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The colors of natural scenes benefit dichromats

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ABSTRACT

Dichromacy impairs color vision and impoverishes the discrimination of surface colors in natural scenes. Computational estimates based on hyperspectral imaging data from natural scenes suggest that dichromats can discriminate only about 10% of the colors discriminated by normal trichromats. These estimates, however, assume that the colors are equally frequent. Yet, pairs of colors confused by dichromats may be rare and thus have small impact on overall perceived chromatic diversity. This study estimated, empirically, how much dichromats are disadvantaged in discriminating surface colors drawn from natural scenes. The stimulus for the experiment was a scene made of real three-dimensional objects painted with matte white paint and illuminated by a spectrally tunable light source. In each trial the observers saw the scene illuminated by two spectra in two successive time intervals and had to indicate whether the colors perceived in the objects in the two intervals were the same or different. The spectra were drawn randomly from hyperspectral data of natural scenes and therefore represented natural spectral statistics. Four normal trichromats and four dichromats carried out the experiment. It was found that the number of pairs that could be discriminated by dichromats was almost 70% of those discriminated by normal trichromats, a proportion much higher than anticipated from estimates of discernible colors. Moreover, data from model simulations show that normal trichromats and dichromats use lightness differences for discrimination in about 40% and 50% of the discriminable pairs, respectively. Together these results suggest that the color distributions of natural scenes benefit the color vision of dichromats.

1. Introduction

Normal human color vision is trichromatic, based on three types of cone photoreceptors with photopigments absorbing light in the short-, medium- and long-wavelength regions of the visible spectrum (Solomon & Lennie, 2007). It evolved from the Old World primates who developed trichromatic vision about 40 million years ago (Jacobs, 2009), probably as an adaptation for foraging (Mollon, 1989; Osorio & Vorobyev, 1996). It allows discrimination of several million surface colors (Linhares, Pinto, & Nascimento, 2008a; Pointer & Attridge, 1998). With the possible exception of tetrachromatic women (Jordan, Atkinson, & Mollon, 2006) the genetic anomalies underlying color deficiencies imply limitations in color discrimination either because photopigments are spectrally closer, as in anomalous trichromats, or missing, as in dichromats or monochromats (Neitz & Neitz, 2011).

Dichromacy is most frequent in the red-green range of the spectrum because the photopigments are X-linked and individuals lack either the long-wavelength-sensitive (L) cones (protanopes) or the middle-wavelength-sensitive (M) cones (deuteranopes). It affects a small number of females, about 0.02%, but a larger number of males, about 2% (Sharpe, Stockman, Jägle, & Nathans, 1999).

The missing M or L photopigment may be replaced by the other but in some cases the photoreceptor is missing completely (Carroll, Neitz, Hofer, Neitz, & Williams, 2004) and there is disruption of the cone mosaic (McClements et al., 2013). The other red-green photopigment that remains, M or L, may also vary (Neitz, Neitz, & Jacobs, 1995).

Dichromats confound colors that are discriminated by normal trichromats. These confused colors lie along the confusion lines and can only be discriminated by luminance differences (Wyszecki, 1982). Given that many natural colors are close to these confusion lines dichromats may be at a disadvantage in discriminating natural objects using only chromatic cues (Hendley & Hecht, 1949). Dichromats, however, do not seem impaired in other visual aspects associated with color, e.g. in visual memory of colored images of natural scenes (Gegenfurtner, Wichmann, & Sharpe, 1998) and in color constancy with natural stimuli (Álvaro, Lillo, Moreira, Linhares, & Nascimento, 2015;

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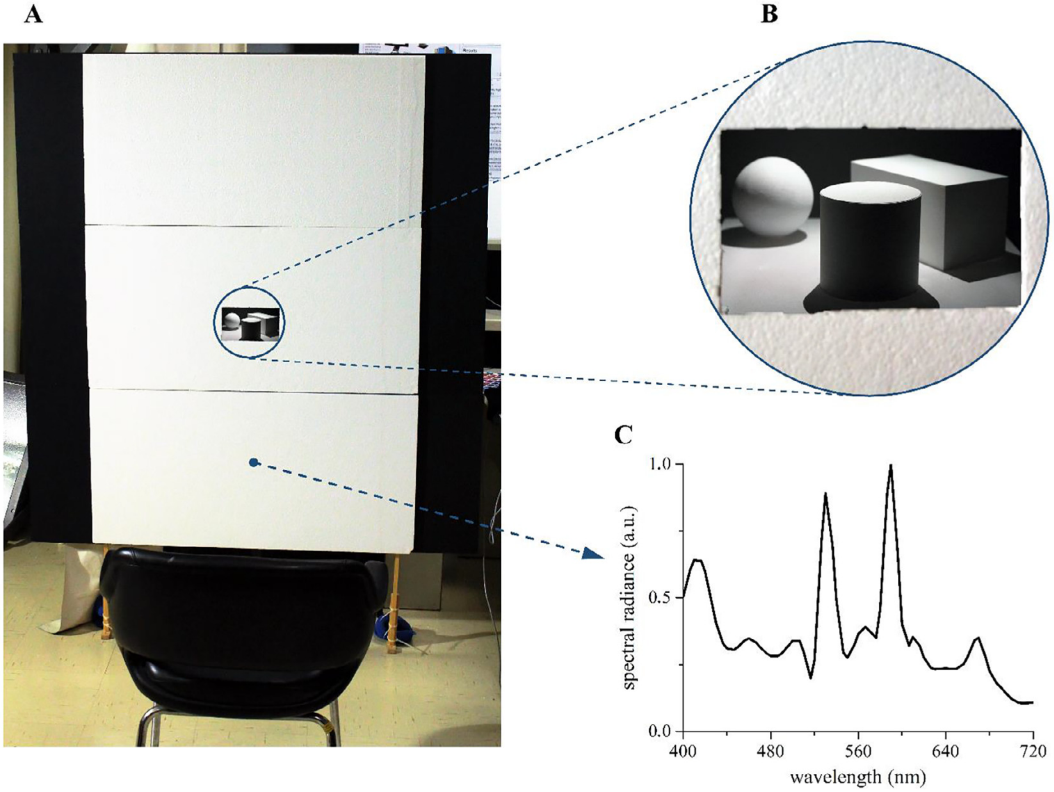

