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Characterization of Red-Green and Blue-Yellow Opponent Channels

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Abstract. *The responses of opponent channels have been modeled in the past as a linear transformation of cone absorption values L, M, S. The authors asked two related questions: (i) which form of transformation is psychologically most plausible and (ii) is a linear transformation the right model, in the first place. The authors tested positions of unique hues for seven subjects in an xy chromaticity diagram as well as in a Boynton–MacLeod chromaticity diagram in log-coordinates. The results show that neither of the two opponent channels can be adequately approximated by a single straight line. The red-green channel can be approximated by two straight lines. The blue-yellow channel can be approximated by a quadratic function, whose middle section coincides closely with the daylight locus. These results show that linear models do not provide an adequate description of opponent channels. Our further analysis shows that there is a correlation between the red and the green directions.* **©** *2007 Society for Imaging Science and Technology.*
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INTRODUCTION

A trichromatic theory has been dominant in the field of color vision since the time of its formulation. It was originally proposed by Thomas Young[1] and then popularized by Helmholtz.[2] According to this theory, there are three receptors in the human eye that produce color sensations of blue, green, and red. Other colors are produced by combinations of these three. Despite its success in accounting for various color phenomena, the theory has failed to explain some important phenomena such as color blindness, simultaneous color contrast, color afterimages, etc. These color phenomena are explained by the opponent process theory proposed by Hering.[3] According to the opponent process theory, color is coded in the visual system in three channels: red-green, blue-yellow, and bright-dark. Green is a negative red, and blue is a negative yellow. As a result, no color appears simultaneously both red and green or blue and yellow. The theory received considerable attention after it had been tested and confirmed by Hurvich and Jameson's binocular fusion experiment.[4]

There are currently two theories accounting for the opponent color mechanisms. One postulates three stages and the other postulates two (Hurvich and Jameson suggested that two stages are sufficient[5]). Vision science and the psychophysics community use a three-stage theory: (1) LMS cone excitation, (2) cone-antagonistic processing that can be derived as a linear transformation of the first stage, and (3) a higher-order chromatic mechanism of the cone-antagonistic information. For the third stage, there exist two different chromatic mechanisms to obtain unique red and unique green, and one single mechanism for unique blue and unique yellow.[6–8] A more detailed description of the three-stage theory can be found in the recent work by Wuerger, Atkinson, and Cropper.[8] The two-stage theory is widely used in imaging systems research and applications.[9–18] Essentially, this theory takes the first two stages from the three-stage theory and ignores the third one, assuming that the third stage contributes little. By doing this, the two-stage theory is computationally quite simple because it does not include the nonlinear transformation of the third stage. But the computational simplicity of the two-stage theory comes at the price of providing a less accurate description of the color coding in the human visual system. A natural question is whether the approximation errors in the two-stage theory are justifiable. For example, if the errors are smaller than individual variability, then eliminating these errors will have no practical consequences for the color imaging industry. The main motivation behind our study is to provide empirical results that shed light on this question.

Our results show that an accurate description of each observer's color judgments requires the third stage, as suggested by the three-stage theory. Furthermore, we provide evidence showing that the blue-yellow channel cannot be modeled by a single straight line (contrary to Wuerger et al.'s finding). Finally, our results strongly suggest that these nonlinearities are not small as compared to individual variability and, therefore, should be included in imaging applications,

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such as image quality prediction, compression, broadcasting, color management, etc.

The human visual system acquires spectral information by means of three types of cones with maximum sensitivity in the, long, medium, and short wavelengths (L,M,S). This information is then represented by the responses of three opponent channels. There has been a substantial amount of research on the transformation between the responses of cones (LMS) and the responses of opponent channels (OPP). Most transformations have been assumed to be linear and are represented as a 3×3 matrix. There is also another device-independent space that is used to represent colors. This is the CIE XYZ space.[19] CIE XYZ is often used in engineering applications. The transformations between XYZ and OPP and between XYZ and LMS have also assumed to be linear by Smith and Pokorny,[20] Stockman, MacLeod, and Johnson,[21] and Stockman and Sharpe.[22]

The nature of color representation is critical in the color imaging industry. When images are processed, one tries to minimize the perceived error between the transformed and the original images. It is, therefore, important to know which space provides an adequate representation of the color percept, so that the error can be computed in this space. Visible difference predictors are computational tools that try to accomplish just that.[16–18] Color images are often represented in the CIE XYZ space. But the percept uses the OPP space. Therefore, the visible difference predictors have to transform the former into the latter before the perceived difference is computed. As pointed out just above, the imaging community assumes that a linear transformation can be used to characterize the relation between these two spaces. However, if a linear transformation is not adequate, the visible difference will not be predicted accurately. Another application of OPP space is found in the compression of images to utilize the fact that the human eye is not as sensitive to chromatic values as it is to luminance. Therefore, the human visual system can afford to lose more information in the chrominance signals than in the luminance signal. In this application, precise decomposition of images into opponent colors is a key factor for more effective and optimal compression results.

There has been growing evidence indicating that the linearity assumption may not be valid.[23–29] Before we discuss details of the violations of the linear model, we introduce five different transformations between XYZ and OPP and highlight differences and similarities among them. These transformations will be called Zhang,[9] Hurvich,[10] Flohr,[11] Hunt,[12–14] and Wandell.[14,15] Each of these transformations is represented as follows:

$$\begin{bmatrix} X \\ Y \\ Z \end{bmatrix} = [A]\begin{bmatrix} O_1 \\ O_2 \\ O_3 \end{bmatrix} = [C_l \;\; C_{rg} \;\; C_{by}]\begin{bmatrix} O_1 \\ O_2 \\ O_3 \end{bmatrix}, \qquad (1)$$

where C_l, C_{rg}, and C_{by} are the columns of A. The matrices are described in detail in Appendix A.1 (available as Supplemental Material on the IS&T website, www.imaging.org).

The columns of A provide isoluminant and isochrominant modulations in the CIE xy chromaticity diagram: C_l specifies the direction of isochrominant modulation and C_{rg} and C_{by} define the directions of isoluminant modulation. For the isoluminant modulation that isolates the red-green opponent mechanism, the response of the blue-yellow mechanism is supposed to be zero. Similarly, the red-green mechanism response to the blue-yellow stimulus also should be zero. The two opponent-color directions specified by the vectors C_{rg} and C_{by} for each of the five transformations are shown in Fig. 1. The vector C_{rg} is the direction of the red-green channel and C_{by} is the direction of the blue-yellow channel. Unique spectral hues (green, blue, yellow) as identified by Hurvich and Jameson[4] for subject DJ are represented in Fig. 1 as circles.

