

# Variations in normal color vision. II. Unique hues

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We examined individual differences in the color appearance of nonspectral lights and asked how they might be related to individual differences in sensitivity to chromatic stimuli. Observers set unique hues for moderately saturated equiluminant stimuli by varying their hue angle within a plane defined by the LvsM and SvsLM cone-opponent axes that are thought to characterize early postreceptoral color coding. Unique red settings were close to the +L pole of the LvsM axis, while green, blue, and yellow settings clustered along directions intermediate to the LvsM and SvsLM axes and thus corresponded to particular ratios of LvsM to SvsLM activity. Interobserver differences in the unique hues were substantial. However, no relationship was found between hue settings and relative sensitivity to the LvsM and SvsLM axes. Moreover, interobserver variations in different unique hues were uncorrelated and were thus inconsistent with a common underlying factor such as relative sensitivity or changes in the spectral sensitivities of the cones. Thus for the moderately saturated lights we tested, the unique hues appear largely unconstrained by normal individual differences in the cone-opponent axes. In turn, this suggests that the perceived hue for these stimuli does not depend on fixed (common) physiological weightings of the cone-opponent axes or on fixed (common) color signals in the environment. © 2000 Optical Society of America [S0740-3232(00)01809-3]

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## 1. INTRODUCTION

Human color vision is thought to depend on two general stages: Light is initially absorbed by the long-, medium-, or short-wavelength sensitive (L-, M-, or S-) cone receptors, and the signals from the receptors are then combined to form different types of postreceptoral channels. However, the number and nature of these postreceptoral transformations remain poorly defined. The principal dimensions underlying postreceptoral color vision were first suggested by measures of color appearance. Any aperture color can be described by a combination of the four perceptually unique hues: red, green, blue, or yellow, yet no light appears both red and green or both blue and yellow.<sup>1,2</sup> Such observations led Hering to postulate that the sensation of color directly reflects the responses in two opponent channels coding red–green or blue–yellow sensations.<sup>3</sup> Because a single channel signaled either red or green depending on the polarity of its response, these two hues could not be perceived simultaneously. By this account, most hues (e.g., orange) appear mixed because they reflect the component responses from both channels (e.g., red plus yellow), while the unique hues appear pure because they stimulate one channel but leave the second channel in equilibrium.

Such models account well for the phenomenology of color vision but predict cone transformations different

from those that are typically observed in physiological recordings or in psychophysical measurements of sensitivity and adaptation.<sup>4</sup> These types of studies suggest that postreceptoral color coding is organized in terms of two dimensions that correspond to opposing signals from the L and M cones (LvsM) or to signals from the S cones opposed by a combination of signals from the L and M ones (SvsLM). Any color can be represented in an opponent-modulation space whose two chromatic axes correspond to the level of SvsLM or LvsM activity.<sup>5</sup> Yet within this space the four unique hues do not lie along the four poles of the cardinal axes. For example, Fig. 1 plots the unique-hue settings for a single observer (MW) within the LvsM versus SvsLM plane (from the study of Webster and Mollon<sup>6</sup>). Only the +L pole of the LvsM axis may be close to a perceptually pure color (unique red), while the remaining poles appear as mixtures of the primary hues (blue–green for the +M pole, blue–red for the +S pole, and yellow–green for the –S pole). Thus—with the possible exception of unique red—the unique hues do not correspond to activity along a single cardinal axis. Moreover, whether any suprathreshold stimuli can isolate a single postreceptoral color mechanism is doubtful, for a variety of results suggest that postreceptoral color coding involves multiple mechanisms tuned to different color directions.<sup>4</sup> Thus the perceived hue at any stimulus di-

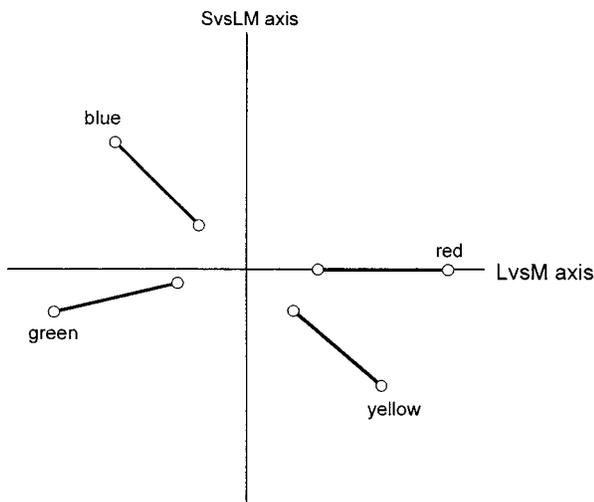


Fig. 1. Locus of unique hues in cone-excitation space, measured for a single observer. Points plot the chromatic angles corresponding to unique red, green, blue, or yellow (from the study of Webster and Mollon<sup>6</sup>).

rection may depend on the distribution of activity across a large number of mechanisms.

The different cone combinations implied by measurements of sensitivity and adaptation versus color appearance have led to two alternative accounts of the basis for hue sensations. On the one hand, models built on the assumption that color appearance reflects an underlying representation in terms of two mechanisms isolated by the red–green and blue–yellow perceptual axes have postulated a third stage of color vision, in which early postreceptoral channels tuned to the cardinal axes are recombined to yield the perceptual mechanisms.<sup>7,8</sup> On the other hand, it has been suggested that observers may learn to associate hues with prominent stimulus variations in the environment rather than with special (e.g., isolating) states of neural activity.<sup>9,10</sup> For example, different phases of daylight vary predominantly along a blue–yellow axis, and blue–yellow sensations may therefore reflect our perceptual representation of the daylight locus,<sup>9–12</sup> though not necessarily through the responses of an explicit blue–yellow mechanism. By this account there is no need to postulate further recombinations of the cardinal cone-opponent axes, for a pure yellow may reflect a particular ratio of activity across mechanisms, rather than the isolation of a single mechanism.

By either account, it is clear that both the perceptual hue axes and the cardinal cone-opponent axes represent important and salient aspects of human color vision. It is therefore important to ask how these different representations are related. In our study we explored this relationship by examining the patterns of variability in color appearance and sensitivity. Subjects with normal color vision are known to vary widely in their unique hue settings.<sup>13,14</sup> Substantial individual differences at peripheral stages of the visual system, which will produce variability in the cardinal axes, are also well established.<sup>15–17</sup> Yet the possible correlations between variations in the cardinal axes and color appearance have not been examined.