Fig. 1. Front view of the test setup for the 10° stimuli (A), close view of the test scene (B), and the radiance spectrum of the discharge lamp (OSRAM HQI 150W RX7s) reflected by the white Styrofoam mask that served as the adapting illuminant for the experiment (C). The white Styrofoam mask illuminated by the adapting illuminant provided an adapting field. A rectangular aperture on this mask allowed the scene to be seen by the observer. The set up for 2° stimuli was the same but with a smaller viewing aperture and proportionally smaller test objects.

Baraas, Foster, Amano, & Nascimento, 2004, 2010; Linhares et al., 2008a; Rüttiger, Mayser, Sérey, & Sharpe, 2001). In some tasks, they seem to be even better than normal trichromats, e.g. cone-isolating stimuli at high temporal frequencies (Sharpe, de Luca, Hansen, Jägle, & Gegenfurtner, 2006) or camouflage detection (Morgan, Adam, & Mollon, 1992; Saito et al., 2005). They can also use color names much like normal trichromats (Montag & Boynton, 1987; Montag, 1994; Wachtler, Dohrmann, & Hertel, 2004), can discriminate most of the objects in everyday life and only rarely show evidences of their color deficiency, e.g. in selecting the colors of clothes, working with man-made color codes, judging ripeness and the cooked state of food (Cole, 2004), in the medical profession (Pramanik, Khatiwada, & Pandit, 2012; Spalding, 2004) or in artistic activities (Lanthony, 2001). This unexpectedly good performance in real conditions could be related with the fact that in some viewing conditions, e.g. large-viewing-fields, dichromats become trichromats (Nagy, 1980; Scheibner & Boynton, 1968; Smith & Pokorny, 1977) showing some red-green discrimination (Nagy & Boynton, 1979) through mechanisms that require large temporal and spatial summation (Montag, 1994) but which are poorly understood (Broackes, 2010; Crognale, Teller, Yamaguchi, Motulsky, & Deeb, 1999).

Estimates based on the dichromatic perceptual model of Brettel, Viénot, & Mollon (1997) and on how much the object color volume (Wyszecki, 1982) is compressed in dichromacy predict that dichromats see less than 1% percent of the object colors that normal trichromats can see (Perales, Martínez-Verdú, Linhares, & Nascimento, 2010). These estimates assume that lightness is a chromatic dimension that is used for discrimination. They also assume that all colors of the theoretical object color volume occur in nature. More realistic estimates based on spectral imaging data from natural scenes suggest numbers of about 7% (Linhares, Pinto, & Nascimento, 2008b) corresponding to a relative pairwise discriminability less than 1% if the colors occur with the same frequency (see Appendix A). These estimates suggest a larger impairment than observed in dichromats' everyday life. One hypothesis is that pairs of colors confused by dichromats are rare in natural conditions and thus have small impact on the overall perceived chromatic diversity of the environment. In fact, the colors of natural scenes are mainly distributed around a yellow-blue axis (Montagner, Linhares, Vilarigues, & Nascimento, 2016; Webster & Mollon, 1997) which although not collinear with the tritan line may still facilitate dichomats' discrimination through the S-cone pathway.

The goal of the present work was to empirically quantify how much dichromats are disadvantaged in discriminating the colors of natural objects if those colors are viewed with the same frequency as in nature. Thus, a discrimination test based on spectral data from hyperspectral imaging of natural scenes was implemented. The spectral data were used for the illumination of a real scene assembled in the laboratory with three-dimensional objects with flat reflectance spectra so that the reflected light appeared to come from surfaces sampled from natural scenes. The set-up was built in such a way that the objects of the scene look as having a tunable intrinsic color. The spectrally tunable light source reproduces the spectra with high accuracy and therefore the methodology avoids the usual assumptions about dichromat's photoreceptor spectral sensitivities that have to be made when doing display monitor experiments. The experiment was carried out by color normal observers and dichromats. It was found that dichromats discriminate almost 70% of the colors normal observers discriminate when making paired comparisons and therefore the impairment is, in practice, relatively small. The discrimination data can be predicted using the model of dichromatic color perception due to Brettel et al. together with the actual distributions of colors in natural scenes and confirms the hypothesis that the frequency of occurrence of natural colors benefits dichromats.