The transformations of Hurvich and Flohr are almost identical. Let us assume that Hurvich and Jameson's unique hues shown in Fig. 1 are an adequate representation of colors in the human visual system. (Recall, however, that there is individual variability with respect to unique hues.) Then, the transformation by Hurvich and Flohr seems to be the best for both blue and yellow. However, in the case of green, the model by Hunt or Wandell would be better than the one by Hurvich and Flohr. Clearly, none of these transformations seem to be adequate for all three unique hues.

The question of psychophysical plausibility of linear models has been examined by Larimer, Krantz, and Cicerone[6,7] Burns, Elsner, Pokorny, and Smith,[23] Ayama, Nakatsue, and Kaiser,[24] Ikeda and Uehira,[25] Chichilnisky and Wandell,[26] Zaidi,[27] Webster, Miyahara, Malkoc, and Raker,[28,29] and Wuerger et al.[8] Some measurements were performed with a mixture of monochromatic lights and others with computer generated stimuli.

Larimer et al.[6] reported that the blue-yellow opponent channel (red-green equilibria) satisfied Grassmann-type additivity laws. Specifically, the combination of unique blue

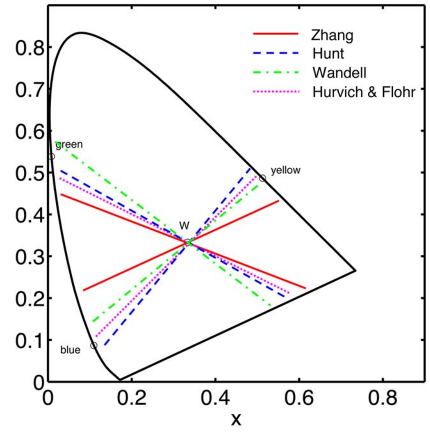

Figure 1. Opponent-channel directions of five opponent-channel matrices in the CIE xy chromaticity diagram. The point "W" is the equal energy "white."

and unique yellow remains an equilibrium color (neither red nor green). However, another experiment conducted by them showed nonlinear additivity in the red-green opponent system (blue-yellow equilibria).[7] A similar result was described in the most recent study by Wuerger et al.[8] From the findings of nonlinearity of unique red and unique green in cone space, they postulated that there are three chromatic mechanisms required to account for the four unique hues: two color mechanisms that yield unique red and unique green, respectively, and one chromatic mechanism for unique blue and unique yellow. Burns et al. noted from two observers that constant hue loci were typically curved (this is called the Abney effect[30]) in the chromaticity diagram.[23] Each of their unique hue loci was fairly straight except the curved unique blue locus. However, their unique reds were not collinear with unique greens. Similar results are found in Valberg's determination of four unique hue curves.[31]

Rather than using the mixture of monochromatic lights as in Larimer et al., Burns et al., Ikeda and Uehira, and Ayama et al.'s experiments, Chichilnisky and Wandell used stimuli generated on a computer monitor.[26] They also concluded that the opponent classification was not linear and described it by using a piecewise linear model. Recently, computer generated stimuli have been widely used to measure not only the loci of unique hues, but also the loci of constant hues,[32,33] and all the loci look similar to those of previous findings with monochromatic color stimuli.[34,35]

A recent study by Webster et al. is quite representative for the current understanding of the relation between the cone absorptions and opponent channels.[28,29] They measured the direction of unique hues for several subjects. In their experiment, the initial adaptation to the gray background lasted 3 min, and the intertrial adaptation lasted 3 s. The color stimulus was presented for 280 ms. Each trial presented moderately saturated stimuli. Figure 2 shows the opponent-color directions of one of their subjects in the *xy* chromaticity diagram. The red-green direction cannot be approximated by a single straight line. The same is true for the blue-yellow direction.

In this paper, we provide a further test of the linearity assumption for the transformation from LMS to OPP and XYZ to OPP. Similar studies on the unique hue characterization have been done in the past and the results described in this paper conform to those former findings. Compared to previous studies, our psychophysical experiment used more subjects, and the exposure duration was unlimited. Using unlimited exposure duration more closely approximates natural viewing conditions. Our discussion focuses on the correlation between the red and the green directions, and on the relation between the daylight locus and the entire blue-yellow channel. It is important to point out that when we refer to opponent colors, we refer to colors in the opponent (perceptual) color space, rather than to colors in the chromaticity diagram. Specifically, in the chromaticity diagram, opponent colors do not have to lie on a single straight line going through the point representing an achromatic color. In fact, they do not.

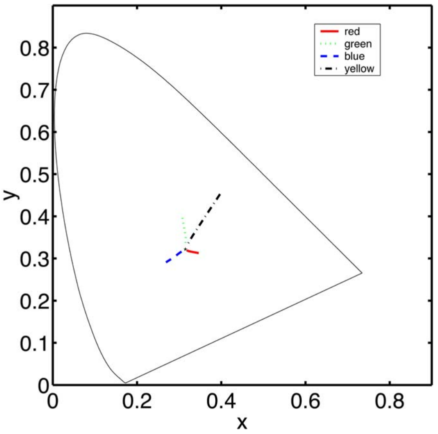

Figure 2. Opponent-color directions of one subject in the *xy* chromaticity diagram measured by Webster et al. (p. 1548, Fig. 2, observer EM).[29]

Before testing the subjects in the main experiment, we had them perform the standard color deficiency tests.

