Research Article
Vol. 42, No. 5 / May 2025 / Journal of the Optical Society of America A B245

Journal of the Optical Society of America A
OPTICS, IMAGE SCIENCE, AND VISION

Achromatic loci in normal and anomalous trichromats

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Received 8 November 2024; revised 18 January 2025; accepted 18 January 2025; posted 22 January 2025; published 21 February 2025

The stimuli that appear achromatic anchor color space and exhibit multiple properties that reflect an alignment of color vision with spectral characteristics of the chromatic environment. We examined how well this alignment is preserved in individuals with anomalous trichromacy. Observers viewed stimuli spanning a range of chromaticities and luminance contrasts relative to a nominal gray background of varying luminance, and classified the stimuli as achromatic (white or gray) or chromatic (one of eight color terms). For color-normal observers, the achromatic categories were constrained in size and tended to vary along a blue–yellow axis, with a bias toward blue. Anomalous observers had larger achromatic regions and less evidence for a blue–yellow orientation. However, the range of stimuli labeled as achromatic was often substantially smaller than the range predicted by their threshold sensitivity losses. This discrepancy is consistent with partial compensation of color perception or color naming for the altered spectral sensitivities of anomalous trichromats.

https://doi.org/10.1364/JOSAA.546890

1. INTRODUCTION

Among the vast tapestry of colors, achromatic colors such as white or gray are special because they correspond to the neutral or null stimuli that anchor the perceptual space, forming the norms relative to which all chromatic colors are referenced. For example, hue refers to the direction or way in which the stimulus differs from gray, while saturation refers to the perceived magnitude of the difference. The nature of these achromatic loci is thus important for understanding both the perceptual and neural representation of color [1].

The properties of achromatic stimuli have been explored in many studies (e.g., Refs. [2–4]). Color discrimination is best around the white or adaptation point [5–7], consistent with optimizing sensitivity relative to the norm. The perception of white also remains relatively stable across age or retinal location, suggesting that the norm is calibrated and updated to match observers with varying spectral sensitivity to a stable property of the color environment [1,4,8,9]. A further common finding is that achromatic settings are more variable along the blue–yellow hue dimension relative to orthogonal dimensions, such as reddish-green. This has been found both for relative sensitivity to different chromatic directions within the observer and for individual differences in white settings across observers [2,4,10,11]. This bias has also been explained by a match between visual coding and the statistics of the visual environment. Natural lighting varies predominantly along the blue–yellow daylight axis, and the gamut of colors within scenes also often varies most along bluish–yellowish directions [12–15]. The gain of visual responses might be set to give equal weight to the variance along different dimensions of color space, so that as the range of signals increases, the sensitivity is correspondingly reduced [12,16].

Biases in achromatic settings have also been found within the blue–yellow axis. Winkler *et al.* [10] found that chromaticities along the blue direction are more likely to be classified as achromatic than the equivalent chromatic contrasts in the yellow direction. This asymmetry could relate to the finding that we tend to discount the bluish hues of shadows [17], and may be more likely to attribute bluish hues to changes in the color of the lighting and yellowish hues to changes in the color of the surface. Related asymmetries have also been observed in color constancy, where observers are less sensitive to illuminant changes in a bluish direction compared to changes in a yellowish direction (and thus exhibit greater constancy across the bluish illuminants) [18,19]. These asymmetries may reflect higher-level inferences or priors about illumination and reflectance that could further affect achromatic percepts. For example, memory colors for objects can also bias the chromaticity that looks achromatic to an observer [20].

In the present study, we explored the nature of achromatic percepts in observers with color vision deficiencies and how these differ from color-normal trichromats. Congenital color vision deficiencies affect about 8% of the European male population, and typically result from changes in the genes encoding the photopigment opsins of the long- and medium-wavelength cone photoreceptors (L and M) [21]. Individuals who lack one of the cone types are dichromats and have only a single long- or medium-wavelength-sensitive receptor and short-wavelength-sensitive (S) cone. However, in most cases (about 6% of males), the individual has three different cone types, but the spectral peaks are shifted. In deuteranomalous observers, the normal M pigment is replaced by a pigment with a peak shifted toward the L cone, while protanomalous individuals instead have the normal M cone and a pigment with a peak shifted toward the M cone. In both cases, the reduced difference in spectral sensitivity between the longer-wavelength pigments reduces the L versus M difference signal that conveys one dimension of chromatic information. Consequently, sensitivity along this dimension is reduced relative to normal trichromats. This is detected in color discrimination or color matching tasks, which are the basis for color vision assessments, and could also be manifest as an expanded range for the stimuli that "look" white or are desaturated. However, several recent studies have explored the possibility that color coding in anomalous trichromats at least partially compensates for the sensitivity losses predicted by the cone sensitivities [22,23]. For example, suprathreshold color differences along the L versus M dimension are rated as larger than the equivalent cone-contrast differences in normal trichromats [24,25], and naming and categorizing colors, even for dichromats, can be very similar to normal trichromats [26,27]. This compensation could occur at many levels, from cognitive strategies for how colors are experienced or communicated, to gain changes in the neural responses to colors [28]. One goal of our study was to explore this potential compensation in the context of achromatic colors by examining the range of chromaticities that are judged as achromatic in normal and anomalous trichromats.

A second goal was to examine whether achromatic settings in anomalous trichromacy exhibit the same kinds of properties that are found in normal trichromacy. This includes the biases for white judgments both along and within the blue–yellow or daylight axis of color vision that were described above. Again, these biases are thought to reflect an adaptation to the chromatic statistics of the environment, and we asked whether color coding in anomalous trichromats can also support these calibrations. To explore these questions, we used a naming task where observers selected the color term describing a large sample of chromaticities and luminance contrasts spanning the nominal white point. We focus on the range of stimuli that were labeled as white or gray, and how these ranges differ between normal and anomalous trichromats. One prediction is that the percepts of the anomalous observers are equivalent to color-normal observers for stimuli that produce the same cone excitations. By this account, the achromatic settings should span an increasingly broader range of chromaticities in proportion to the observers' sensitivity loss. Since these losses are primarily for the differences in the L and M cone signals, they should largely reflect a proportional change in the L versus M contrast needed for an equivalent response. Note that this is typically what is illustrated in simulations of what the world appears like to someone with a color deficiency. However, such simulations rarely incorporate principles of adaptation and compensation [25,29,30]. This compensation leads to the alternative prediction that the category boundaries should have similar extents and properties as the color-normal observers, or in other words, that they are equivalent for the same physical stimuli, despite the differences in cone excitations. To test these alternatives and the magnitude of potential compensation, we compare the color naming responses to the observers' threshold L versus M sensitivity.