2. Methods

2.1. Experimental setup

Fig. 1 shows the experimental setup with the test scene assembled inside an illumination booth with a size of 66 cm (width) × 48 cm (length) × 46 cm (height). The objects were three geometric objects: a sphere, a cylinder, and a parallelepiped. They were fixed to an acrylate plate, supported by a Styrofoam support which was slightly tilted towards the observer. The objects and the acrylate plate were uniformly sprayed with a white matte powder (Spray-Rotrivel U, CGM Cigiemme s.r.l) which gave an approximately lambertian finish with a reflectance spectrum flat in the visible spectral region. The visible booth's wall was painted with a Munsell N7 matt emulsion paint (VeriVide Ltd, Leicester, UK). When normalized the spectral reflectance of this paint and that of the matte powder were almost identical (RMSE = 0.05) and reflected virtually the same chromaticity; in the conditions of the experiment the mean $\Delta E_{L^*a^*b^*}$ was 0.7 with a standard deviation of 0.2, i.e. color differences indistinguishable to the human eye. The test scene inside of the booth was illuminated by a spectrally tunable light source (OL 490 Agile Light Source, Gooch & Housego), based on the Digital Light Processor (DLP) technology. With this set-up it is possible to tune the color of the test scene to any arbitrary spectral composition without having to resort to metameric methods of color reproduction, e.g. monitor displays, which always need assumptions about the visual system of dichromats. The spectrally tunable light source was calibrated with a spectral resolution of 20 nm and its light was delivered to the scene from above by an optical diffuser (10DKIT-C2 25°, Newport) placed at the end of the flexible optical fiber light guide. This guaranteed a level of uniformity of about 90% over the visible part of the scene.

Between the observers and the booth there was a Styrofoam mask with a flat white surface with an aperture that allowed the observers to see the test scene. The size of the white surface was 99.5 cm (width) × 149 cm (height) corresponding to a visual angle of 57° × 79° at the distance of 93 cm. Relatively to the test scene position, the white surface was at 54 cm and the observer was at a viewing distance of 147 cm. With this configuration the visual angle of the aperture width (17 cm) and scene width (26 cm) was 10°. A similar configuration but with proportionally smaller aperture and test objects was used to test for a 2° viewing angle. The white surface was illuminated by a discharge lamp (OSRAM HQI 150W RX7s) located at 240 cm from the experimental setup and at an angle of approximately 45° such that no light contaminated the test scene. This illuminant was considered the adapting illuminant and its spectrum as reflected by the white surface is represented in Fig. 1C. The spectrum had a correlated color temperature (CCT) of 5200 K, a luminance of 30 cd/m^2 and was uniform across the white surface.

2.2. Stimuli

The stimulus for the experiment was the three-dimensional scene inside the booth which simulated objects reflecting as in natural scenes. Two geometrical conditions were tested, 10° and 2° viewing. The geometry of the scene was selected to mimic natural viewing conditions of complex objects producing shadows and heterogenic light fields to induce the perception of colored objects rather than surfaces illuminated by colored lights. The colors of the objects inside the booth were produced by selecting spectra from natural scenes obtained by hyperspectral imaging from 400 nm to 720 nm. These data were obtained from single pixels from four natural scenes of an existing database (Foster, Amano, Nascimento, & Foster, 2006; Linhares et al., 2008a). The four scenes are shown in Fig. 2 and their color volume expressed in CIELAB are represented in Fig. 3. Natural scenes in this context were interpreted as representative of our everyday environment, typically rural with vegetated areas or urban with man-made objects and buildings. Importantly, they exclude the kinds of artificial scenes constructed specifically for research. The four scenes were selected to represent rural and urban environments and their colors span a considerable volume of the color space of natural colors.

The scenes were assumed illuminated by the discharge lamp, thus with a CCT of 5200 K. This illuminant was selected to be the same as the adapting illuminant which spectrum is presented in Fig. 1C.

The test scene was viewed monocularly to avoid diplopia resulting from viewing the scene binocularly through the aperture of the Styrofoam mask located at a different plane. Because the observers were viewing the scene through this aperture the test scene appeared to contain a group of objects of an intrinsic color illuminated by the discharge lamp, rather than white objects illuminated by a colored illuminant.

2.3. Procedure

Each trial consisted of a sequence of three time intervals where the scene could be observed, separated by a dark inter-stimulus interval (ISI) of 0.5 s. Fig. 4 illustrates the sequence. In the first interval the adapting illuminant was presented, i.e., the same as the light reflected from the Styrofoam mask, for 1.5 s. Then, spectrum 1 and spectrum 2 illuminated the scene with spectra drawn from random pixels of one of the four scenes tested, lasting 0.5 s each, and separated by a dark ISI of 0.5 s. In each session, the spectra from only one natural scene were tested. For the 10° condition the 4 scenes were tested 3 times each in separate sessions in a counterbalanced design. Each observer carried out 12 sessions of 220 trials each, giving a total of 2640 test trials plus 240 control trials where spectrum 1 and spectrum 2 were made deliberately equal to estimate false alarm rates. The 2° condition was tested a few months later in the same way, except for one observer (normal trichromat) that only completed 8 sessions (2 sessions for each scene).

Thus, the design corresponds to a one-alternative forced choice (1AFC) version of a same-different task (Kingdom & Prins, 2010). The task of the observers was to indicate whether the color of the objects was the same or different. No indication was given to the observers about which type of scene was being tested.

2.4. Observers

Four normal trichromats and four dichromats carried out the experiment in the 10° condition and the same but one normal trichromat carried out the experiment in the 2° condition. The normal trichromats were students aged 20, 22, 23, and 23 years (1 male and 3 females). The dichromats were 2 protanopes and 2 deuteranopes aged 26, 41, 42, and 49 years (3 males and 1 female), respectively. Each had normal or corrected-to-normal visual acuity. Their color vision was tested with Rayleigh anomaloscope (Oculus Heidelberg Multi Color), Cambridge Color Test (Regan, Reffin, & Mollon, 1994), Ishihara plates and the Color Assessment and Diagnosis (CAD) Test (Carmona, 2006). The experiments were performed in accordance with the tenets of the Declaration of Helsinki and informed consent was obtained from all observers.