COLOR DEFICIENCY TEST

Subjects

We tested five male observers (SL, WJ, OA, GF, KL), one of whom is the first author of this paper, and two female observers (BZ, YB). We used two tests: Ishihara's test for color deficiency[36] and the Farnsworth–Munsell 100-hue test.[37] Five observers wore normal untinted glasses for their eyesight correction. Both tests were done under daylight D65 simulated by a viewing booth (GretagMacbeth SpectraLight II, 617 Little Britain Road, New Windsor, NY 12553). Subjects SL, BZ, WJ, GF, and KL had perfect scores for all 25 Ishihara plates, while YB and OA responded incorrectly on some plates. Specifically, OA responded incorrectly on plate #19, and YB on plates #5, 7, 9, 12, 16, 17, and 22. According to the instruction for the interpretation of the test result, YB's color vision is not regarded as normal, but since she read 15 plates out of the first 21 plates normally, she cannot be treated as a color deficient, either. In fact, her result of the Farnsworth-Munsell 100-hue test indicated she had good color discrimination ability as described next. With a more sophisticated color vision test such as anomaloscope, YB was found to have a normal color vision.

The Farnsworth–Munsell 100-hue test directly measures the subject's ability to perform general color discrimination. It enables subjects with normal color vision to be categorized into the classes of superior (total error score is less than 16), average (total error score from 16 to 100), and low (total error score greater than 100) color discrimination. Figure 3 shows the results for each subject. Subjects SL, GF, and KL achieved a zero error score on this test. These subjects also scored perfectly on the Ishihara test. BZ and WJ's color vision can also be treated as superior since they had only one wrong arrangement of purplish colors and cyanish colors, respectively (their error score was 4). Recall that these subjects obtained perfect scores on the Ishihara test. Subjects YB and OA gave more incorrect answers with error score 16, and thus can be categorized as normal observers with

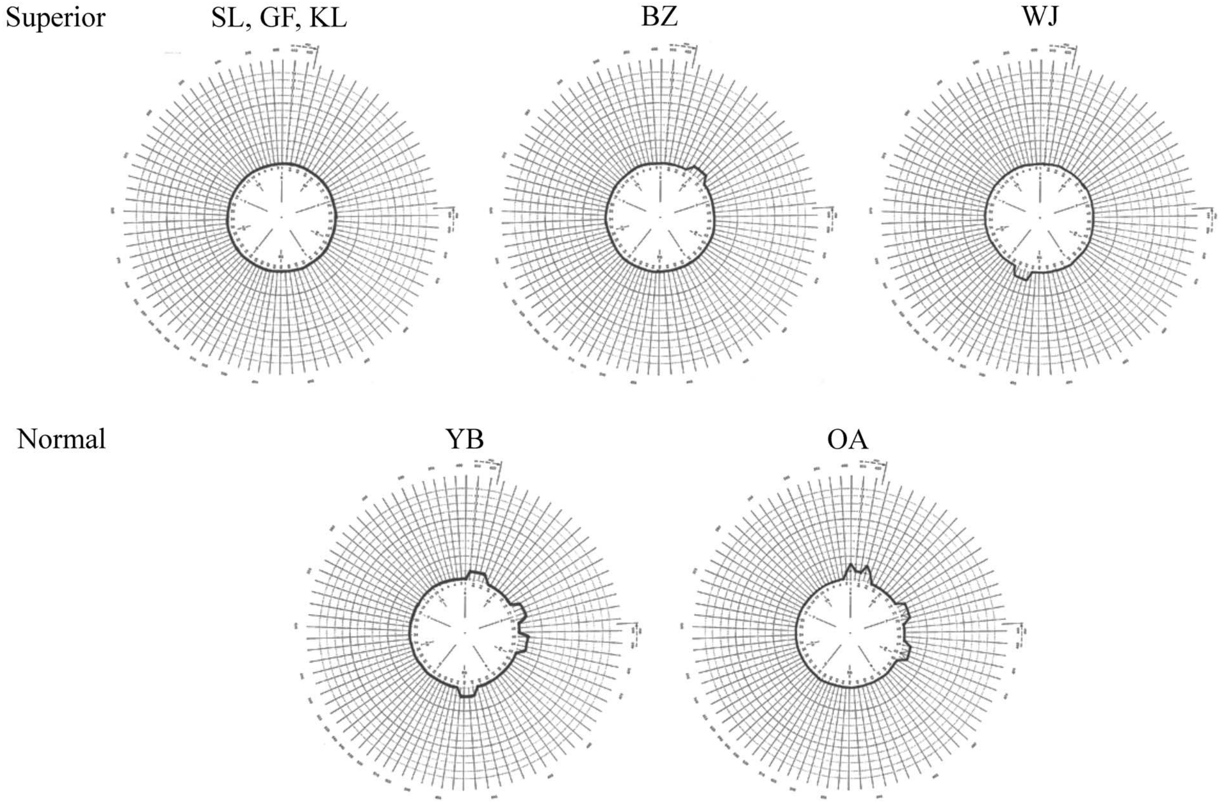

Figure 3. Results of the seven subjects in the Farnsworth-Munsell 100-hue test. Perfect performance is represented by a perfect circle. The number of bumps represents the number of errors, and the height of the bumps represents the magnitude of each error. For example, OA made four errors.

average color discrimination ability compared to the other subjects.

EXPERIMENT

General Methods

Apparatus and Stimuli

A calibrated cathode ray tube (CRT) computer monitor (EIZO FlexScan T965, EIZO Nanao Technologies Inc., 5710 Warland Drive, Cypress, CA 90630) was used to display stimuli in a darkened room. The calibration was done by a PR705 spectroradiometer (Photo Research Inc., 9731 Topanga Canyon Place, Chatsworth, CA 91311-4135) using a procedure similar to that described by Berns, Motta, and Gorzynski.[38] To evaluate the performance of the calibration, 125 patches using the combination of five digital values (0, 32, 96, 145, 245) were generated and tested. CIE color differences were computed between the measurements from the patches and predictions from the calibration. The results showed average $\Delta E^*_{ab}=0.5$ and maximum $\Delta E^*_{ab}=1.62$.

The subject viewed the stimuli from a distance of approximately 20 in. A square patch with size 2×2 deg^2 was shown at the center of the monitor. The background was uniform neutral gray color with the chromaticity value of ($x=0.33$, $y=0.33$) and a luminance value of 20 cd/m^2.