To assess these correlations we examined variations in

unique-hue settings for moderately saturated, nonspectral lights. Such stimuli are the most relevant for characterizing color perception under natural viewing conditions, for they approximate more closely the stimuli that observers will be exposed to in the natural environment. In contrast, most previous studies of individual differences in the unique hues have used monochromatic and thus highly saturated lights. Variability in unique-hue settings may exhibit different patterns for monochromatic versus broadband stimuli because the effective spectra of broadband stimuli may be differentially affected by changes in the cone spectral sensitivities.<sup>18,19</sup> The two types of stimuli may also point toward different variables for interpreting individual differences. For example, spectral lights that appear unique yellow are typically near 570–580 nm. For these moderately long wavelengths the contribution of S cones is negligible, and researchers have therefore focused on the relationship between unique yellow settings and the ratio of L to M cone signals.<sup>20–22</sup> Yet as Fig. 1 suggests, for nonspectral stimuli unique yellow corresponds instead to a ratio of LvsM to SvsLM activity and thus is defined by the relationships between signals in all three cone classes. We show that for all of the unique hues these ratios—or hue angles—vary substantially among color normal observers.

To explore a possible basis for the variation in unique-hue angles, we asked to what extent they could be equated across observers by normalizing the cone-opponent spaces of individual observers, to identify either a common physiological or a common environmental correlate of the unique hues. Such results are important for assessing to what extent the signals underlying unique hue settings reflect strongly constrained rules—e.g., that specify fixed transformations of the cone signals or strongly constrained stimuli in the environment—versus rules that allow more variable transformations or are perhaps more susceptible to individual experience. For example, as noted above, unique blue and yellow correspond to different ratios of SvsLM to LvsM activity. It is therefore possible that individual differences in the stimuli that observers perceive as pure blue or yellow can in part be accounted for by individual differences in the relative sensitivity to the SvsLM and LvsM axes (so that blue and yellow correspond to fixed ratios of signals along the two cardinal axes). This hypothesis is readily confirmed in an *individual observer*. The SvsLM or LvsM axis can be selectively desensitized by contrast adaptation, and the change in relative sensitivity to the two axes induces predictable rotations in the hue angles corresponding to different perceived colors.<sup>6,23</sup> For example, reducing sensitivity to the LvsM axis causes a previously unique yellow to appear greenish (a rotation toward the SvsLM axis), and causes the hue angle corresponding to unique yellow to rotate toward the LvsM axis (by an amount that preserves a constant ratio of LvsM to SvsLM activity for unique yellow). We asked whether unique yellow corresponds to a constant SvsLM to LvsM ratio across *different observers*, by asking whether variations in their unique yellow settings were tied to variations in their sensitivity ratios. However, we instead failed to find any evidence for a relationship between relative sensitivity to the car-

dinal axes and unique hue settings across observers. Moreover, in contrast to the predictions for relative sensitivity differences across the cones or for changes in the spectral sensitivities of the cones, there was no correlation between hue angles corresponding to different unique hues. These results thus suggest that normal variations in peripheral factors may place little constraint on the perceived hues of the moderately saturated lights we tested.

## 2. METHODS

A detailed description of the display and stimulus specification is given in the accompanying paper.<sup>17</sup> As described there, stimuli were shown on a monitor and consisted of equiluminant ( $30 \text{ cd/m}^2$ ) pulses of color presented in a 2-deg square field, centered on a  $6.4 \times 8.4$  deg neutral gray background ( $30 \text{ cd/m}^2$  and chromaticity of Illuminant C). The chromatic contrasts of the pulses were defined by their variations relative to this neutral point within a threshold-scaled version of the MacLeod–Boynton<sup>24</sup>  $r, b$  chromaticity diagram, scaled so that

$$\text{LvsM contrast} = (r_{mb} - 0.6568) * 2754$$

$$\text{SvsLM contrast} = (b_{mb} - 0.01825) * 4099.$$

Observers made unique-hue judgments for conditions and stimuli that were very similar to those described in the accompanying paper for measuring chromatic sensitivity.<sup>17</sup> The monitor was viewed binocularly in an otherwise dark room from 250 cm. Observers first adapted for 3 min to the gray background. Test stimuli were then presented while subjects made forced-choice judgments about their perceived color (e.g., responding either “too red” or “too green” for unique yellow settings.) The pulsed tests were shown at full contrast for 280 ms and ramped on and off with Gaussian envelopes ( $\sigma = 80$  ms). During a run the contrast ( $\sim$ saturation) of the stimulus was fixed, while the chromatic angle was varied across trials by using two randomly interleaved staircases to define the angle at which the alternate responses occurred with equal probability. The field returned to gray for 3 s between each presentation. Control runs with longer intertrial intervals (up to 8 s) yielded very similar settings, suggesting that the hue angles were not biased by adaptation to the test pulses. Hue angles were measured over a range of contrasts for six observers (the authors and two additional subjects) for whom we also collected measures of sensitivity to the LvsM and SvsLM axes.<sup>17</sup> Further unique-hue settings at a single contrast were collected for an additional 45 subjects who participated for course credit. All subjects had normal color vision as assessed by the Ishihara pseudo-isochromatic plates.

## 3. RESULTS

### A. Unique Hues and Scaling of the LvsM and SvsLM Axes

Figure 2 shows for six individuals the hue angles for red, green, blue, and yellow at contrasts ranging from 10 to

60. Each point is the mean of six settings. The results are consistent with general characteristics observed previously for the unique hues<sup>6,25–29</sup> (e.g., see Fig. 1). For most observers the angles defining the unique hues were roughly independent of contrast over the range of contrasts tested. Unique red was close to the  $+L$  axis, and the remaining hues fell at intermediate angles. Consequently, for all observers the red–green axis was clearly “bent,” so that unique red and green do not correspond to complementary colors. For some of the observers (e.g., EM and JS) unique blue and yellow were also clearly not collinear, though for others (e.g., MW and VR) they did appear consistent with a single color-opponent axis.

Differences in the hue settings across subjects were substantial. For example, for these six observers the unique yellow locus varied from  $-32$  to  $-69$  deg (equivalent to a variation in dominant wavelength from roughly 580 to 570 nm, respectively; see Table 1). Again, we asked whether these differences might reflect differences in observers’ sensitivity to the cone-opponent axes. Suppose for example that unique yellow corresponded to a fixed ratio of signals within the SvsLM and LvsM axes. Then the differences across observers might be tied to differences in their relative sensitivity to these axes. To explore this possibility, we compared the sensitivity ratio predicted by the green, blue, or yellow hue angles (as given by the tangent of the hue angles), with the sensitivity ratio that we estimated for these observers from thresholds or contrast adaptation.<sup>17</sup> Plots of these comparisons are shown in Fig. 3. For blue settings the range of variation predicted by differences in the hue angles and differences in the direct sensitivity estimates are roughly comparable (twofold). Thus differences in the sensitivity ratio are large enough to be consistent with the observed variations in blue. However, the sensitivity estimates underestimate the fourfold range of variation implied by the yellow and green settings. Moreover, for none of the hues is there a clear suggestion that the hue angles and the sensitivity ratios inferred from the thresholds or adaptation are related.