2. METHODS

A. Participants

The study was conducted at two different test sites (University of Nevada, Reno and University of New South Wales, Sydney) employing the same displays and testing procedures. The two sites were included to increase the rate of recruitment. Participants included a total of 27 observers (12 females and 15 males), with 11 completing the tasks at UNR and 16 at UNSW. Participants' ages ranged from 19 to 67 years ($M = 29.8$ years, $SD = 12.3$ years). The participant groups included normal trichromats (four in Reno and eight in Sydney), deuteranomalous observers (four in Reno and six in Sydney), and protanomalous observers (four in Reno and one in Sydney). The color vision status of each participant was assessed using the Rayleigh match on an anomaloscope (Oculus). Participation was with informed consent, and all procedures followed protocols approved by each university's IRB Board.

B. Stimuli and Apparatus

Stimuli were displayed on Display++ monitors (Cambridge Research Systems) calibrated with a Photo Research PR655 spectroradiometer. The stimulus was a 2 × 2 array of uniform square fields, each subtending 4.76 deg ×4.76 deg and separated by 0.34 deg. The total array subtended 9.85 deg × 9.85 deg and was centered on the 33.7 deg ×49.4 deg background of the display (Fig. 1). Each square was surrounded by a narrow black border to distinguish it from the background [or a dim (5 cd/m^2) border when the background was instead black]. These outlines remained on continuously, while the color within the field was pulsed at 500 ms on, 2000 ms off, as described below and shown in Fig. 1. For color naming, the four fields all contained the same color, while for the threshold measurements, the color was shown in only one of the fields, chosen randomly on each trial.

Chromaticities were defined in a variant of the color spaces developed by MacLeod–Boynton [31] and Derrington–Krauskopf–Lennie [32], and were based on the standard cone fundamentals of Stockman and Sharpe [33,34]. Chromatic stimuli were represented in terms of the signals along the L versus M and S versus LM axes at constant luminance. The space was centered on a gray point with a chromaticity equal to

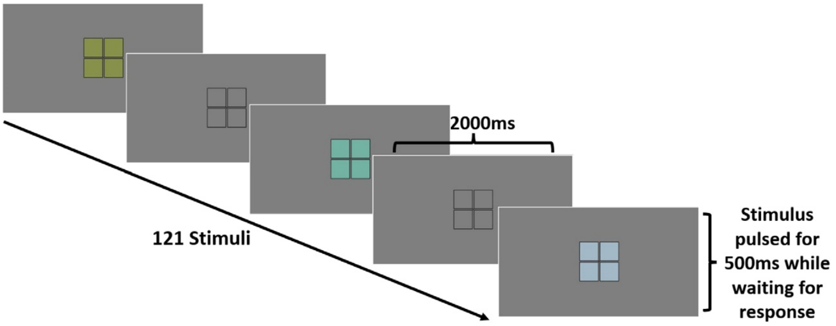

Fig. 1. Schematic illustration of the stimulus and test sequence used in the color naming task. The same chromaticity was shown in the four fields and alternated with the neutral background stimulus until the observer selected a response. In the contrast threshold task, the stimulus was instead shown in only one field randomly chosen on each trial, with observers responding to identify the field.

D65 (CIE 1931 $x, y = 0.313, 0.329$), which was used as the background chromaticity and as the neutral reference point for the stimuli. MacLeod–Boynton values along the axes were multiplied by 2500 (L versus M) or 5000 (S versus LM) to roughly equate distances (chromatic contrasts) along each axis (in terms of multiples of threshold for detecting a change from the gray origin for color-normal observers). The conversion between contrast units in our space and the corresponding l, s MacLeod–Boynton coordinates [33] was thus given by

$$\text{L versus M} = 2500 * (l_{mb} - 0.6981) \,,$$

$$\text{S versus LM} = 5000 * (s_{mb} - 0.02065) \,,$$

where 0.6981 and 0.02065 are the l, s coordinates of D65.

The experiment sampled 121 contrasts, forming an 11 × 11 grid of chromaticities centered on the nominal gray and spanning values from −60 to +60 along each axis in steps of 12 units (Fig. 2). The test stimuli always had a nominal luminance of 20 cd/m^2, but were empirically adjusted for individual observers so that they were equiluminant with the 20 cd/m^2 background chromaticity. On different runs, the background luminance was set to 0, 10, 20, or 40 cd/m^2, so that the target squares were presented as increments (background 0 or 10), decrements (40), or equiluminant (20) with respect to the background.

This common space was used for testing and analyzing the results of all observers. A limitation of this procedure is that the stimuli were not corrected for individual differences in spectral sensitivity, which, for example, can introduce metamerism errors (e.g., for the simulated D65 illuminant) or alter the stimulus directions isolating the cardinal axes for different observers [29]. These differences can be large even among color-normal observers [35]. However, they typically have not been found to predict aspects of color appearance in color-normal observers [36,37], and the principal advantage of a common space is that responses across observers can be directly compared for the same physical stimuli (rather than the same cone excitations).

C. Procedure

Participants viewed the display binocularly from a distance of 60 cm and responded with a handheld numeric keypad. The room was illuminated only by the display.

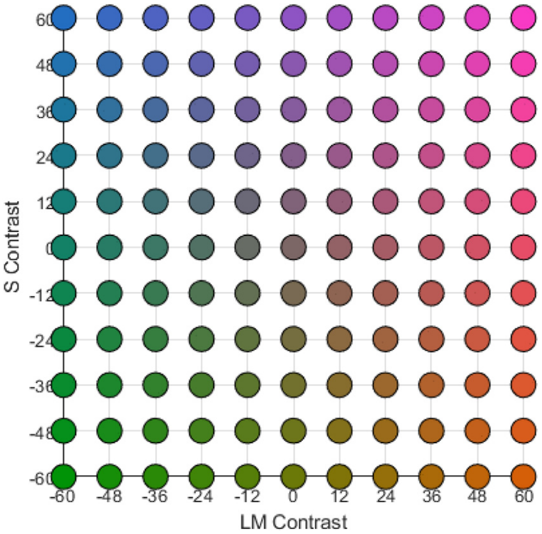

Fig. 2. Test grid of chromaticities used for the color naming experiment, defined by chromatic contrasts relative to the neutral point along the L versus M and S versus LM axes.