Ten stimuli were generated for each color (red, green, blue, yellow) by using different mixtures of the red, green, and blue phosphors of the CRT monitor. For example, to generate the ten red stimuli that were used to find unique red, each patch was generated by setting the red phosphor to its maximum intensity, the green phosphor to one of ten evenly spaced digital values ranging from 15% to 85% of its maximum, and the blue phosphor to a random value. These ten values for the green phosphor produced ten different levels of saturation of the red patch. This mixture looked red, but not necessarily unique red. The range of the random setting of the blue phosphor corresponded to $\pm 15\Delta E^*_{ab}$ units around the unique red of subject SL (this range contained unique reds of the remaining subjects). The subject's task was to adjust the intensity of the blue phosphor to make the mixture look unique red (i.e., neither bluish red nor yellowish red). Unique green was determined the same way as unique red. In the case of unique blue, the subject adjusted the intensity of the red phosphor to cancel green for ten different saturations of blue. Unique yellow was determined similarly by asking the subject to adjust the intensity of the green phosphor to cancel red. Note that the luminance of stimuli with different saturations and hues was not the same. It is known that luminance has little or no effect on the color settings chosen as unique.[6,7] We directly tested this assumption in a control experiment described in Appendix A. 2

(available as Supplemental Material on the IS&T website, www.imaging.org).

Procedure

There were four sessions. Each session consisted of ten trials and tested only a single color, i.e., red, green, blue, or yellow. The individual trials measured unique hue at different levels of saturation. In each trial, the subject viewed the patch in the center of the CRT monitor. A slide-bar was provided on the monitor for the subject to adjust the color of the patch. Changing the position of the slide-bar changed the intensity of one phosphor (the other two phosphors stayed at the initial setting). At the beginning of each trial, the phosphor intensity corresponding to the center position of the slide-bar was randomized to prevent the subject from using this position as cue to color. The subject's task was to adjust the patch to a unique hue. Each trial was preceded by 3 min of adaptation to a neutral gray background. This duration was chosen based on the results of a preliminary experiment, which is described next. Each trial lasted about 1 to 2 min. One session lasted about 1 h. Each subject was limited to one session a day.

Note that since each trial lasted up to 2 min, the subject's visual system adapted to the color displayed. As a result, this color was not constant throughout the trial, but was nevertheless close to the unique hue that the subject was supposed to produce. For example, in a trial where unique red was produced, the patch had only a small component of blue or yellow. Therefore, it is reasonable to expect that the adaptation changed the appearance of the patch with respect to the red component, but not much with respect to the blue or yellow components. The effect of adaptation (if present) is likely to lead to increased variability of judgments from trial to trial, but not to systematic errors because (i) the initial intensity of the variable phosphor was random and (ii) the ten levels of saturation were presented in random order. This conjecture was verified in a control experiment described in the next section.

Preliminary Experiment

The first author was the subject. The subject repeated ten trials for the same stimulus but with different durations of adaptation between trials: 0, 1, 3, and 5 min. In each trial, SL viewed the stimulus (medium saturated red) after he adapted to the neutral gray background for the given period of adaptation. As in the main experiment, the subject's task was to adjust the patch to a unique hue by changing the position of the slide-bar.

Figure 4 shows the subject SL's settings of unique red using four different durations of adaptation. It is seen that the 0 and 1 min adaptation periods produce systematic changes in the perceived color of the stimulus: the values of x and y systematically increase with the trial number. Specifically, the slope of the regression line is significantly different from zero ($p < 0.05$). On the other hand, 3 and 5 min of adaptation produce no systematic changes in the perceived color. The slope of the regression line was not significantly different from zero. Therefore, in the main experiment we used a 3 min adaptation between trials. To further minimize the effect of adaptation, the stimuli were presented in a random order in the main experiment.

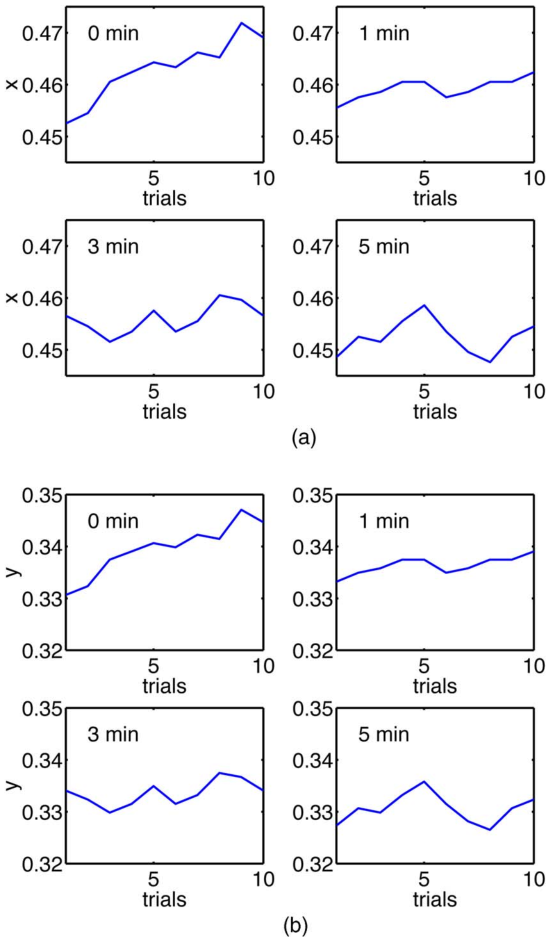

Figure 4. Subject SL's settings of unique red (medium saturation) using four different durations of adaptation, (a) variation in chromaticity x and (b) variation in chromaticity y, as function of trial number.

Results

Figure 5 shows the opponent-channel directions for each subject in the xy chromaticity diagram. It can be seen that the red-green channel cannot be represented by a single straight line. The red and the green parts of this channel can be approximated by straight line segments, but these segments meet at an angle different from 180°. Similarly, the blue-yellow channel cannot be represented by a straight line; a single curved line seems more appropriate.

To verify whether a piecewise linear regression is adequate, we performed a regression analysis separately for each subject and each color. Specifically, linear and quadratic functions were used and the significance of the quadratic term was tested. The results for each subject are shown in Table I.

It is seen that the quadratic term was significant for the blue part of the blue-yellow channel for six out of the seven subjects. An additional analysis shows that the quadratic term is significant for the blue-yellow channel in all subjects.