3. Experimental results

Fig. 5 shows the results of the experiment for normal observers (N) and dichromats, protanopes (P) and deuteranopes (D) for the two viewing conditions. Fig. 5A represents the average across observers of pairs of spectra identified as different. Data was based on 2640 trials for each observer except for the normal observer that did only 8 sessions in the 2° condition (see Section 2.3). Error bars represent the standard deviation across observers.

For the 10° condition, average performance is about 80% for normal observers and protanopes and about 10% lower for deuteranopes. As these results are affected by observers' criterion the discrimination

Fig. 2. Images of the four natural scenes tested. Scenes A and B are from rural environments. Scenes C and D are from urban environments. The scenes represented in A and B are from the Minho region, C is from Braga and D is from Porto, all in Portugal. They belong to an existing database (Foster et al., 2006). The colors of the scenes were simulated as illuminated by the adapting illuminant. In each trial of the experiment two pixels were selected randomly and their radiance spectra were used to illuminate successively the objects inside the booth. Each scene was tested in different experimental sessions.

index *d′* (Swets, Tanner, & Birdsall, 1961) was computed for each observer. The computation was based on the assumption of a 1AFC, same-different task by the differencing mode (Kingdom & Prins, 2010). Fig. 5B shows the average *d′* values across observers. For normal observers *d′* was about 4 and for dichromats about 3, expressing relatively high discrimination performance. To express this discrimination performance in a more familiar way the percentages of pairs of spectra discriminated were computed as if all observers had the same criterion. This was done by inverting the *d′* computations (Kingdom & Prins, 2010). These data are represented in Fig. 5C. For normal observers the discrimination was 67%, for protanopes 45% and for deuteranopes 46%. Thus, performance of dichromats was about 67% of that of normal observers. Fig. 6 represent the data in Fig. 5C for rural scenes (A and B) and urban scenes (C and D). Performance is systematically higher for urban scenes for the three groups of observers. For the 2° condition, results are similar within a few percent, no significant effect of the viewing geometry was found.

4. Predictions from models

Discrimination performance depends on the distribution of colors in natural scenes. Fig. 7A shows by the black solid line the distribution of color differences expressed in the CIELAB color space based on 10,000 pairs drawn randomly from the four natural scenes used in the experiment assumed illuminated by the adapting illuminant described in Section 2. The dashed line shows the same data for the illuminant D65. The two distributions are quite similar suggesting that the artificial illuminant used in the experiment has similar effects to the natural illuminant D65. Fig. 7B shows by the black solid line the corresponding cumulative distribution. The average value of 67% corresponds to Δ*E* CIELAB of about 24 units. This is large compared with the value for perceiving color differences in images, of about 2.4 units (Aldaba et al., 2006; Liu, Huang, Cui, Luo, & Melgosa, 2013). However, the specific value derived here was relative to the criterion assumed in the inverted calculations from d′ values. In addition, the task here was discrimination of images viewed in succession, not side-by-side, and therefore a larger threshold is expected.

A similar computation was carried out for dichromats. Under the assumption of the dichromatic model of Brettel et al. (1997) the distribution of color differences expressed in CIELAB color space was computed and is represented in Fig. 7A by a solid red line for protanopes and a solid green line for deuteranopes. These distributions have a shape similar to that for normal observers (black solid line) except that their maxima are shifted towards lower values. Fig. 7B shows the corresponding cumulative distributions. The value of 45% corresponds to a Δ*E* CIELAB of about 30 units. This suggests that the discrimination threshold for dichromats when expressed in CIELAB space is somewhat higher than that for normal observers.

Fig. 7C shows the distribution of color differences expressed in CIELAB color space computed without the L^* component, i.e., representing pure chromatic differences and Figure E the distribution computed only with the L^* component, i.e., representing pure lightness differences. Figure (D) and (F) show the corresponding cumulative data. The color codes for the lines are the same as in (A) and (B). For normal observers about 44% of pairs that were discriminated could have been discriminated by lightness alone. For dichromats this number