Prior to the naming experiment, participants first completed a minimum-motion task to determine their luminance sensitivity [38]. Settings were made for 0.95 c/deg gratings displayed within the four fields and with chromatic contrasts along the L versus M or S versus LM axes. The null values were used to adjust the relative luminances of the display primaries for all subsequent experiments. Luminances were also converted from the CIE V lambda function, measured by the spectroradiometer, to the function defined by the Stockman and Sharpe fundamentals [39].

In a second preliminary experiment, contrast thresholds were measured for detecting differences from the neutral gray along both poles of the L versus M, S versus LM, and luminance axes. The test stimulus was shown for 500 ms in one of the four fields, and contrast was varied in a four-alternative forced-choice staircase, with the threshold determined by the last 9 of 13 reversals. Each stimulus was measured three times, and the reported thresholds are based on the mean settings across the two pooled poles for each axis.

In the color naming task, the observer was shown each chromaticity in random order. The stimulus was pulsed in the squares for 500 ms on and 2000 ms off, and continued until the observer responded by pressing one of nine keys to categorize the color as white or gray, or one of eight chromatic color categories (the primary hues red, green, blue, yellow; or the binary hues orange, purple, blue–green, and yellow–green) (Fig. 1). The responses options and keys remained visible as text shown at the bottom of the display. The full set of stimuli were shown two separate times on each of the background luminances, with the order of the backgrounds counterbalanced.

3. RESULTS

Figure 3 shows the contrast thresholds for the normal and color-anomalous observers for each of the three test axes. One of the observers classified as a normal trichromat based on the assessments showed substantially elevated thresholds along all three of the axes. This observer is indicated by the triangle in the figure and was excluded from the analyses. Thresholds along the S versus LM and luminance axes did not significantly differ for three groups [S versus LM: $F(2,23) = 2.5$, $p = 0.10$; lum: $F(2,23) = 0.05$, $p = 0.95$]. For the L versus M stimuli, the thresholds ranged from 3 to 20 times higher for the anomalous observers, with large individual differences and a larger range of differences among the deuteranomalous participants. The L versus M thresholds were significantly higher for both anomalous groups compared to the color normals [deutan versus normal: $t(19) = 4.87$, $p = 0.001$; protan versus normal: $t(14) = 8.34$, $p = 0.001$]. Alternatively, the mean L versus M differences between the two anomalous groups were not significant [$t(13) = 2.01$, $p = 0.07$]. Based on these differences, the equivalent cone excitation (no compensation) prediction is that the group differences in achromatic settings should also differ by roughly the same factor as the L versus M threshold differences.

Figure 4 summarizes the color naming responses. The different panels show the pooled responses for the color-normal, deuteranomalous, and protanomalous observers for each of the four background luminance levels, while each point depicts the modal response for the color term selected for that chromaticity. The extent of the achromatic region is confined for color-normal and smaller for the 10 and 20 cd/m^2 backgrounds, while expanding for the stronger increments and decrements (0 and 40 cd/m^2 backgrounds). (Note again that the luminance contrast was set by varying the background luminance relative to the fixed test luminance.) The modal values for the deuteranomalous observers show a similar pattern but tend to cover a larger range at each background level. In contrast, the modal achromatic region for the protanomalous observers extends

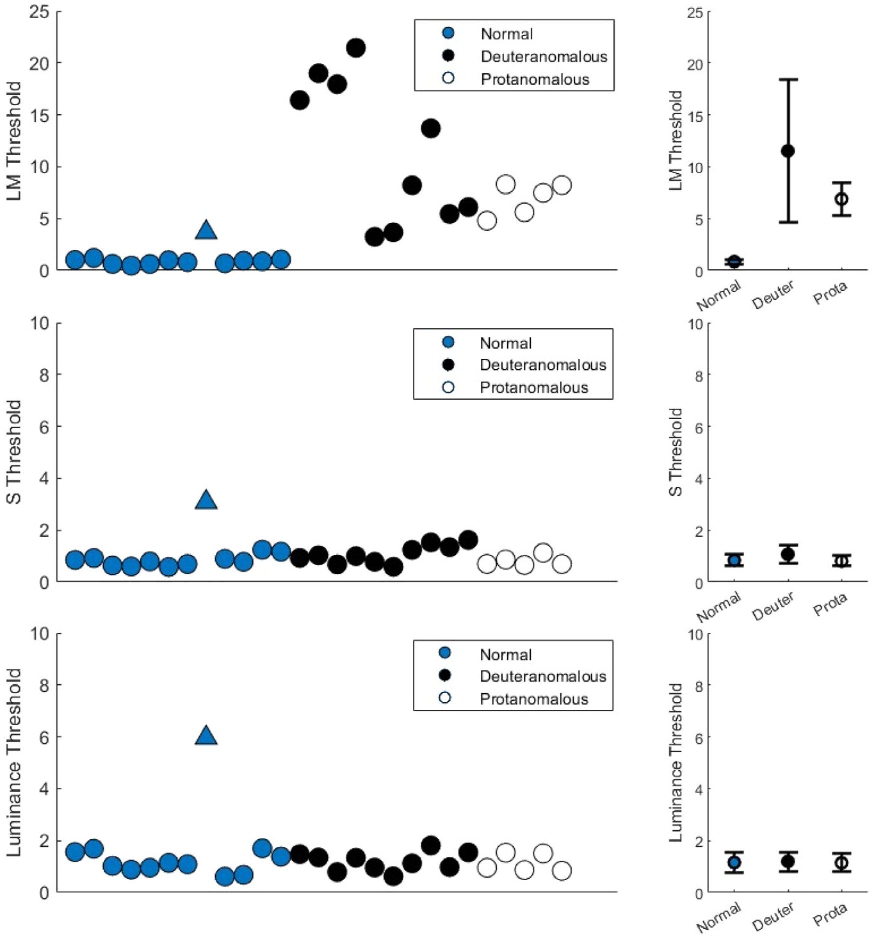

Fig. 3. Contrast thresholds for detecting a change from the neutral gray along the L versus M, S versus LM, and luminance axes, compared for the three test groups. The left panels plot the mean values for individual observers, while the right panels plot the mean values and standard deviations for each group. The observer indicated by the triangle was excluded from analyses based on their outlying thresholds.