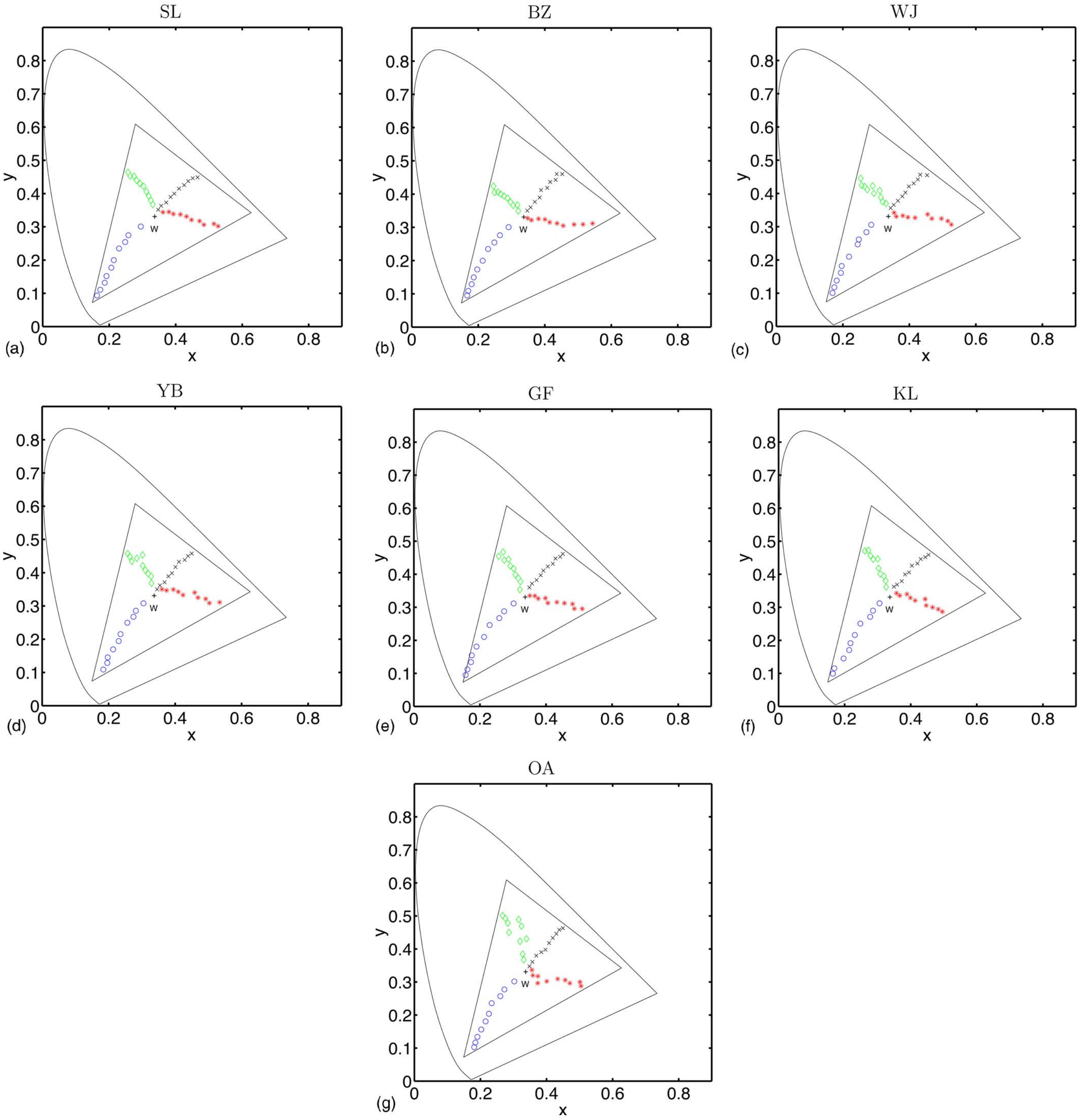

Figure 5. Unique hues for each subject in *xy* chromaticity diagram. Red(stars)-green(diamonds) and blue(circles)-yellow(crosses). Individual data points represent settings in individual trials. "W" is the point that corresponds to equal energy white. The triangle in the diagram represents the gamut of the computer monitor that was used in the experiment.

Therefore, we independently approximated the red and green settings by two straight line segments, and the blue-yellow settings by a single quadratic function. Using two separate functions (a quadratic one for the blue channel and a linear one for the yellow channel) is likely to improve the fit, but at the expense of using more parameters.

Figure 6 shows the results from Fig. 5, but with best fitting lines for blue-yellow (dash-dotted line), red-green (dashed line), and daylight locus (solid line) superimposed. The dashed lines for the red and green parts are the best fitting lines for the data. By the best fitting line, we mean a line minimizing the sum of squared distances of data points from this line in the direction orthogonal to the line. The actual computations were completed by singular value decomposition (SVD). In the conventional regression, the sum of squared differences in the direction of the variable to be