### B. Relationships between Different Unique Hues

As a second test for a possible relationship between the hue loci and sensitivity, we examined the relationships between *different* hue settings. If the variations in different hue loci had a common basis, then these variations should be correlated. For example, suppose again that the chromatic angles defining unique yellow, blue, and green did all correspond to fixed ratios of SvsLM to LvsM signals. Decreasing or increasing the SvsLM sensitivity in an observer would cause all of the unique hues to rotate toward or away from the SvsLM axis, respectively. Thus blue and yellow should be positively correlated, while both would be negatively correlated with green settings. We therefore tested for covariations in the hue settings as a further test of sensitivity influences on the unique hues. Comparing different unique hues directly had the advantage over the preceding experiments that they might reveal more directly the sensitivity ratios relevant to color appearance and could be quickly measured on a large number of observers. Subjects in this experiment included students in an undergraduate psychology

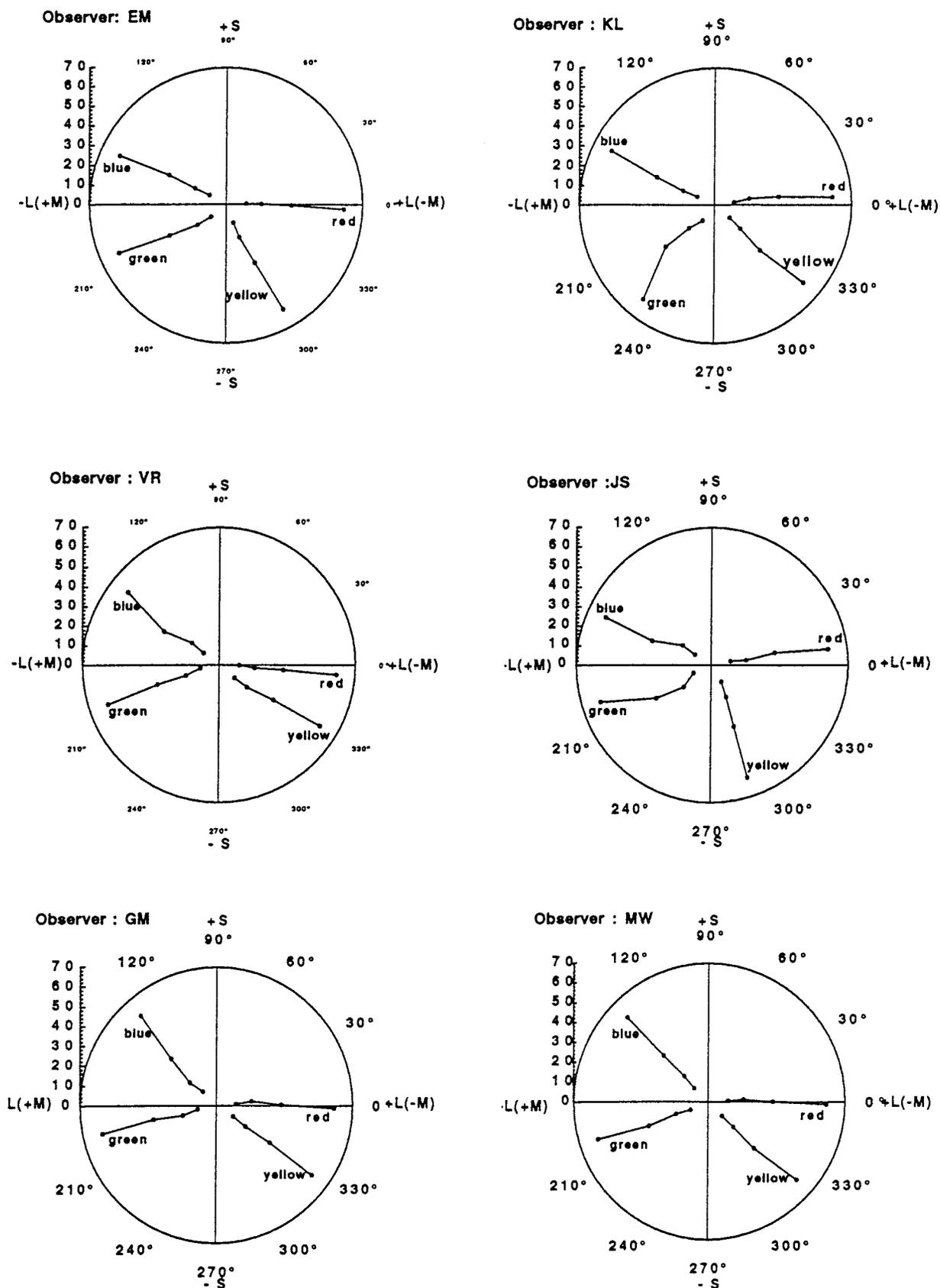


Fig. 2. Locus of unique hues within the SvsLM and LvsM plane. Curves plot the loci of unique red, green, blue, or yellow settings for stimuli that range in contrast from 10 to 60. Each panel plots the settings for an individual observer.

**Table 1. Unique-Hue Settings for All Subjects ( $n = 51$ )<sup>a</sup>**

Hue Angle	Unique Hue			
	Yellow	Blue	Red	Green
Mean Hue Angle	-50.3	144.6	0.4	205.1
Dominant Wavelength	574	477		545
Standard Deviation	9.2	10.3	5.4	12.6
Range	-70.6 to -31.3	121.0 to 163.3	-9.0 to 12.3	172.6 to 241.1
Dominant Wavelength	570 to 580	465 to 486		491 to 562

<sup>a</sup> Values give chromatic angle in degrees within the threshold-scaled LvsM and SvsLM space.