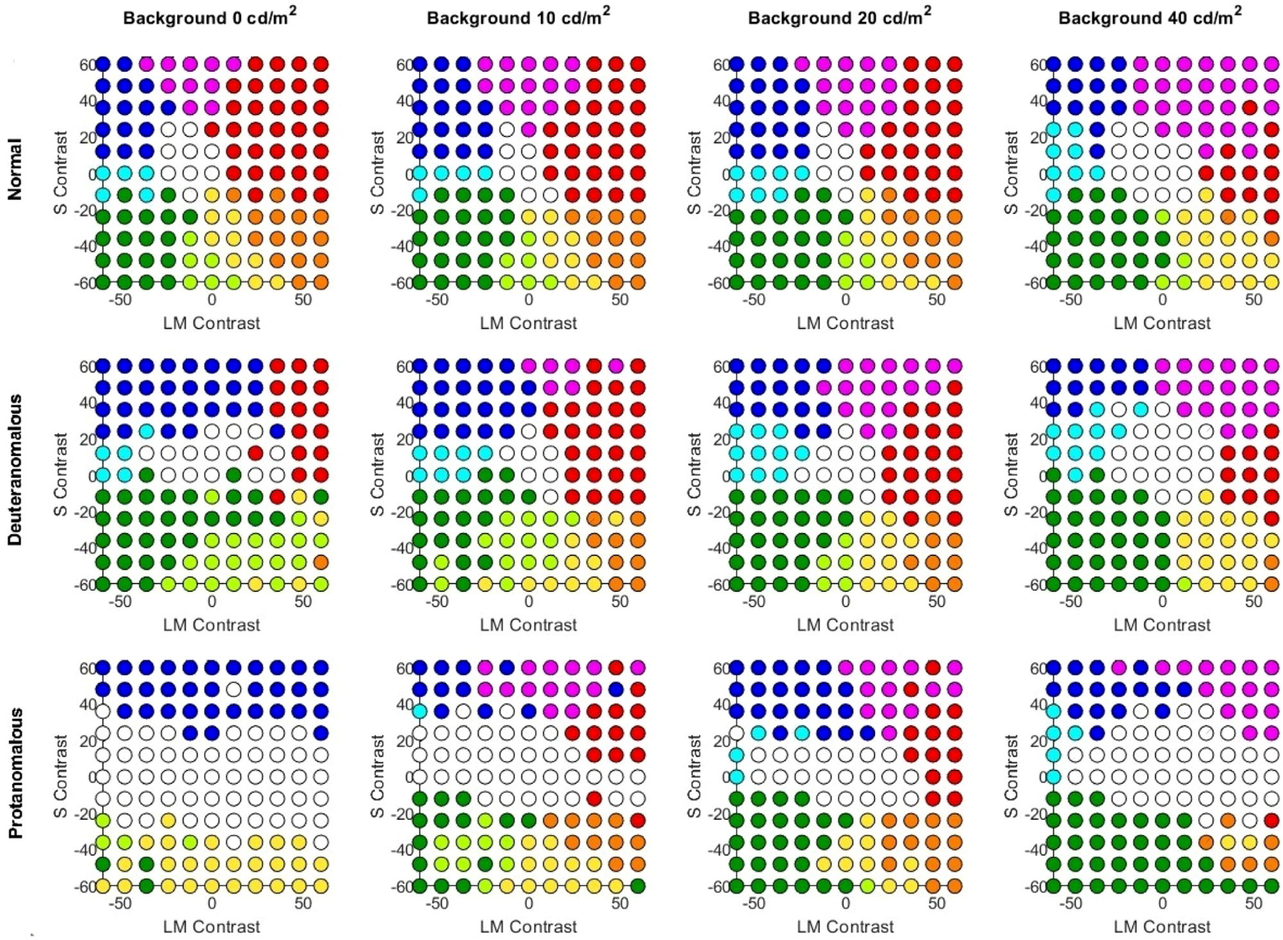

Fig. 4. Color naming responses for the three groups of observers. Each point shows the modal color response for each of the stimuli. Columns show the patterns for each background luminance. The test luminance was fixed at 20 cd/m^2 throughout.

across almost the full range of L versus M contrasts at each of the lightness levels.

As noted, for the present study, we focused only on the achromatic settings, and therefore recoded the responses as either achromatic or chromatic for subsequent analyses. We then examined the characteristics of the white category for individual observers.

The first case was a simple count of the number of stimuli in the set that were labeled as white or gray. These values are summarized in Fig. 5, and recapitulate the general pattern seen in Fig. 4—with more stimuli seen as achromatic for the high-contrast increments or decrements and with larger achromatic regions for the deuteranomalous observers and substantially larger still for the protanomalous group. Differences in the number of achromatic responses were evaluated with a repeated-measures ANOVA (three participant groups by four background luminance levels), with the dependent measure taken as the log of the percentage of achromatic responses (to assess relative rather than absolute differences). This revealed a main effect for both the color vision type [$F(2,92) = 67.3$, $p < 1e\text{-}15$] and the background luminance level [$F(3,92) = 24.7$, $p < 1e\text{-}11$], but no interaction between them [$F(6,92) = 0.47$, $p = 0.83$]. Thus, the relative differences in the mean achromatic responses for the color-normal and anomalous observers did not significantly differ with the background level.

Figure 6 shows that the groups also differed in the centroid of the achromatic category. For the color normals, the values are consistently clustered in the blue quadrant, where the S versus LM values are higher (positive) and L versus M values lower (negative) than the background gray level. This was assessed by one-sample t-tests separately evaluating the mean shifts along the S versus LM or L versus M axes, pooled over the four background luminance levels. The average values along both axes significantly differed from the neutral gray point [$LM_{\text{mean}} = -7.03$, $t(43) = -9.01$, $p < 1e\text{-}10$; $S_{\text{mean}} = 5.65$, $t(43) = 6.45$, $p < 1e\text{-}8$]. This is consistent with the greater tendency to label "blue" chromaticities as white or gray, as found by Winkler *et al.* [10]. For the deuteranomalous group, there is greater spread in the mean values, with a significant shift only along the S versus LM axis [$LM_{\text{mean}} = 3.74$, $t(39) = -1.90$, $p = 0.064$; $S_{\text{mean}} = 7.37$, $t(39) = 6.58$, $p < 1e\text{-}7$]. Thus, in this case, the centroids tended to fall in the upper two quadrants that correspond to S-cone increments, which dichromats are more likely to associate with blue [40]. Finally, for the smaller sample of protanomalous observers, a significant bias was not found [$LM_{\text{mean}} = 1.51$, $t(19) = -0.93$, $p = 0.36$; $S_{\text{mean}} = 2.36$, $t(19) = 1.25$, $p = 0.23$].