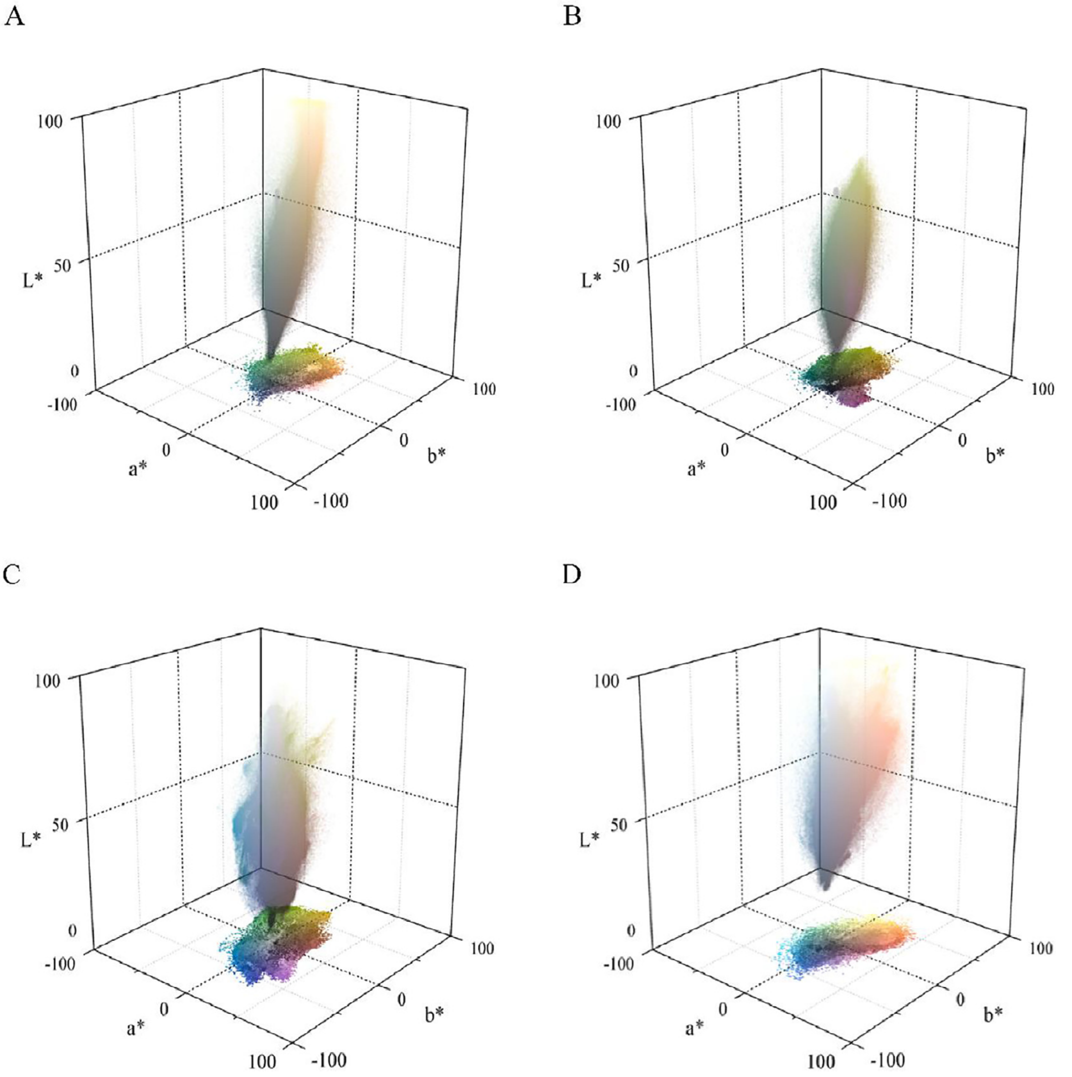

Fig. 3. Color volume of each natural scene represented in Fig. 2. The illumination was the adapting illuminant with a CCT of 5200 K and the colors are represented in the CIELAB color space for the CIE 1964 standard observer.

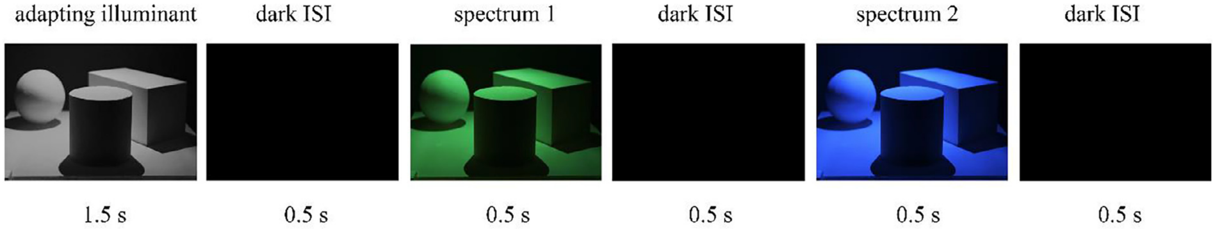

Fig. 4. Stimuli sequence of each trial. The experiment was a 1AFC single alternative same-different test. The adapting illuminant was kept on for the first 1.5 s of the trial. The two test spectra and the three dark ISI lasted 0.5 s each. The adapting illuminant was the same in all trials but spectrum 1 and spectrum 2 varied between trials.

is 50%. Thus, despite their color deficiency, dichromats use often pure chromatic cues to discriminate objects in natural scenes.

Fig. 8 represents the same data of Fig. 7A and B but represented for rural scenes (A&B, solid lines) and urban scenes (C&D, dotted lines). Color differences are systematic larger for the urban scenes which is well correlated with the performance data shown in Fig. 6.

The illumination simulated in the tested natural scenes was the same as that used for the adapting field, produced by the discharge lamp shining on the Styrofoam mask. Although this light source is different from daylight the distributions of color differences it produces are very similar, thus the discrimination levels inferred here are very similar to those expected in natural conditions.

5. Discussion

Color discrimination for dichromats with natural environment spectra was found to be about 45%, just 22% less than the corresponding performance of normal trichromats. This result translates into a reduction of 33% in dichromats' discrimination relatively to normal discrimination. Dichromats in natural environments are therefore less disadvantaged than implied by models that do not take into account the distributions of natural spectra. Model simulations suggest that the