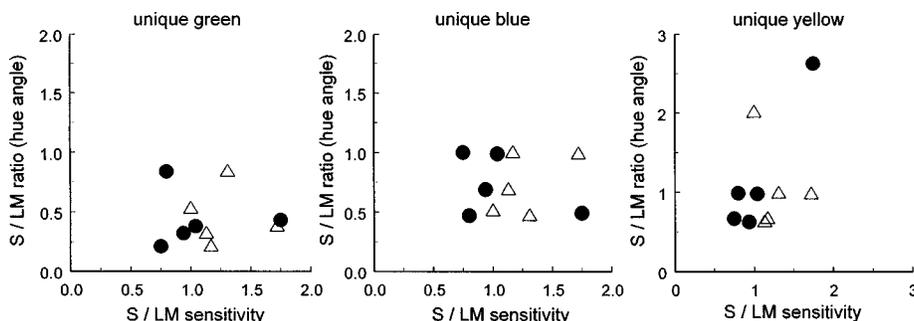


Fig. 3. S/LM sensitivity ratios estimated from hue angles compared with estimates from thresholds (circles) or adaptation (triangles). Estimates from unique hues are based on the tangent of the observer’s mean unique hue angle.

course who participated for course credit. During a single session each of the unique hues at a contrast of 30 was measured four times (following an initial, discarded practice run). A subset of subjects repeated the same measures during a second session as a test for reliability. The settings for some students were highly variable, presumably for reasons unrelated to their color vision (e.g., estimating the wrong hue on some trials). We therefore excluded subjects whose range was greater than one standard deviation above the mean range for the group for any single hue. Thirteen observers were excluded by this criterion.

Figure 4 plots the hue angles for each subject within the LvsM and SvsLM space, and Fig. 5 shows histograms of the chromatic angles for each hue. The figures illustrate large variations in all of the hue angles. Within our chromatic plane the loci for red were the most constrained (covering a range of 20 deg centered on the +L axis), whereas unique green varied over a range of 60 deg (Tables 1 and 2). Tables 1 and 2 also give the dominant wavelength of the hue angles for blue, green, and yellow. For blue and yellow the means and range are comparable to previous measurements of the unique hues in monochromatic lights,<sup>14,22,30</sup> consistent with the largely linear equilibrium axes for these hues.<sup>25,28</sup> Alternatively, our unique green settings were biased toward longer wavelengths than unique green estimates for spectral lights, consistent with a curvature in the loci for unique green.<sup>25,29</sup>

Despite the large interobserver differences in each of the hues, the variations across different hues were in all cases unrelated. The correlation matrix for the four hues is given in Table 3. Surprisingly, none of the correlations between different hues reaches significance. In Table 3 the values in the upper-right cells were calculated from

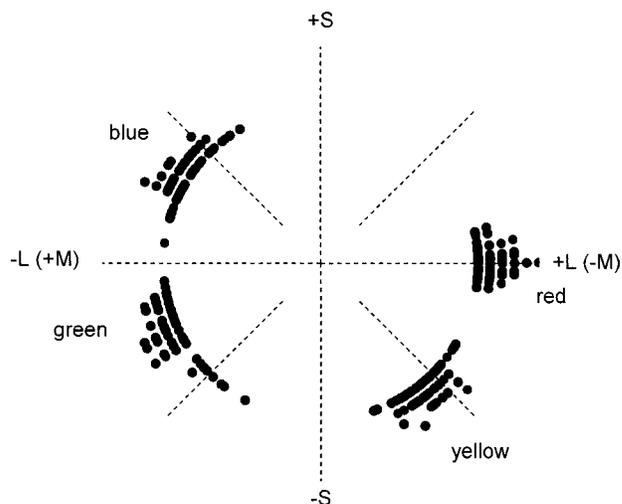


Fig. 4. Locus of unique hues within the SvsLM and LvsM plane. Each point plots the chromatic angle that appeared unique red, green, blue, or yellow for one of the 51 observers. All stimuli had a fixed contrast of 30.

the data of all 51 observers. The diagonals show the correlations between the same hues over two different days based on 31 observers who participated in two sessions. These values show that red, blue, and yellow were set with good reliability, whereas settings for green were highly variable (even relative to the large differences across observers). Uncertainty in the settings for individual hues could thus mask a weak relationship between different hues. To give the sensitivity hypothesis the best chance for succeeding, we therefore further restricted the analysis to the subset of subjects who made the most reliable hue settings, by selecting subjects whose total range of hue settings was at or below the median range

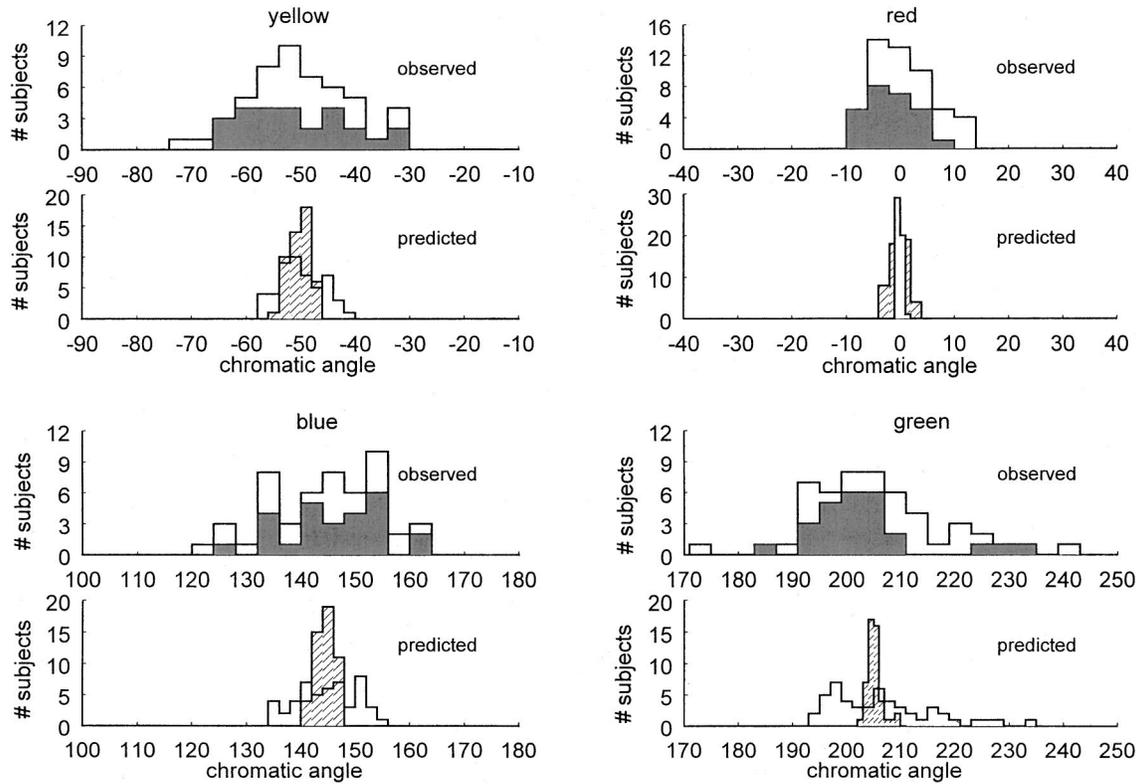


Fig. 5. Histograms of the distributions of hue angles. For each of the four hues, the upper panel plots the measured hue settings, for the full set of 51 observers (unshaded bars) or for the subset of 26 observers who set the hues most consistently (shaded histogram). The lower panel for each hue shows the range of hue angles predicted by assuming that all observers with different spectral sensitivities choose hues that match the same physiological weightings of the cardinal axes (unshaded bars) or choose hues that match the same environmental stimuli (shaded bars). The predictions were based on reconstructing the sensitivities of the 49 Stiles and Burch observers.