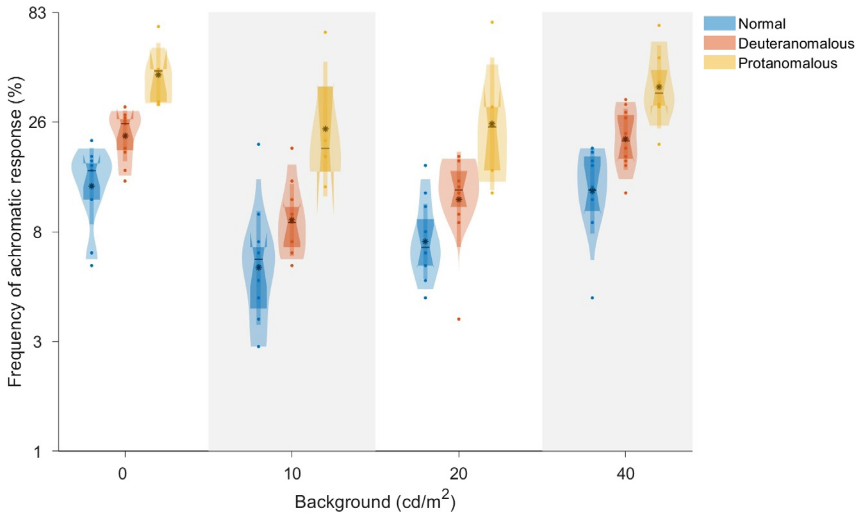

Fig. 5. Percentage of stimuli labeled as achromatic by the individual observers. The four panels are for the four different background luminance levels.

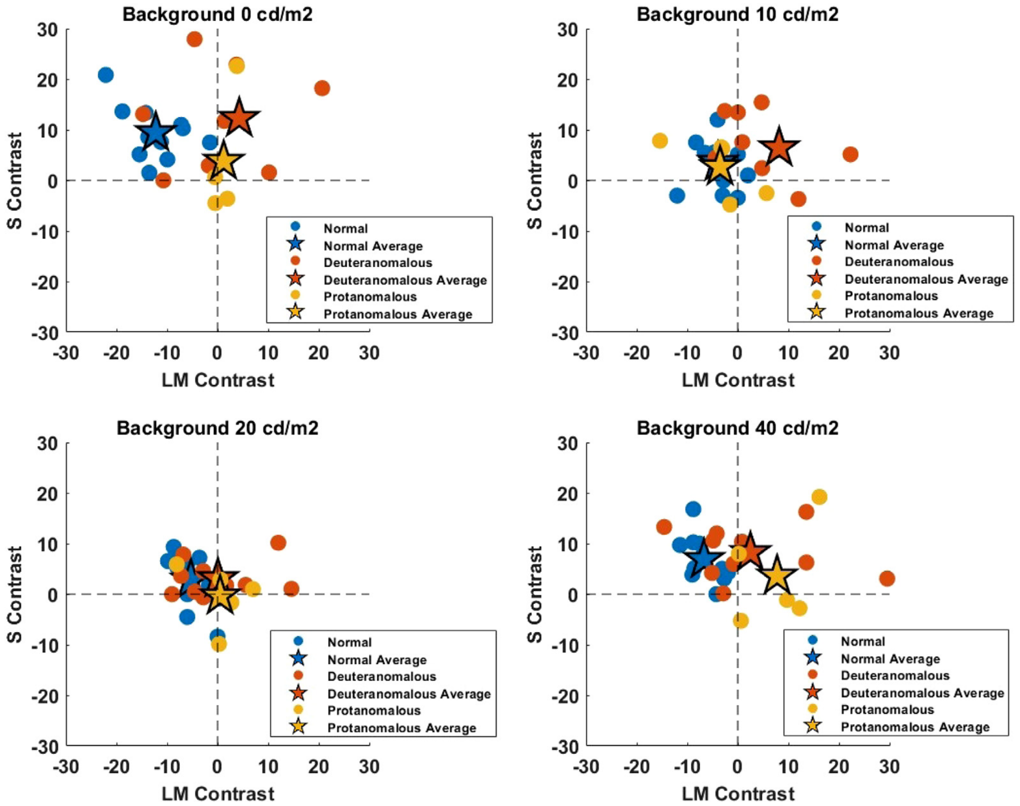

Fig. 6. Centroids of the achromatic regions shown for individual observers and the group means at the four background levels.

To further summarize the achromatic region, we fit ellipses to the responses, varying the center, major, and minor axes, and orientation to maximize the number of achromatic responses within the ellipse and the number of chromatic responses outside. For this, the two separate runs at each luminance were combined, and the fit was optimized to capture the number of stimuli that were classified as achromatic at least one of the two times, while excluding stimuli that were labeled as chromatic both times. Examples of the resulting ellipses for three individual observers are shown in Fig. 7, which also includes the ellipse corresponding to their detection thresholds (which was measured only for the 20 cd/m^2 background). This is included to emphasize the point that the achromatic region is, in fact, much broader than the threshold for detecting a change from the neutral gray stimulus.

The plots in Fig. 8 show the estimated areas of the achromatic category based on the fitted ellipses. For reference, a square block of 4 adjacent stimuli would correspond to a circular region with a radius of 8.4 and an area of 226 ($10^{2.4}$), and would occupy