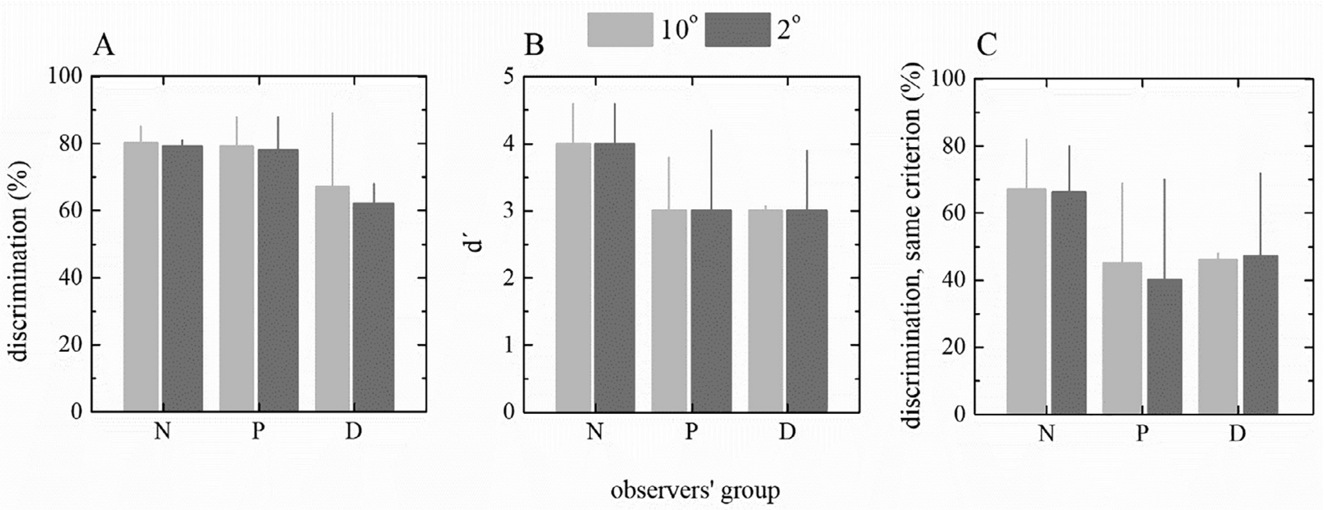

Fig. 5. Results from the experiment for normal observers (N) and dichromats, protanopes (P) and deuteranopes (D). (A) Average pairs of colors identified as different. (B) Average discrimination index d′ computed for an 1AFC, same-different task by the differencing mode (Kingdom & Prins, 2010). (C) Average pairs of colors identified as different derived by the discrimination index d′ assuming that all observers have the same criterion. Data based on 2640 trials for each observer except for the normal observer that did only 8 sessions in the 2° condition (see Section 2.3). Error bars represent standard deviation across observers.

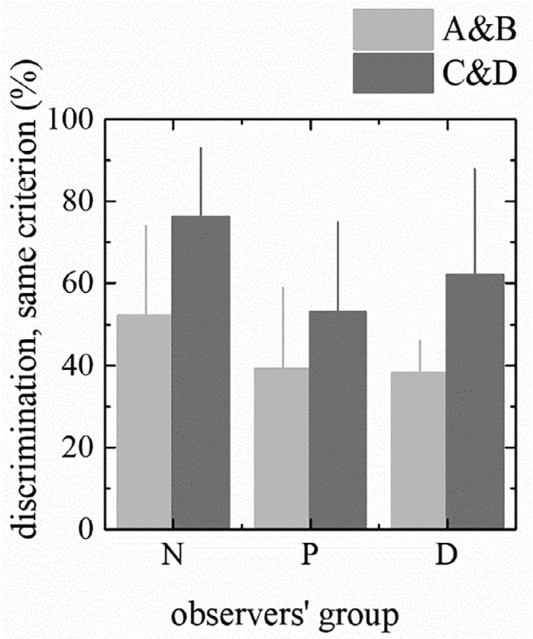

Fig. 6. Data as in Fig. 5C represented for rural scenes (A and B) and urban scenes (C and D) for the 10° condition. Data for the 2° condition are similar.

dichromatic discriminations are based 50% on lightness differences, a value that for normal trichromats is about 44%.

Discriminations for rural scenes was lower than for urban scenes. This result is consistent with the corresponding distribution of color differences shown in Fig. 8. Significantly, the estimates based on the model of Brettel et al. predict about the same performance for protanopes and deuteranopes for rural scenes but higher performance for deuteranopes for urban scenes, which is what was found in the experiment. It is possible, however, that these dichromats are large-field trichromats and use to some extent their residual red-green discrimination. Or, they use some other more complex mechanisms (see Broackes, 2010; Crognale et al., 1999). The experiment in the 2° viewing condition rules out that they use these mechanisms for color discrimination as they perform the same in both viewing conditions. Also, if the contribution of these mechanisms was substantial performance would not be consistent with the Brettel et al. model and would be higher. Thus, the good performance seems to result from the favorable distribution of colors in nature.

The results suggest that the discrimination threshold for dichromats expressed in the CIELAB color space are larger than for normal trichromats. This result is consistent with the fact that protanopes and deuteranopes have higher tritan thresholds than normal trichromats (Regan et al., 1994). It is also consistent with a study that measured thresholds for dichromats and for normal observers seeing stimuli simulated for dichromatic perception (Nascimento, Linhares, João, Santos, & de Almeida, 2015). Fig. 9 shows data drawn from that study for an average of 10 normal observers and for the four dichromats tested in the present study. Thresholds were obtained from a discrimination experiment and are expressed as a function of the hue angle. Open symbols show the data for the two deuteranopes (A) and the two protanopes (B). The solid continuous line shows the average of 10 normal observers when seeing the stimulus derived using the Brettel et al. model for deuteranopes (A) and protanopes (B). Data shows that the actual thresholds for dichromats are systematically higher than those obtained by normal observers seeing the simulation for dichromats.

Dichromats had a performance almost as good as trichromats in distinguishing colors of natural scenes in general, but for discriminating in particular between fruits and foliage the trichromats may have the advantage (Osorio & Vorobyev, 1996), consistent with frugivory being the main reason for the development of trichromacy in pre-historic primates (Mollon, 1989). The better-than-expected results of dichromats in this study could help explain why dichromacy continues to occur in modern populations and why dichromacy remains the most common form of color vision in mammals (Jacobs, 2009). Dichromacy must allow satisfactory discrimination in natural scenes, otherwise trichromacy would probably be more frequent among species of mammals. This idea is consistent with a spectral analysis suggesting that the receptors of dichromatic mammals coincide with the optimal spectral tuning predicted for discrimination in natural scenes (Chiao, Vorobyev, Cronin, & Osorio, 2000).