**Table 2. Unique-Hue Settings for the Most Consistent Subjects ( $n = 26$ )<sup>a</sup>**

Hue Angle	Unique Hue			
	Yellow	Blue	Red	Green
Mean Hue Angle	-50.2	146.1	-1.83	203.3
Dominant Wavelength	574	478		542
Standard Deviation	9.5	9.1	4.3	10.9
Range	-63.5 to -31.3	125.6 to 162.4	-9.0 to 6.17	186.6 to 232.1
Dominant Wavelength	571 to 580	468 to 486		504 to 560

<sup>a</sup>Total variability in hue settings equal to or below the median range for all observers. Values give chromatic angle in degrees within the threshold-scaled LvsM and SvsLM space.

**Table 3. Correlations between Different Unique-Hue Settings<sup>a</sup>**

Unique Hue	Unique Hue			
	Yellow	Blue	Red	Green
Yellow	<b>0.97</b>	0.88	-0.23	-0.22
Blue	<b>0.31</b>	<b>0.93</b>	0.88	-0.12
Red	<b>0.30</b>	<b>0.38</b>	<b>0.92</b>	0.80
Green	<b>0.15</b>	<b>-0.13</b>	<b>-0.01</b>	<b>0.54</b>

<sup>a</sup>Values give the correlations between hue angles for all observers ( $n = 51$ , upper-right cells) or for the subset of observers who made the most consistent settings ( $n = 26$ , lower-left cells, in boldface). Values along the diagonal show the correlations for the same hue measured across two daily sessions. None of the measured correlations across different unique hues is significant.

for the entire group. For these subjects the repeated settings of each individual varied over a range of 10 deg or less for red, blue, and yellow and over 20 deg or less for unique green. This resulted in high reliabilities for red, blue, and yellow, though consistency for the green settings was still marginal (Table 3). Yet even for this subset of observers the correlations across different hues remained in all cases insignificant. Thus our results suggest that variations across the unique hues are surprisingly independent.

### C. Unique Hues and Individual Differences in Spectral Sensitivity

The preceding results suggested that there is little relationship between the chromatic angles that are perceived as unique hues and the relative sensitivity to the SvsLM and LvsM axes. As a final analysis we examined the variations in unique hues that would be predicted by changes in the spectral sensitivities of the cone mechanisms rather than by their relative scaling. To assess normal variations in the cone sensitivities, we used the analysis of MacLeod and Webster<sup>16,31</sup> to reconstruct individual spectral sensitivities for the 49 observers in the color matching study of Stiles and Burch.<sup>32</sup> (Details of this reconstruction are described in the accompanying paper.<sup>17</sup>) We then calculated the unique hues for these individuals predicted by two different assumptions: (1) that the hue angles are determined by fixed physiological signals in the observer or (2) that the unique hues correspond to fixed color signals in the environment. We consider these alternatives in turn.

#### 1. Fixed Physiological Signal

In this case we assumed that the unique hues were set by fixed directions within the SvsLM and LvsM plane. We then calculated how the stimulus directions required to produce these ratios would be biased by changes in the cone sensitivities, owing to differences in preretinal screening or photopigment absorption spectra. Note that, like the sensitivity-ratio hypothesis we rejected above, this approach essentially assumes that the unique hues are determined by a fixed weighting of the cone signals (as might occur if these weightings were specified genetically). For the calculations, we assumed that these weightings were given by the S/LM ratio implied by the mean hue settings for our observers (Table 1). We then calculated for each Stiles and Burch observer the stimu-

lus angle (relative to their individual responses to the white point) at which this ratio occurred.

Figure 5 plots the distribution of hues predicted by the variations in color matching among the Stiles–Burch observers. These are shown by the unshaded histograms plotted below the empirical distributions for each hue. Because these predictions are based on finding constant directions within each individual's cone-opponent plane, they are similar in principle to analyzing how changes in spectral sensitivity alter the stimulus directions determining the cardinal axes (see Fig. 5 of the accompanying paper.<sup>17</sup>) In fact, the distribution for unique red is identical to the distribution defining the LvsM axis, since we assumed an angle of 0 deg (the +L axis) for unique red. This distribution is very narrow, spanning a range of only 2 deg, and thus clearly fails to account for the 20-deg range of variation in the observed unique red settings. Alternatively, the predicted range of angles for the other hues is large and thus comes much closer to the spread of hue angles actually observed. However, as Table 4 shows, the predicted variations in the different hues are very highly correlated. Thus, like the scaling hypothesis, the changes in spectral sensitivity again fail to account for the independence of the different unique hues.

#### 2. Fixed Environmental Stimulus

A dissociation between color sensations and chromatic sensitivity could arise if the hue loci for the conditions we examined are tied more to physical properties of the outside world than to physiological properties of the observer.<sup>9,10</sup> Jordan and Mollon<sup>18,19</sup> suggested that there might in fact be comparatively little interobserver variability in hue judgements for natural reflectance functions (though focal colors named in Munsell chips do show some individual differences.<sup>33</sup>) They suggested that observers might learn to associate concordant hue percepts with real-world reflectances. These percepts would correspond to different physiological signals depending on the specific makeup of the observer (e.g., whether the observer had a higher or lower density of preretinal pigments). By this argument, variations in the hues of monochromatic lights arise because narrowband lights are no longer subjected to the spectrally selective filtering by the individual's visual system and thus no longer produce the same ratio of cone signals.

The hypothesis of Jordan and Mollon points to the importance of searching for the basis of color appearance

**Table 4. Correlations between Different Unique-Hue Settings Predicted by Individual Differences in Color Matching<sup>a</sup>**

Unique Hue	Unique Hue			
	Yellow	Blue	Red	Green
Yellow		0.99	−0.77	−0.93
Blue	<b>0.97</b>		−0.77	−0.97
Red	<b>0.62</b>	<b>0.77</b>		0.80
Green	<b>0.19</b>	<b>0.37</b>	<b>0.84</b>	

<sup>a</sup> Values give the correlations between hue angles for observers with different spectral sensitivities, based on reconstructing sensitivities for the 49 Stiles and Burch observers. Upper-right cells show the correlations predicted if the unique hues correspond to constant S/LM ratios equal to the mean observed ratios. Lower-left cells (in boldface) show the correlations predicted if the unique hues correspond to a constant color signal in the environment, simulated by spectra for Munsell chips viewed under Illuminant C.

