered so far.

Third, the finding has broader implications for theories of aesthetics. Since Fechner founded the field of aesthetics research in the late 19th century, experimental research has sought to identify general principles of aesthetics (27). One contemporary theory proposes that the more fluently a stimulus can be processed, the more it is liked (28). It has been proposed that stimuli with greater contrast, clarity, symmetry, familiarity, and prototypicality are processed more fluently by an observer (29), and relationships between fluency and preference have been documented for stimuli such as music (30), faces (31), voices (32), and art (33). Prior work has found greater preference for focal than nonfocal colors (34), but an explicit link between color preference and fluency has not been demonstrated previously. Here we show that, for males, the general principle of fluency (measured by ease of naming, i.e., naming response time) at least partially accounts for color preference. Importantly, we also show that when genetic mutation (e.g., dichromacy) affects stimulus fluency, the relationship between fluency and preference holds for males. Finally, we show that there can be group differences in the extent to which fluency predicts preference, because the relationship between fluency and color preference was present only for tri- and dichromat males, but not for females. Further investigation of such group differences may clarify the conditions under which fluency contributes to preference, as opposed to alternative mechanisms such as complexity or novelty (35). More broadly, the current finding that group differences in color preference (e.g., differences between trichromats and dichromats) are accounted for by biological components of color vision resonates with the debate on the relative contributions of culture, environment, and genes to individual differences in perception (1–3).

Combined, the findings on cone contrast and color naming suggest that the more psychological specificity colors have, the more they are preferred. By “psychological specificity” we mean the extent to which colors produce the greatest response in the visual system and the extent to which they are salient, distinctive, and less prone to be confused with other colors. For example, dichromat preference peaks at colors with the strongest response in the yellow–blue mechanism and that are easiest for dichromats to name. As Palmer and Schloss (18) argue, human color preferences could be essentially adaptive, and people could be more likely to interact, survive, and reproduce successfully if they prefer some colors over others (19). Because color perception has adaptive uses related to the speed and ease of processing (e.g., when locating something useful or dangerous), it seems logical that males prefer colors that are easy to name and therefore process. The lack of such a relationship for females deserves further investigation and could reveal important differences in the underlying mechanisms of male and female color preference. The current investigation reveals the aesthetic response of dichromats to their colored world and provides greater understanding of dichromacy, why we like some colors more than others, and general theories of aesthetics.

## Methods

**Participants.** Participants were 15 males and 17 females with normal color vision and 17 deuteranope males and 15 protanope males with dichromatic color vision. There were no significant group differences in age (mean age: trichromat males = 29.40 y, SD = 6.49; trichromat females = 28.29 y, SD = 9.73; protanopes = 34.00 y, SD = 8.60; deuteranopes = 27.82 y, SD = 8.59),  $F(3,60) = 1.72, P = 0.17$ . All participants were native Spanish speakers; 18 were students from Universidad Complutense de Madrid, but most were research volunteers from the local area. Their color vision was tested with a set of psychophysical tests (36–38). None had tritan defects. To assign them into groups, participants with color-vision deficiencies also performed a Rayleigh match in a Nagel anomaloscope (Tomey, AF-1). The research was conducted according to the principles of the Declaration of Helsinki, and all participants gave informed consent. This research was approved by the Universidad Complutense de Madrid – Hospital Clínico San Carlos review board.

**Stimuli and Experimental Set-Up.** The 24 stimuli (Fig. S1) were close approximations of the saturated (S), light (L), and dark (D) sets from the BCP (18). The saturated set comprised good saturated examples of red (R), orange (O), yellow (Y), chartreuse (H), green (G), cyan (C), blue (B), and purple (P). The light and dark sets were approximately halfway between those of the corresponding hue in the saturated set and Munsell Chroma 1. Munsell value (lightness) was approximately halfway between that of the corresponding hue in the saturated set and Munsell value 9 (light) or 1 (dark). We also used a set of focal stimuli that were the best exemplars of the 11 basic color categories named in Spanish (11) and included the best exemplars of red, green, yellow, blue, orange, pink, purple, brown, black, gray, and white (Fig. S1). The chromaticity coordinates for the 35 stimuli were verified with a Minolta CL-200 lux-colorimeter (Table S2). All stimuli were presented as circular patches (8°) on a calibrated 24-inch in-place switching LCD monitor with a hood in a dark room (LaCie 324i; resolution of 1,920 × 1,200 pixels; reference white:  $Y = 18,195 \text{ cd/m}^2, x = 0.36, y = 0.35$ ). The center of the monitor was at participants' eye level, at a distance of 65 cm.

**Design and Procedure.** Participants completed a color-preference task and a color-naming task, with task order counterbalanced across participants. For the color-preference task, stimuli were presented individually in the center of a gray background ( $Y = 32.35 \text{ cd/m}^2, x = 0.35, y = 0.35$ ). A line representing a rating scale (22° horizontal, 1° vertical) was presented below the colored circle, and participants were required to move the cursor from its neutral position in the middle of the scale to indicate their degree of preference for the stimuli. Text (12-point Arial font) below each endpoint specified what that end of the scale represented (0, *nada*, not at all; 10, *mucho*, very much). A trial began with a 500-ms fixation cross (1° diameter) and a simultaneous whistle, followed by 500 ms of gray background. The stimulus remained on the screen until the participant indicated how much they liked the color by sliding the cursor along the rating scale and clicking the confirmation button. After performing 24 practice trials, participants rated each stimulus twice in a pseudorandom order (without consecutive stimulus repetitions).

The naming task was identical, except that participants were required to name rather than rate the colors, and each stimulus remained on the screen for 2.5 s. Participants were instructed to name aloud the color using one of the 11 Spanish basic color terms: *rojo* (red), *verde* (green), *amarillo* (yellow), *azul* (blue), *naranja* (orange), *rosa* (pink), *morado*, (purple), *marrón*, (brown), *negro* (black), *gris* (gray), or *blanco* (white). Response time was registered as the start of the verbal response using a unidirectional condenser microphone (Fonestar FMC-616) and a digital recorder (Olympus VN-711PC) for backup purposes. The experimenter manually registered color names and verbal artifacts (i.e., dubious interjections, changes in response). Participants took an average of 12 min to complete the full experiment. For both tasks, participants were instructed to answer as quickly but precisely as possible.

**ACKNOWLEDGMENTS.** We thank Jenny Bosten for helpful comments on an earlier version of this manuscript. This work was funded by Universidad Complutense de Madrid Research Grant BE48/09 (to L.Á.), European Research Council Starting Grant (project "CATEGORIES") 283605 (to A.F.) and Ministerio de Economía y Competitividad Grant PSI2012-37778 (to J.L., H.M., and L.Á.).

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