The analysis of pure chromatic differences shown in Fig. 7 shows that these are very frequent for normal trichromats, and that the distribution for dichromats is not dramatically different. It is well known that pure chromatic edges are common in natural scenes (Hansen & Gegenfurtner, 2009) a result that also supports the idea that dichromats are well equipped to discriminate natural objects.

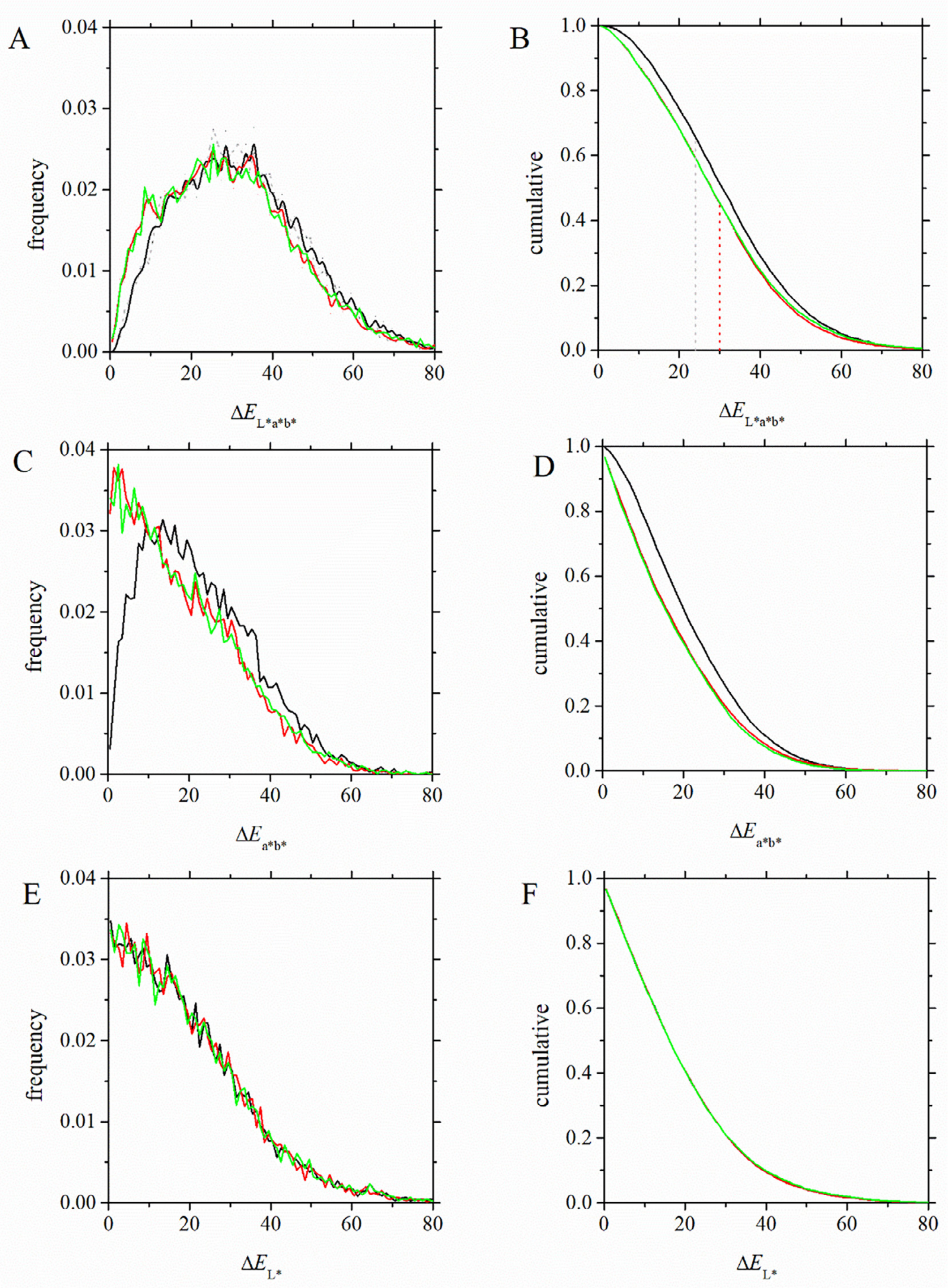

Fig. 7. Predictions from Brettel's model of dichromatic color perception. (A) Distribution of color differences expressed in CIELAB color space for normal observers (black solid line). Corresponding data for protanopes (red solid line) and deuteranopes (green solid line) using Brettel's model to predict the color perception of dichromats. Data based on a random sampling of 10,000 pairs from the 4 images tested (see Fig. 2). The dotted line shows the distribution for normal observers assuming D65 instead of the illuminant used in the experiment. (B) Cumulative data derived from the distributions in A for normal observers (black solid line) and dichromats, protanopes (red solid line) and deuteranopes (green solid line). The dotted straight lines indicate the threshold level necessary to obtain the discrimination of Fig. 5C. (C) Distribution of color differences expressed in CIELAB color space computed without the L^* component, i.e., representing pure chromatic differences. (E) Distribution of color differences expressed in CIELAB color space computed only with the L^* component, i.e., representing pure lightness differences. (D) and (F) Cumulative data for the distributions in (C) and (E), respectively. The colors of the lines represent the same as in (A) and (B). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The discrimination performance measured here was obtained with uniform colored object surfaces. Real objects are not uniform and thresholds for natural textures are known to differ from those for uniform surfaces (Giesel, Hansen, & Gegenfurtner, 2009; Hansen, Giesel, & Gegenfurtner, 2008). Nevertheless, the relative discrimination between normal trichromats and dichromats in real conditions is not expected to change much as the individual chromatic diversity of objects is likely to favor an impaired visual system.