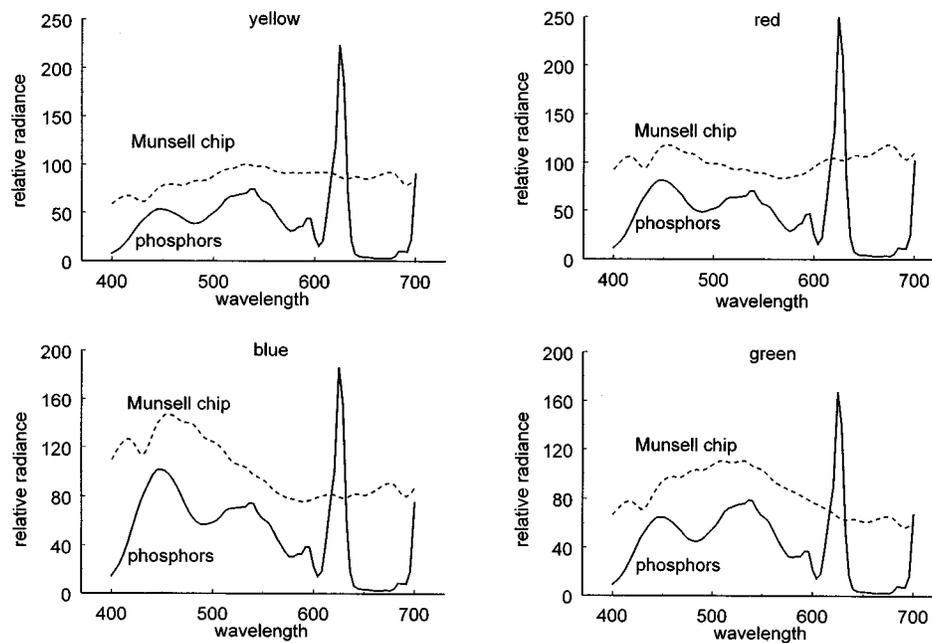


Fig. 6. Spectra used to calculate how the variations in the hue settings depend on the stimulus color signal. Naturalistic color signals were constructed by simulating Munsell chips viewed under Illuminant C (dashed curves). Solid curves show the monitor spectra with the equivalent chromaticity.

within the context of the stimuli to which observers are normally exposed. The spectra for our monitor stimuli are obviously much broader than the monochromatic lights traditionally used to measure the unique hues, yet they vary much less smoothly than typical natural color signals. Could differences in hue settings on our monitor reflect differences in the spectral filtering characteristics of observers who would have agreed on the perceived hue of natural surfaces? To assess this possibility, we again used the hypothetical Stiles–Burch observers, but this time we calculated how these observers would encode natural surfaces viewed under natural illumination. Since our reference chromaticity equaled Illuminant C, we approximated an Illuminant-C source from the first three basis functions that Judd *et al.*<sup>34</sup> derived for natural daylight. Surfaces were simulated Munsell chips based on the first three basis functions derived for Munsell reflectance spectra by Cohen.<sup>35</sup> The chips were chosen so that the color signals under the illuminant had a contrast of 30 and again equaled the mean angle chosen for each hue by our observers. The resulting spectra are illustrated in Fig. 6, along with the monitor phosphor spectra giving the same chromaticity. For each observer we calculated the S/LM ratio for each unique hue based on the Munsell spectra (given by the hue angle relative to their response to the Illuminant C spectrum). Finally, we calculated the color angle that was necessary to give the same S/LM ratio for the phosphor spectra (again relative to their response to the Illuminant-C reference, which we assumed represents their “learned” white point).

Again, if observers with different spectral sensitivities agreed on the hues of the Munsell surfaces, then the cone ratios corresponding to these hues must differ, and thus for the monitor stimuli different phosphor combinations would be necessary to equate these cone ratios. Note that in this case the observers’ settings should be unaf-

ected by differences in the scaling of their cone-opponent axes, for this scaling would affect the Munsell and monitor stimuli in the same way. However, Fig. 5 shows that the monitor stimuli are dispersed by changes in the shapes of the cone spectra (see shaded histograms in the panels for the predicted distributions). Interestingly, in this case the range of angles predicted for each of the hues is comparable ( $\sim 7$  deg) but underestimates the range of 20 to 40 deg that we actually measured. Moreover, the changes in spectral sensitivity again predict highly correlated changes in some pairs of hues, such as blue and yellow (Table 4), although, notably, the relationships between the green and blue or yellow are now weak. Thus the predicted relationships between the different hues are again inconsistent with the pattern that we found. Of course, the environmental stimuli defining the unique hues may be different from the spectra that we chose (for Illuminant C itself appears slightly bluish under neutral adaptation), but the relevant spectra should be similarly broad and thus should similarly account for only a small proportion of the variance in the hue settings, while again predicting strong correlations between the hues.

The implication of these analyses is that the variations in the unique hues are too large and too independent to be accounted for by either a fixed physiological weighting or a fixed color signal in the environment. In turn, this implies that the hue loci for our moderately saturated stimuli are largely unconstrained by normal variations in the peripheral factors that we considered, even though these factors substantially alter an observer’s sensitivity to chromatic stimuli.

#### 4. DISCUSSION

The LvsM and SvsLM axes are often loosely described as “red–green” and “blue–yellow” axes, respectively, yet the

discrepancies between the cardinal cone-opponent and color-appearance axes are large. Understanding these discrepancies and their basis remains a central question in color science. It is well recognized that variations in S-cone excitation do not correspond to a blue–yellow variation, for S-cone signals also contribute substantially to red–green sensations.<sup>36,37</sup> The relationship between the LvsM axis and red–green appearance is less clear. Unique green is clearly shifted off the LvsM axis, requiring less S-cone excitation than the equiluminant white.<sup>6,25,27</sup> On the other hand, we found that unique red judgements do tend to cluster around the LvsM axis. For our observers, the range of unique red settings was an order of magnitude too large to be accounted for by expected individual differences in the LvsM axis, yet the mean locus across observers was not significantly different from the +L axis. This result differs from that of De Valois *et al.*,<sup>27</sup> who found that unique red was instead systematically shifted off the LvsM axis toward angles requiring increasing S-cone excitation.