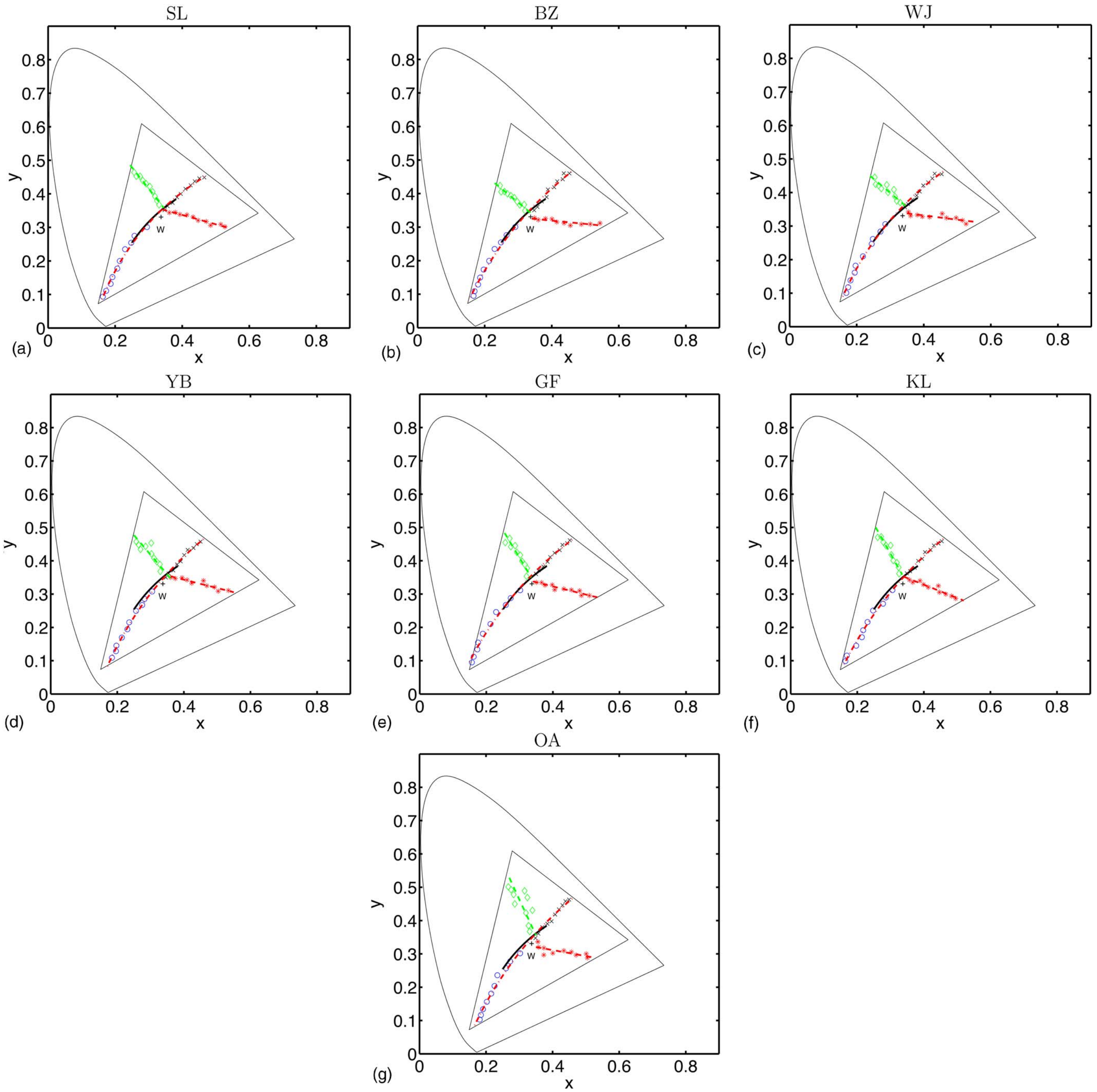

Figure 6. Opponent-channel colors for each subject with the best fitting lines for blue-yellow (dash-dotted line), red-green (dashed line), and daylight locus (solid line) superimposed.

predicted is minimized. However, in our analysis we are not interested in making predictions about either y or x. Therefore, there is no reason to minimize errors in either of these two directions. In fact, since the task was to adjust the hue so that it is unique, it is reasonable to assume that the errors can be adequately modeled by distribution along a direction orthogonal to the opponent-channel direction. Thus, the best approach seems to be the one that minimizes the sum of squares of shortest distances between the data points and the resulting straight line. This is done by determining the eigenvector that is associated with the larger eigenvalue for a given data set. The direction of this vector represents the slope of the best fitting line. The intercept is obtained by assuming that the line goes through the center of the gravity of the data set.

For the blue-yellow data, we cannot do the same analysis because for quadratic regression, there is no direction that can be used as a common orthogonal direction for all data points. Instead, we performed the regression in a new coordinate system. We first compute the eigenvector for the blue-yellow data whose direction maximizes the variance. Then, we rotate the x-coordinate system in such a way that

Table I. *p*-values for testing the significance of the quadratic term in the regressing line approximating the data for individual subjects. *p*-values less than 0.05 indicate that the quadratic term is statistically significant.

	R	G	B	Y	B-Y
SL	0.92	<0.05	<0.05	<0.05	<0.05
BZ	0.06	0.64	<0.05	0.14	<0.05
WJ	0.25	0.50	<0.05	0.06	<0.05
YB	0.44	0.06	<0.05	0.10	<0.05
GF	0.96	<0.05	<0.05	0.08	<0.05
KL	0.24	0.06	0.25	0.13	<0.05
OA	0.55	0.83	<0.05	0.97	<0.05

the new x axis coincides with this direction (we call the new coordinate system, $x'-y'$). As a result, y' is nearly orthogonal to blue-yellow everywhere. Next, we run a quadratic regression that minimizes errors along the y' direction. These lines are shown in Fig. 6. The daylight locus is a quadratic function computed by Judd.[39] It is drawn within the daylight phase: 4000–25 000 K. Note that for all subjects, the best fitting line for blue-yellow closely coincides with the daylight locus.

Figure 7 shows the relationship between the angle θ_R of the red part and the angle θ_G of the green part of the red-green opponent channel for each subject. Each angle was obtained by measuring the angle between the x axis and the fitted line in Fig. 6. The error bars in each direction indicate ± one standard deviation of the estimated angle. The orientation of the best fitting line in each graph coincides with the direction of the eigenvector that is associated with the larger eigenvalue for the given data. It is seen that there is a systematic relation between the two angles. The squared correlation coefficient is $r^2=0.38$ [Fig. 7(a)]. If the data point representing subject OA is excluded (this data point is characterized by large standard errors), the squared correlation coefficient is substantially higher ($r^2=0.83$) [Fig. 7(b)].

Figure 8 shows the opponent-channel colors in a Boynton–MacLeod chromaticity diagram[40] in log-coordinates: $\log[S/(L+M)]$ versus $\log[L/(L+M)]$ space. The quantum absorption rates L, M, S were computed from the tristimulus values X, Y, Z using the matrix from Kaiser and Boynton.[19] The daylight locus (solid line) and best fitting lines for each opponent channel are superimposed. All lines in the graph were obtained via the same method used to determine the lines in the xy chromaticity diagram as shown in Fig. 6. In this space, the daylight locus seems to correspond to a straight line: The squared correlation coefficient computed from 20 equally spaced points from the daylight locus curve is equal to 0.99. Lee also observed that the daylight locus can be approximated by a straight line in log-log coordinates,[41] and this feature was used by Wei, Pizlo, Wu, and Allebach in their model for color constancy.[42] Again, neither the blue-yellow nor the red-green direction can be adequately approximated by a single straight line.