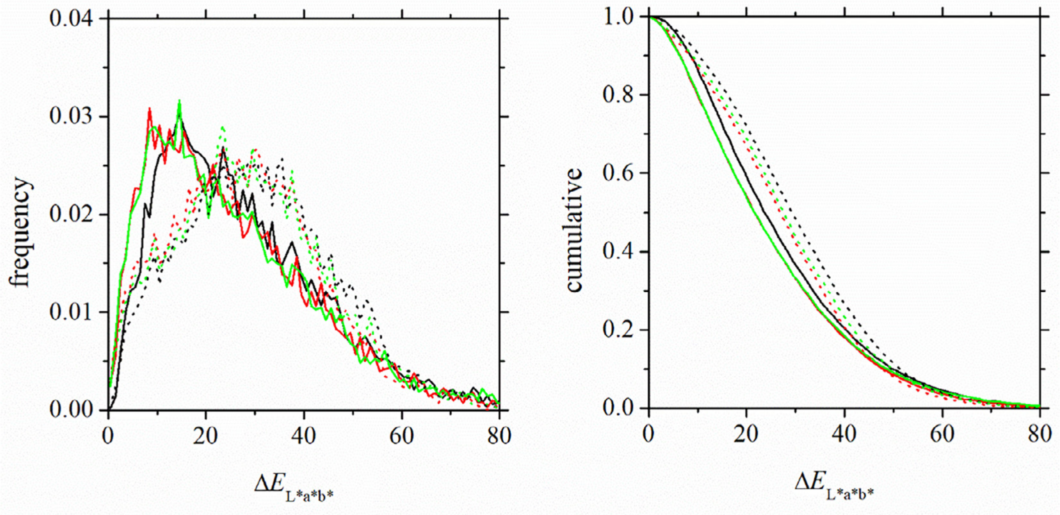

Fig. 8. Same data as in Fig. 7A and B but represented for rural scenes (A&B, solid lines) and urban scenes (C&D, dotted lines).

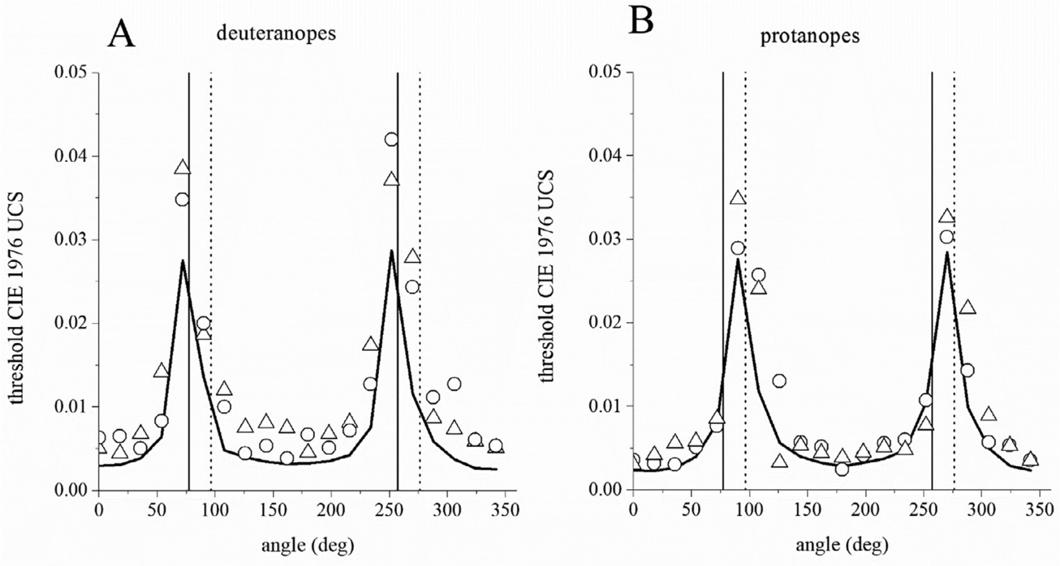

Fig. 9. Thresholds from a discrimination experiment expressed as a function of the hue angle. The open symbols show the data for the two deuteranopes (A) and the two protanopes (B) that were observers in the current experiment. The solid continuous line shows the average of 10 normal observers when seeing the stimulus derived using the Brettel's model for deuteranopes (A) and protanopes (B). The vertical lines indicate the confusion directions for dichromats, solid lines for deuteranopes and dashed lines for protanopes.

In summary, although dichromats perceive fewer colors than normal trichromats the color diversity of natural environments matches their visual capabilities and the colors they confound are infrequent. Overall, their discrimination is close to that of normal trichromats.

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Appendix A

Assume that the normal observer sees n distinguishable colors and the dichromat confounds a fraction of those colors and distinguish only n′. If the colors occur with the same frequency, the fraction of distinguishable pairs of colors for the normal would be $(n^2 - n)/n^2$ and for dichromats $(n'^2 - n')/n^2$. The ratio of the two is $(n'^2 - n')/(n^2 - n)$. Thus, if the number of discernible colors for the normal observer is $2.3 * 10^6$ (Linhares et al., 2008a,) and n′ is 7% of this value (Linhares et al., 2008b), the predicted relative level of discriminability would be about 0.5%.

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