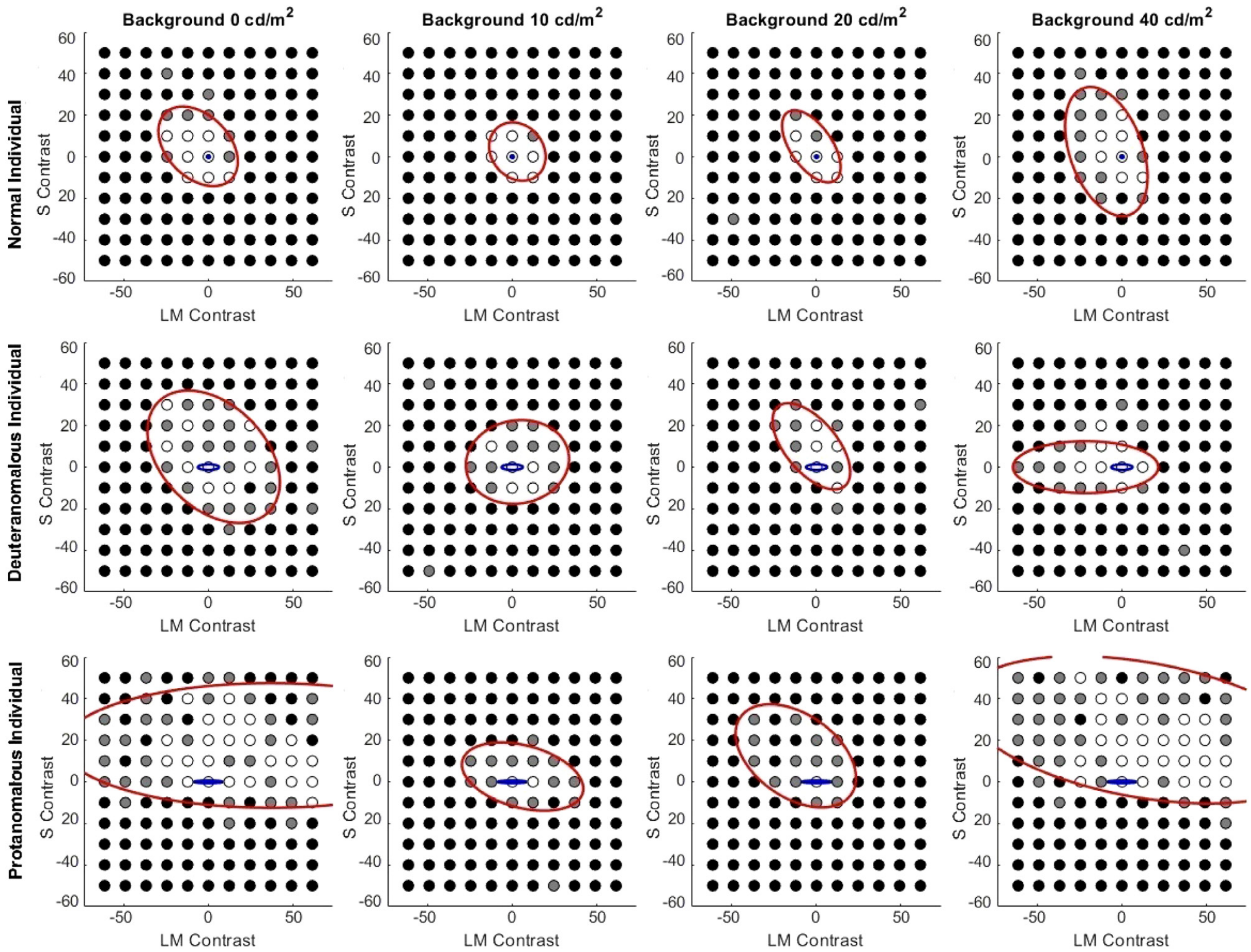

Fig. 7. Examples of the achromatic versus chromatic responses for an individual color-normal, deuteranomalous, or protanomalous observer at each of the four background luminance levels. White circles indicate the stimuli that were labeled as achromatic on both runs (white), gray as achromatic on one run but chromatic on the other, or black as chromatic on both runs. Red contours show the fitted ellipses to approximate the achromatic region. Blue ellipses show the detection thresholds for the L versus M and S versus LM axes (which were measured only for the 20 cd/m^2 background).

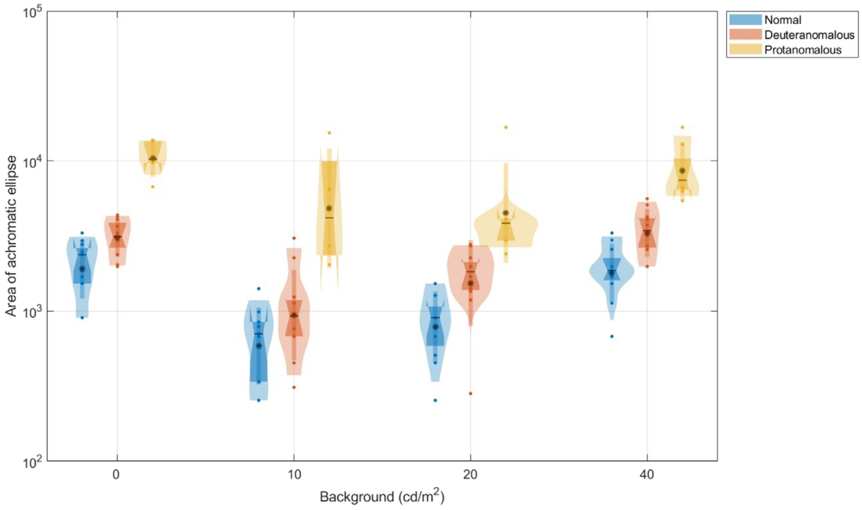

Fig. 8. Areas of the achromatic category for each observer based on the fitted ellipses. The four sets show the distributions for each of the four background luminance levels.

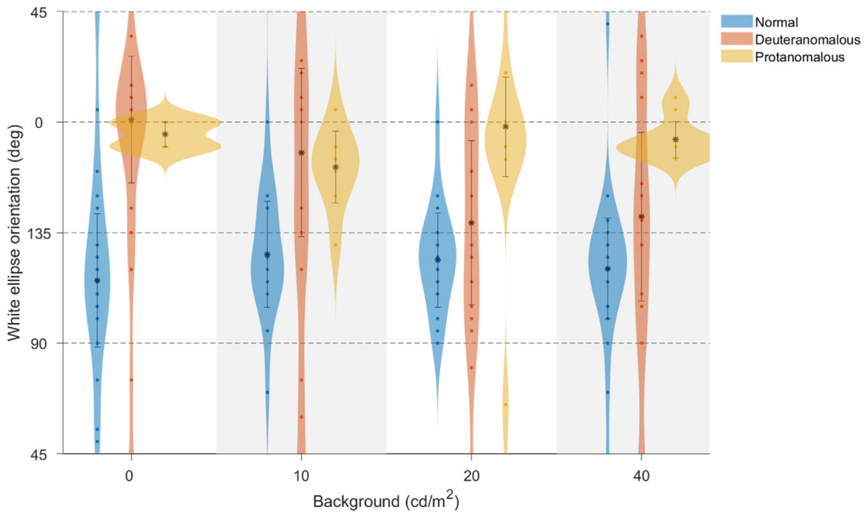

Fig. 9. Orientation of the achromatic regions for each observer and background luminance based on the fitted ellipses.