While red versus green and blue versus yellow represent mutually exclusive sensations, our results support previous evidence indicating that the opponent pairs are not strongly coupled. For example, judgments of red and green or blue and yellow scale differently with eccentricity, suggesting that they do not depend on a single underlying process.<sup>38,39</sup> The independence of the color-opponent poles is further suggested by the observation that red versus green or blue versus yellow are not collinear within cone-opponent space.<sup>25–27</sup> Our results reinforce the conclusion that the different hue sensations are decoupled, because they suggest that there is little correlation across observers between the settings for the four unique hues. This result is particularly surprising in the case of blue and yellow settings, for at least in some observers they fall very close to defining complementary poles of a single linear axis<sup>25,28</sup> (see Fig. 2).

The weak relationships between the hue settings also imply that the hue judgments are not strongly constrained by normal variations in color sensitivity, which should lead to correlated changes in different axes of color space. In particular, our results failed to show a relationship between the hue loci and the relative sensitivity to the SvsLM and LvsM axes or between the hue loci and peripheral factors that modify the shapes of the cone spectral sensitivities. Again, differences in a factor such as the S/LM sensitivity ratio could plausibly have affected the hue judgments on a number of grounds. First, changing the scaling in a single observer (e.g., through contrast adaptation) does induce corresponding changes in the chromatic angles defining the unique hues.<sup>6</sup> Second, the variability in the relative scaling across observers may, for some hues at least, be comparable in range to the range implied by the variations in the unique hues (see Fig. 3). Third, we showed that if the rules defining the axes of color experience reflected a specific, fixed weighting of the cardinal-axis signals or reflected a common learned feature of the environment, then the stimuli required for the hue judgments should reflect variations in the weightings imposed by factors affecting the cone-opponent axes. Finally, under some conditions the unique-hue settings have been found to be systematically

related to individual differences in peripheral color vision, such as in the relative number of cones<sup>21</sup> (but see Refs. 20 and 22), or the eye pigmentation of the observer.<sup>18</sup>

Yet despite such *a priori* arguments, the absence of measurable correlations between the hue loci for our stimuli suggest that the variations in the unique hues are largely independent of the sensitivity differences across observers. Because of the low reliability for some settings (e.g., unique green), we cannot reject a pattern of weak correlations, but then the implied influence of the factors that we considered must be correspondingly weak. Independent variations in different unique hues have also been observed by others,<sup>40,41</sup> as has independence between measurements of observers' hue settings and spectral sensitivities.<sup>18</sup> Moreover, a similar result is suggested by studies showing largely normal color judgements in observers with highly compromised color sensitivity. For example, Scheffrin *et al.*<sup>42</sup> found that most diabetic observers that they tested made unique-hue settings within the range of normal controls despite large measured losses in S-cone sensitivity. Miyahara *et al.*<sup>43</sup> found that carriers of anomalous trichromacy had highly biased L/M cone ratios but nevertheless made unique yellow settings that were within the range of normal observers. Further, Crognale *et al.*<sup>44</sup> examined color vision in a subject with congenital cone dystrophy. This subject lacked L cones and had abnormally low M- and S-cone sensitivity but made unique-hue settings that were within normal limits for green and blue (though unique yellow and red fell outside the range we have found for normal observers). Thus even observers with markedly different chromatic sensitivities may make concordant appearance judgments.

Such results are difficult to reconcile with a fixed physiological transformation (i.e., a fixed, common weighting of the cone signals) as the basis for the unique hues. It remains possible that the hue loci depend in a simple way on variations in a physiological factor that we have not considered (e.g., in the degree of rod intrusion); yet then different factors that selectively affect specific hues would be required to account for the independent variations in the different hues. This constraint eliminates many of the known peripheral sources of variation in normal color vision, since these sources instead have more global influences on the cone signals for the desaturated lights that we tested. Moreover, variations in hue-specific factors that arise at more central levels of the visual system could dilute the influence of more-peripheral factors, but they should not remove that influence entirely.

The alternative of a fixed environmental basis for the unique hues (e.g., a common learned color signal) also appears inconsistent with the large range of hue settings that we observed. Specifically, our results do not point to a substantial decrease in interobserver differences in perceived hue as the spectra become more broadband or naturalistic. It is possible that observers do show more consistent judgments for real surfaces under natural viewing conditions, but our analysis suggests that this is unlikely to result from changes in the color signal that defines the surface (though it could conceivably result from the much richer context in which these color signals are judged).

On the other hand, if hue judgments do depend on learned characteristics of the environment, then differences in these judgments could plausibly be expected from differences in the visual diets of observers. Shepard<sup>12</sup> noted that natural daylight provides a consistent environmental variable that could underlie a common color organization. However, the color statistics of natural images—of collections of natural surfaces viewed under daylight—vary substantially, and thus different natural contexts may be characterized by very different color signatures.<sup>45</sup> Adaptations to these statistics shape the signals underlying color vision<sup>45</sup> and thus could shape the stimulus dimensions that define an individual's perceptual organization of color. However, it remains to be tested whether differences in the color environment are correlated with hue judgments and whether the environment varies in ways that predict independent variations in the loci for different hues. We are currently exploring these questions.