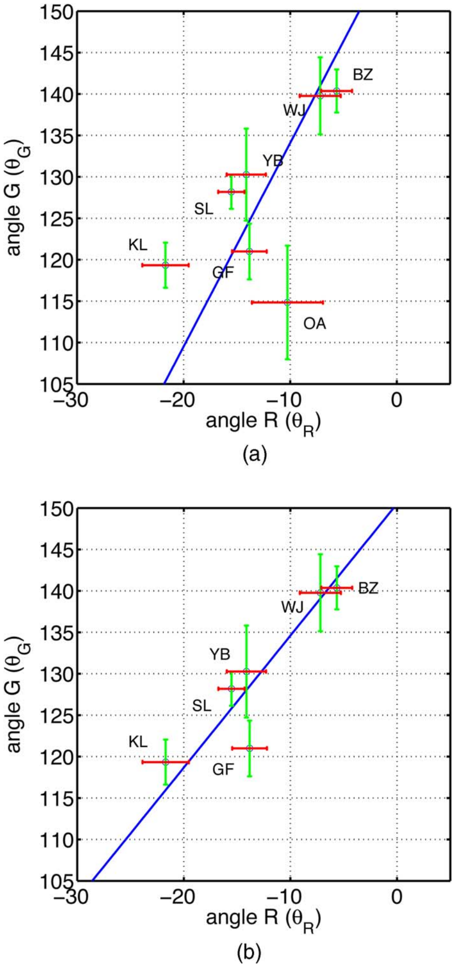

Figure 7. Angle between the red line and the green line (the unit is degrees): (a) for seven subjects ($\theta_G=1.14\theta_R+142.0$, $r^2=0.38$) and (b) for the six subjects remaining after subject OA is excluded ($\theta_G=1.38\theta_R+147.8$, $r^2=0.83$). Solid lines represent best fitting lines obtained by a regression on the given data. The error bars in each direction indicate ± one standard deviation of the estimated angle.

DISCUSSION

For linear models of color vision to be adequate, it is necessary that the two equilibrium lines be straight lines in the xy chromaticity diagram. We (and others) have shown that these lines are not straight lines in xy space. It follows that linear models do not provide an adequate description of the opponent channels.

As shown in Fig. 5, there is not much variability across subjects with respect to unique blue and unique yellow. On the other hand, there is some variability across subjects with respect to the directions of the lines representing unique red and unique green, although the two directions appear to be correlated. Figure 9 shows the distributions of maximally saturated unique hues measured by the seven subjects. Variations in unique blue and unique yellow are relatively small compared to those in unique red and unique green. The

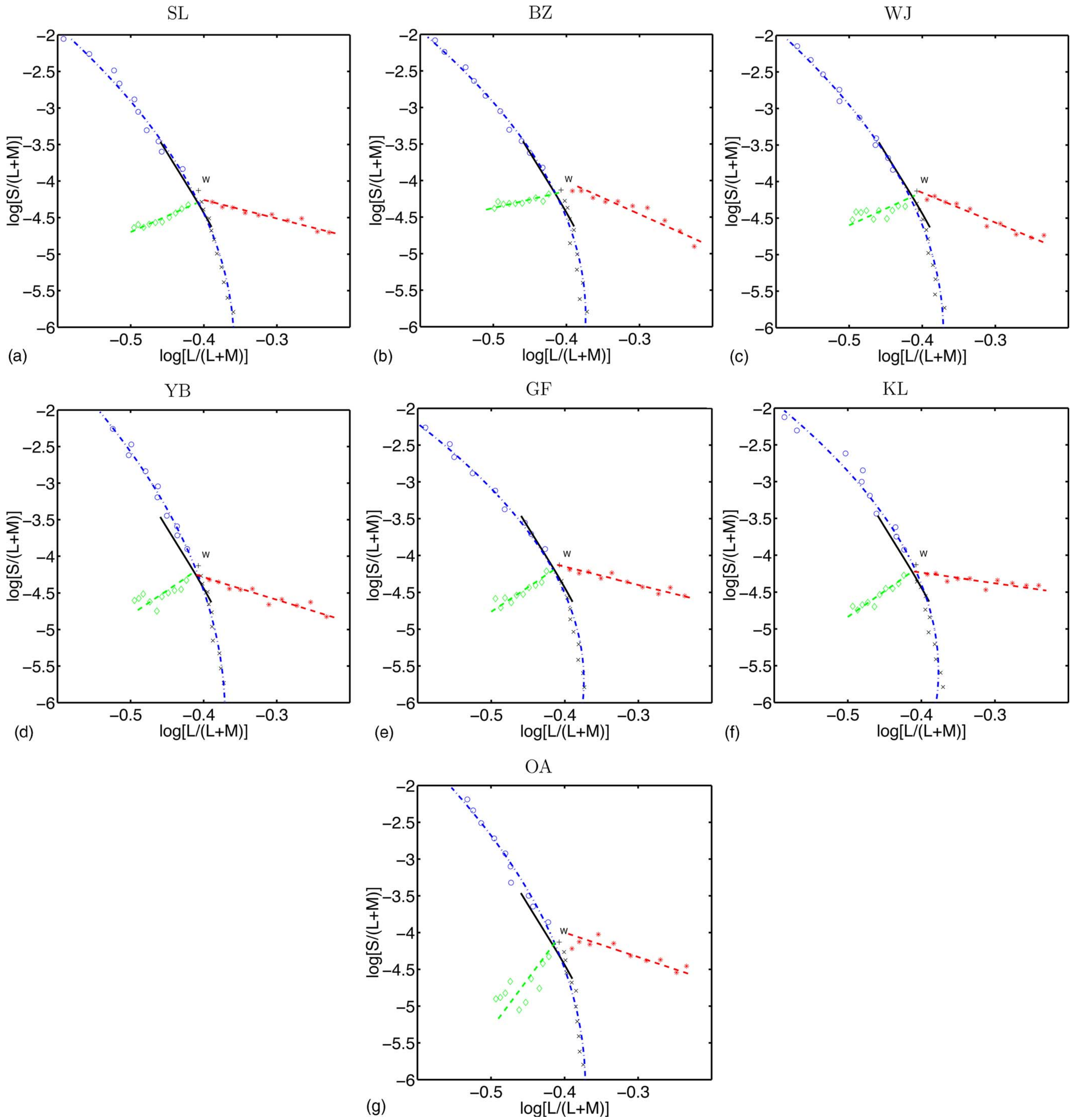

Figure 8. Opponent-channel colors for each subject in log[$S/(L+M)$] vs. log[$L/(L+M)$] space with blue-yellow (dash-dotted line), red-green (dashed line), and daylight locus (solid line) superimposed.

range of unique hues in ΔE^{*}_{ab} units is 18 for red, 26 for green, 11 for blue, and 9 for yellow.