1.5% of the area of the entire palette range ($120^2 = 10^{4.2}$). For color normals, the region is constrained and somewhat larger for the deuteranomalous observers, while for some of the protanomalous observers it spanned the majority of the palette colors. Note that the areas predicted for some of these observers (e.g., the protanomalous observer in Fig. 6) actually exceeded the area of the test palette, as the ellipses were not constrained outside the palette.

Consistent with the simple achromatic counts in Fig. 5, for color normals, the achromatic region is smaller for the 10 and 20 cd/m^2 backgrounds and broadens for the stronger increments and decrements. A similar pattern is also evident for the color-anomalous observers, though the average ranges are elevated at all luminance contrasts. These differences were again confirmed with a two-way (three groups by four background levels) repeated measures ANOVA with log area as the dependent measure. There was a main effect of group [F(2,92) = 77.4, p < 1*e*-15] and luminance level [F(3,92) = 27.6, p < 1*e*-12], but the interaction was not significant [F(6,92) = 0.59, p = 0.74], again suggesting that the achromatic regions for the three groups differed by a constant scaling factor.

The final parameter we evaluated was the angle of the fitted ellipses (Fig. 9). For color-normal observers, these are again expected to fall roughly along the blue–yellow (135–315 deg) quadrants of the space, reflecting reduced sensitivity or greater achromatic spread along bluish–yellowish axes, such as the daylight locus. This is evident for the majority of color normals, whose ellipse orientations cluster around angles between 90 and 180 deg (the bluish quadrant) and 270 to 360 deg (the yellowish quadrant). In contrast, there is no clear dominant orientation for the deuteranomalous white categories. For the protanomalous, the biases are primarily along the horizontal (0–180) axis, reflecting the extended spread of the achromatic responses along the L versus M axis for these observers.

As the preceding results illustrate, for the anomalous trichromats, the regions of the gamut that were classified as achromatic ranged from similar to color normals to markedly broader for some individuals. But how much broader should they be? A prediction for this is again given by the differences in contrast thresholds. According to the equivalent cone excitation hypothesis, if the anomalous L versus M threshold was five times higher than for color normals, then a corresponding rescaling of the suprathreshold L versus M signals predicts that the achromatic category should also expand by five times [25], and the shape of the category should be more strongly elongated along the L versus M axis. This prediction was evaluated for the ellipses fit to the observers' settings on the 20 cd/m^2 background, for which thresholds were also collected. For the 15 anomalous observers, the correlations between the angle and area of the ellipses were not significant (r = 0.33, p = 0.23), and neither was correlated with the observer's L versus M threshold (area versus threshold: r = −0.19, p = 0.50; tilt versus threshold: r = −0.28, p = 0.31). There was also little relation evident when both color-normal and anomalous observers (n = 26) were included in the analysis (area versus threshold: r = 0.14, p = 0.50; tilt versus threshold: r = −0.14, p = 0.50).

To further explore this, we also compared the achromatic areas to the relative sensitivity losses for each observer. The predicted scaling was based on the average values for area and threshold for the color-normal observers. The results are shown in Fig. 10, where the dashed lines plot the predicted increase in area for a given increase in threshold. Note that because the S versus LM thresholds were similar across groups, the predicted change in area should primarily scale with the changes in the L versus M sensitivity. Note also that we again measured thresholds only for the 20 cd/m^2 background and used this threshold for all of the predictions. The different slopes of the predictions reflect the differences in the achromatic regions for different luminance contrasts, but are not corrected for possible differences in the chromatic contrast thresholds at the different luminance contrasts (though luminance contrast tends to have weak effects or can even facilitate the detection of chromatic contrast; [41,42]).

For the deuteranomalous observers, the area of the achromatic region increases relatively little despite their higher thresholds, even when these thresholds were up to 20 times higher than the color-normal values; and all of the estimates are below the predicted ratio, a difference that is highly significant

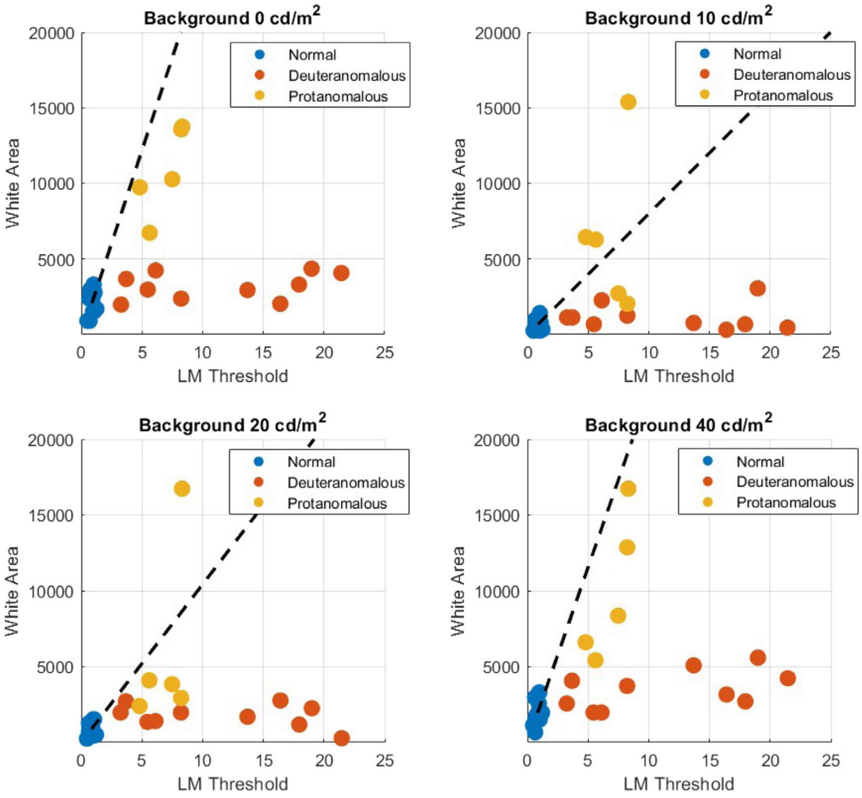

Fig. 10. Comparison of the area of the achromatic category to the contrast detection thresholds for the anomalous observers. The dashed line shows the predicted increase in area with L versus M threshold, assuming the area increases in proportion to the threshold.

based on a sign test (for each background, 10/10 fall below the prediction, $p < 0.0001$). This is consistent with a suprathreshold compensation for their chromatic judgments. Errors in the threshold-scaled predictions would vary the slope of the predicted line, but would have to be implausibly large to account for the nearly flat distribution of values for the deuteranomalous observers. Conversely, the protanomalous observers show a more variable pattern, with a number of the values trending with the predicted change. Thus, for these observers, there is less evidence for compensation in this task.