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## REFERENCES

- I. Abramov and J. Gordon, "Color appearance: on seeing red—or yellow, or green, or blue," *Annu. Rev. Psychol.* **45**, 451–485 (1994).
- L. M. Hurvich and D. Jameson, "An opponent-process theory of color vision," *Psychol. Rev.* **64**, 384–404 (1957).
- E. Hering, *Outlines of a Theory of the Light Sense* (Harvard U. Press, Cambridge, Mass., 1964).
- M. A. Webster, "Human colour perception and its adaptation," *Network Comput. Neural Systems* **7**, 587–634 (1996).
- D. H. Brainard, "Cone contrast and opponent modulation color spaces," in *Human Color Vision*, P. Kaiser and R. M. B. Boynton, eds. (Optical Society of America, Washington D.C., 1996), pp. 563–579.
- M. A. Webster and J. D. Mollon, "The influence of contrast adaptation on color appearance," *Vision Res.* **34**, 1993–2020 (1994).
- R. L. De Valois and K. K. De Valois, "A multi-stage color model," *Vision Res.* **33**, 1053–1065 (1993).
- S. L. Guth, "Model for color vision and light adaptation," *J. Opt. Soc. Am. A* **8**, 976–993 (1991).
- J. Pokorny and V. C. Smith, "Evaluation of single-pigment shift model of anomalous trichromacy," *J. Opt. Soc. Am.* **67**, 1196–1209 (1977).
- J. D. Mollon, "Color vision," *Annu. Rev. Psychol.* **33**, 41–85 (1982).
- H.-C. Lee, "A computational model for opponent color encoding," in *Advanced Printing of Conference Summaries*, SPSE's 43rd Annual Conference (Society for Imaging Science and Technology, Springfield, Va., 1990), pp. 178–181.
- R. N. Shepard, "The perceptual organization of colors: an adaptation to regularities of the terrestrial world?" in *The Adapted Mind*, J. Barkow, L. Cosmides, and J. Tooby, eds. (Oxford U. Press, Oxford, UK, 1992), pp. 495–532.
- D. M. Purdy, "Spectral hues as a function of intensity," *J. Psychol.* **43**, 541–559 (1931).
- B. Scheffrin and J. S. Werner, "Loci of spectral unique hues throughout the lifespan," *J. Opt. Soc. Am. A* **7**, 305–311 (1990).
- V. C. Smith and J. Pokorny, "Chromatic discrimination axes, CRT phosphor spectra, and individual variation in color vision," *J. Opt. Soc. Am. A* **12**, 27–35 (1995).
- M. A. Webster and D. I. A. MacLeod, "Factors underlying individual differences in the color matches of normal observers," *J. Opt. Soc. Am. A* **5**, 1722–1735 (1988).
- M. A. Webster, E. Miyahara, G. Malkoc, and V. E. Raker, "Variations in normal color vision. I. Cone-opponent axes," *J. Opt. Soc. Am. A* **17**, 1535–1544 (2000).
- G. Jordan and J. D. Mollon, "Rayleigh matches and unique green," *Vision Res.* **35**, 613–620 (1995).
- J. D. Mollon and G. Jordan, "On the nature of unique hues," in *John Dalton's Colour Vision Legacy*, C. Dickenson, I. Murray, and D. Carden, eds. (Taylor & Francis, London, 1997), pp. 381–392.
- D. H. Brainard, A. Roorda, Y. Yamauchi, J. B. Calderone, A. Metha, M. Neitz, J. Neitz, D. R. Williams, and G. H. Jacobs, "Functional consequences of the relative numbers of L and M cones," *J. Opt. Soc. Am. A* **17**, 607–614 (2000).
- S. Otake and C. M. Cicerone, "L and M cone relative numerosity and red–green opponency from fovea to midperiphery in the human retina," *J. Opt. Soc. Am. A* **17**, 615–627 (2000).
- J. Pokorny and V. C. Smith, "L/M cone ratios and the null point of the perceptual red/green opponent system," *Farbe* **34**, 53–57 (1987).
- M. A. Webster and J. D. Mollon, "Changes in colour appearance following post-receptoral adaptation," *Nature* **349**, 235–238 (1991).
- D. I. A. MacLeod and R. M. Boynton, "Chromaticity diagram showing cone excitation by stimuli of equal luminance," *J. Opt. Soc. Am.* **69**, 1183–1186 (1979).
- S. A. Burns, A. E. Elsner, J. Pokorny, and V. C. Smith, "The Abney effect: chromaticity of unique and other constant hues," *Vision Res.* **24**, 479–489 (1984).
- E. J. Chichilnisky and B. A. Wandell, "Trichromatic opponent color classification," *Vision Res.* **39**, 3444–3458 (1999).
- R. L. De Valois, K. K. De Valois, E. Switkes, and L. Mahon, "Hue scaling of isoluminant and cone-specific lights," *Vision Res.* **37**, 885–897 (1997).
- J. Larimer, D. H. Krantz, and C. M. Cicerone, "Opponent-process additivity I. Red/green equilibria," *Vision Res.* **14**, 1127–1140 (1974).
- J. Larimer, D. H. Krantz, and C. M. Cicerone, "Opponent-process additivity—II. Yellow/blue equilibria and nonlinear models," *Vision Res.* **15**, 723–731 (1975).
- C. M. Cicerone, "Constraints placed on color vision models by the relative numbers of different cone classes in human fovea centralis," *Farbe* **34**, 59–66 (1987).
- D. I. A. MacLeod and M. A. Webster, "Factors influencing the color matches of normal observers," in *Colour Vision: Physiology and Psychophysics*, J. D. Mollon and L. T. Sharpe, eds. (Academic, London, 1983), pp. 81–92.
- W. S. Stiles and J. Burch, M., "N.P.L. colour matching investigation: final report (1958)," *Opt. Acta* **6**, 1–26 (1959).
- P. Kay, B. Berlin, L. Maffi, and W. Merrifield, "Color naming across languages," in *Color Categories in Thought and Language*, C. L. Hardin and L. Maffi, eds. (Cambridge U. Press, Cambridge, UK, 1997), pp. 21–56.
- D. B. Judd, D. L. MacAdam, and G. Wyszecki, "Spectral distribution of typical daylight as a function of correlated color temperature," *J. Opt. Soc. Am.* **54**, 1031–1040 (1964).
- J. Cohen, "Dependency of the spectral reflectance curves of the Munsell color chips," *Psychon. Sci.* **1**, 369–370 (1964).
- S. K. Shevell and R. A. Humanski, "Color perception under chromatic adaptation: red/green equilibria with adapted short-wavelength-sensitive cones," *Vision Res.* **28**, 1345–1356 (1988).
- J. S. Werner and B. R. Wooten, "Opponent chromatic mechanisms: relation to photopigments and hue naming," *J. Opt. Soc. Am.* **69**, 422–434 (1979).

38. I. Abramov, J. Gordon, and H. Chan, "Color appearance in the peripheral retina: effects of stimulus size," *J. Opt. Soc. Am. A* **8**, 404–414 (1991).
39. C. F. I. Stromeyer, J. Lee, and R. T. Eskew, "Peripheral chromatic sensitivity for flashes: a post-receptoral red-green asymmetry," *Vision Res.* **32**, 1865–1873 (1992).
40. C. E. Harlow, V. J. Volbrecht, and J. L. Nerger, "What determines the population variability in the locus of unique green?" *Invest. Ophthalmol. Visual Sci. Suppl.* **40**, S355 (1999).
41. I. Abramov, J. Gordon, B. E. Scheffrin, and J. S. Werner, "Spectral loci of unique hues: population statistics," *Invest. Ophthalmol. Visual Sci. Suppl.* **35**, 2166 (1994).
42. B. E. Scheffrin, A. J. Adams, and J. S. Werner, "Anomalies beyond sites of chromatic opponency contribute to sensitivity losses of an *S*-cone pathway in diabetes," *Clin. Vision Sci.* **6**, 219–228 (1991).
43. E. Miyahara, J. Pokorny, V. C. Smith, R. Baron, and E. Baron, "Color vision in two observers with highly biased LWS/MWS cone ratios," *Vision Res.* **38**, 601–612 (1998).
44. M. A. Crognale, J. B. Nolan, M. A. Webster, M. Neitz, and J. Neitz, "Color vision and genetics in a case of congenital optic nerve dystrophy," *Color Res. Appl.* (to be published).
45. M. A. Webster and J. D. Mollon, "Adaptation and the color statistics of natural images," *Vision Res.* **37**, 3283–3298 (1997).