In Fig. 6, we showed that the blue-yellow opponent hue locus closely coincides with the daylight locus. To identify the relation between the daylight locus and the entire blue-yellow opponent channel, we rendered 20 blue and yellow Munsell chips under 10 daylight illuminants chosen from the range 4000−25 000 K. These 20 chips were selected from the Munsell book to adequately represent the unique blue-yellow locus of the subject SL. Figure 10 shows the rendering results of 20 Munsell chips. The 20 circles represent 20 Munsell chips, a thick dotted line shows the daylight locus, and the several thin solid lines are the rendering results. It can be seen that the chromaticities of the light reflected by blue and yellow surfaces closely coincide with the loci of unique blue and unique yellow hues, as shown in our measurements (see Fig. 6) and in measurements presented in Gouras' Plate 10(b).[43] This similarity suggests that the blue-yellow channel

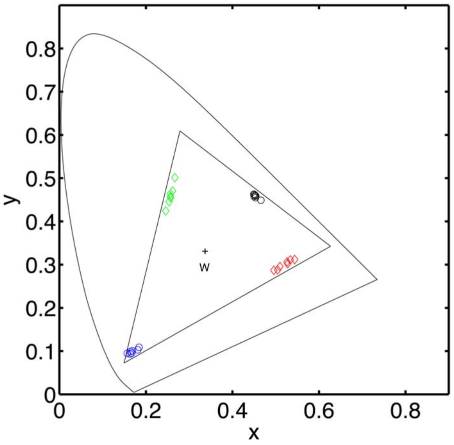

Figure 9. Distributions of maximally saturated unique hues measured by seven subjects. Variations in unique blue and unique yellow (circles) are relatively small compared to those in unique red and unique green (diamonds).

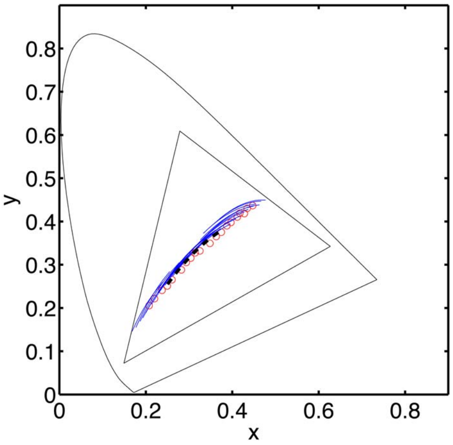

Figure 10. Rendering of 20 blue and yellow Munsell chips under ten daylight illuminants chosen from the range 4000–25 000 K. The 20 circles represent 20 Munsell chips, a thick dotted line shows the daylight locus, and the several thin solid lines are the rendering results.

evolved to efficiently serve in solving color constancy problem: unique blue and unique yellow surfaces will look unique when rendered under any daylight. More generally, changing the daylight when a natural surface is viewed, changes the response of the blue-yellow channel, only. The red-green channel is invariant to such changes.

Consider now the relation between our results and those of Webster et al.[28,29] Figure 8 is log scaled version of the Boynton–MacLeod chromaticity diagram. In the plot, even though the phases of daylight are represented by a straight line, the entire blue-yellow channel cannot be represented by a straight line. The same is true for the red-green channel. This characteristic of the unique hue directions confirms that these directions are not only off the theoretical cardinal opponent axes (the x and y axes of the Boynton–MacLeod diagram), but they also cannot be characterized by straight lines. In many respects, our results are similar to those of Webster et al.[28,29]. Their unique hue settings also showed a certain amount of departure from the cardinal axes (modified Boynton–MacLeod diagram). For none of their observers could the red-green channel be approximated by a single straight line; for some subjects, the same was true for the blue-yellow channel. This fact clearly shows that any simple linear transformation between OPP responses and LMS responses cannot describe the postprocessing stage of the human visual system. Webster et al. described the locus of unique hues as straight lines. Recall, however, that in our results, the blue part of the blue-yellow channel could not be approximated by a straight line. This difference between Webster et al.'s results and ours could be a consequence of the fact that we used a wider range of saturations.

In our experiment, subjects viewed the stimulus for about one minute on the average. This amount of time was necessary for the subject to be able to adjust the color of the patch. A question remains as to the effect of this prolonged adaptation on the directions of the opponent channels. In other words, while the subject is adjusting the color to unique red, does the adaptation affect the saturation of red only, or the hue as well? To verify whether unique hues adjusted in the main experiment still look unique when the exposure duration of the color is short, subject SL ran four sessions, ten trials per session, one session for each hue. After initial adaptation to the gray background for 3 min, a sequence of ten trials began. In each trial, the stimulus was shown for 280 ms. There was a 3 s adaptation period between trials. The trials involved the colors that subject SL chose as unique in the main experiment. The order of saturations was randomized. SL reported that the colors in each session still looked unique. Therefore, we conclude that the long exposure duration in our main experiment did not substantially affect the directions representing opponent channels.

Finally, we would like to point out that the complex relation between cone responses and opponent channels suggests that it may be unwarranted to talk about *color* coding on the retina (as Young-Helmholtz theory claims). Color as a perceptual attribute is associated with the functioning of cortical areas of the brain, rather than of the retina itself. It is more appropriate to talk about coding *spectral* information on the retina. In fact, Hurvich and Jameson made this point very clearly.[44]

CONCLUSION

In summary, our best fitting lines of unique hues in the *xy* chromaticity diagram, as well as in the log scaled version of the Boynton–MacLeod chromaticity diagram, reveal that a linear-model representation of opponent colors is not a precise characterization of the relation between OPP responses and LMS responses (or tristimulus XYZ). A simple nonlinear transformation (e.g., differentiable), however, does not seem to be plausible, either. Before such a model is proposed, one has to design psychophysical experiments that will allow reliable measurement of the relation between cone absorptions and responses of opponent channels for an arbitrary stimulus, not only for unique hues as was done in our study, as well as in prior studies.

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