4. DISCUSSION

In this study, we explored properties of the achromatic category of color and how it varies among observers with normal or anomalous trichromacy. "Gray" is part of the continuum of unique hues, but is special because it corresponds to the null point of all chromatic sensations. It is the only unique color for which a measurable neural substrate can be identified (since the neutral percept corresponds to the neutral point for chromatic adaptation and thus a neural norm in the system [1]). In contrast, the basis for other unique hues (such as pure red or yellow), and whether they really are unique, has been increasingly challenged [13,43–45]. How the achromatic category varies among or within observers is, therefore, especially important for understanding the representation of color. In our case, we did not specifically examine the stimulus that looked purely achromatic or unique gray, but rather the range of stimuli that are classified as achromatic. As illustrated in Fig. 7, this range can be substantially broader than the threshold for detecting a chromatic signal, since even though a hue difference is identifiable at the detection threshold itself [46,47], the achromatic category includes "off-whites," which may be tinged with a hue but are classified by the observer as primarily neutral.

A principal aim of our study was to examine to what extent the properties of the achromatic category in anomalous trichromats preserved characteristics of white settings in normal trichromats. The extent to which achromatic settings are stable across observers with varying trichromacy indicates mechanisms that are shaped by consistent properties of the color environment, rather than variable sensory input. It should also be noted that our relatively large-field stimuli (9.8 deg) may have favored compensation, as color-deficient observers tend to show reduced deficits when the field size is increased [48,49].

With regard to compensation, the achromatic locus itself is similar in the color-normal and anomalous observers. This could be achieved if the neutral point for different observers is calibrated for a common stimulus through adaptation in the receptors, or in the balance of cone inputs to opponent mechanisms [27,50,51]. This adjustment is also similar to the ways in which white settings are compensated for variations in other factors, such as lens or macular pigment density [4,8,9,52].

A second potential calibration is the spread of the achromatic category and whether this tracks the distribution of stimuli in the color environment. As noted, for color-normal observers, the white settings show a consistent blue–yellow bias, potentially reflecting adaptation to the blue–yellow bias in environments [12,15]. Our results replicate this bias for the normal trichromats but did not reveal a similar pattern in the anomalous observers, where the range of achromatic settings was, for many observers, not only expanded but also less consistently oriented, especially for the protanomalous observers. It is possible that the loss of L versus M sensitivity prevents the system from more fully calibrating for this feature of the stimulus diet. However, in other ways, the blue–yellow dimension is faithfully represented in the anomalous observers. For example, hue naming is similar to normal trichromats [26,27], and a recent study found that the equilibrium locus for the blue–yellow axis is similar to the daylight locus for both normal and anomalous trichromats, despite the large differences in their spectral sensitivity [53]. Blue–yellow biases in color constancy also appear partially preserved in anomalous trichromats [54].

A further putative match to environmental colors that we examined was the potential difference between the achromatic percepts for chromaticities along the bluish versus yellowish directions of the color space. As noted, detection of illuminant changes is worse for blue than yellow [19], and Winkler *et al.* [10] found that chromaticities in the blue quadrant of the cone-opponent space were more likely to be classified as achromatic, which may reflect a tendency to attribute bluish tints to the lighting. Our results again confirm this bias for the color-normal observers. For the deuteranomalous observers, the centroid of the category was instead more variable and more generally shifted toward higher S versus LM levels. This could again represent a partial manifestation of the blue bias, as stimuli along this direction of the color space may be perceived as predominantly blue by color-deficient observers [40].

A final compensation we examined was in the area or range of stimuli that were classified as achromatic. As reported by Winkler *et al.* [10], the achromatic category expands for both increments and decrements (though the present results did not reveal clear differences between the equiluminant background and the 10 cd/m^2 background). A similar average trend is also observed for the color-anomalous observers, yet they tend to classify more stimuli as neutral across all levels, as if the achromatic regions are increased at all backgrounds by a similar factor. This is expected from their reduced chromatic sensitivity. However, as shown in Fig. 10, the magnitude of this difference was often substantially less than predicted by their detection thresholds. This suggests that once stimuli exceeded threshold, they were more rapidly classified as chromatic. Evidence for this suprathreshold contrast gain has been observed in a number of behavioral studies [24,55–57], and has been supported by the responses to color contrast in early visual cortical areas [28]. This result is also similar to the perception of spatial contrast. The contrast sensitivity function is bandpass, yet when the contrasts are above threshold, the function becomes flattened, pointing to greater amplification for higher spatial frequencies that offsets their lower threshold sensitivity [58]. However, our study does not reveal the basis for the compensation in the achromatic category, which could range from actual neural gains to learned associations between stimuli and how they are labeled and communicated. Comparing compensation across tasks and in the same observers (e.g., Ref. [56]) will be important for clarifying the nature and number of sensory and cognitive processes shaping color perception and behavior.

In all of these effects, there were large individual differences. These differences are a hallmark of anomalous trichromacy, such that the threshold losses or Rayleigh matches are often a poor predictor of performance [22]. However, the basis for these differences also remains poorly understood. In general, the compensation for contrast (i.e., in the range of the achromatic category) was only partial. This may be because of intrinsic factors that limit how the system can adjust its gain. For example, parvocellular cells encode both chromatic and luminance contrast, and thus must adjust their gain based on both types of input. This may prevent more complete compensation for the selective chromatic losses [29,59].

We also observed pronounced differences between the deuteranomalous and protanomalous groups. The latter exhibited much larger achromatic categories, even though the threshold losses were, on average, more moderate. The settings thus provided less evidence for compensation. We are not sure of the basis for these differences and cannot rule out sampling biases or biased threshold estimates because of the small number of participants tested. However, overall, our results are consistent with many other lines of evidence suggesting that the perceptual experience of color in many anomalous trichromats is not as impoverished as their threshold sensitivity predicts.

Funding. National Eye Institute (EY010834); National Institute of General Medical Sciences (P30 GM145646).

Disclosures. The authors have no conflicts to declare.

Data availability. Data from the study are available upon request.

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