Hue Scaling of Isoluminant and Cone-specific Lights

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Using a hue scaling technique, we have examined the appearance of colored spots produced by shifts from white to isoluminant stimuli along various color vectors in order to examine color appearance without the complications of the combined luminance and chromatic stimulation involved in most previous hue scaling studies, which have used flashes of monochromatic light. We also used spots lying along cone-isolating vectors in order to determine what hues would be reported with a change in activation of only single cone types or of only single geniculate opponent-cell types, an issue of direct relevance to any model of color vision. We find that:

1. Unique hues do not correspond either to the change in activation of single cone types or of single geniculate opponent-cell types. This is well known to be the case for yellow and blue, but we find it to be true for red and green as well.

2. These conclusions are not limited to the particular white (Illuminant C) used as an adapting background in most of the experiments. Shifts along the same cone-contrast vectors relative to different backgrounds lead to much the same hue percepts, independent of the starting white used.

3. The shifts of the perceptual colors from the geniculate axes are in the directions, and close to the absolute amounts, predicted by our [De Valois & De Valois (1993). Vision Research, 33, 1053-1065] multi-stage color model in which we postulate that the S-opponent cells are added to or subtracted from the M- and L-opponent cells to form the four perceptual color systems.

4. There are distinct asymmetries with respect to the extent to which various hues within each perceptual opponent system deviate from the geniculate opponent-cell axes. Blue is shifted more from the S-LM axis than is yellow; green is shifted more from the L-M axis than is red. There are also asymmetries in the angular extent of opponent color regions. Blue is seen over a larger range of color vectors than is yellow, and red over a slightly larger range than green.

5. Such asymmetries are not accounted for by any model that treats red–green and yellow–blue each as unitary, mirror-image opponent-color systems. Although red and green are perceptually opponent, the red and green perceptual systems do not appear to be constructed in a mirror-image fashion with respect to input from different cone types or from different geniculate opponent-cell types. The same is true for yellow and blue. © 1997 Elsevier Science Ltd. All rights reserved.

INTRODUCTION

In many studies observers have named the colors of spectral lights, usually presented as incremental flashes on a dark background (e.g. Boynton & Gordon, 1965; Abramov et al., 1990). Such studies enable one to examine the appearance of various monochromatic lights and provide data from which one can obtain discrimination functions that are as reliable as the classic discrimination results (Jacobs & Gaylord, 1967; Graham et al., 1976).

In the present study we examined color naming, or more precisely, hue scaling, for isoluminant shifts from white to chromatic stimuli rather than for increments of monochromatic light from a dark background as used by previous investigators. There were three reasons for this re-examination of hue scaling. One was that the use of isoluminant stimuli eliminates the interpretative complications results from combining color changes with luminance changes, as in the earlier studies. A second was that extending the hue scaling studies to the extraspectral purple region enables us to determine the relation between the red and green perceptual color vectors. The third was to examine hue scaling in direct relation to the amount of activation produced by specific geniculate opponent-cell types. In addition, we studied
hue scaling for (non-isoluminant) stimuli that differed from the background only by increments and decrements in L- or M-cone activation. Several questions that are central to color vision could thereby be directly addressed.

Our interest in these questions was raised by some implications from a color vision model we recently proposed (De Valois & De Valois, 1993). In the model, we considered not just what arbitrary cone inputs might be combined to produce different unique hues, but rather, we attempted to model the successive processing stages from cones to lateral geniculate (LGN) neurons, and from the LGN to perception. The essence of our model is that the predominant input to all the color systems comes from those LGN opponent cells that difference the L and M cones. We postulate that the output of the S-cone opponent system (S_b) is then combined in different directions with the outputs of the M and L opponent cells (M_o and L_o) at a late processing stage. This would serve to split and rotate the one dominant LGN opponent axis into separate axes corresponding to the RG and YB perceptual color axes. The model predicts that the different perceptual color systems corresponding to this later stage should deviate both from the cone axes and from the geniculate opponent cell axes in predictable ways. We have therefore used hue scaling to test these predictions directly.

**EXPERIMENT 1**

**Methods**

**Stimuli.** The stimuli were presented on an RGB Sony color monitor controlled by a Sun 3/160 computer with a TAAC graphics accelerator. Subjects viewed the monitor binocularly through an aperture that subtended 22 deg at the 58 cm viewing distance used. Each 2 deg stimulus was briefly presented (500 msec) in the center of the display as a color change from a uniform white field. In the principal study, the background was white (Illuminant C: \( x = 0.310, \ y = 0.316, \) 18 cd/m²), and the colored stimulus spots were at the ends of various isoluminant chromatic vectors starting from this white. The L- and M-cone specific (and thus non-isoluminant) stimuli were also presented as shifts from the same background.

In the MacLeod–Boynton isoluminant cone color space as formalized by Derrington et al. (MacLeod & Boynton, 1979; Derrington et al., 1984), the angle \( \phi \) gives the chromatic direction, with 0–180 deg corresponding to the LM-varying axis and 90–270 deg to the S-varying axis. Thus, for stimuli along the 0–180 deg
axis, S-cone activation is constant. In one (0 deg) direction total L-cone activation increases and total M-cone activation decreases proportionately; in the other (180 deg) direction M-cone activation increases and L-cone activation decreases proportionately. For stimuli varying along the 90–270 deg axis, L- and M-cone activation is constant, with variation only in S-cone activation. In one direction [90 deg in our implementation (Rabin et al., 1994)], S-cone activation increases, and in the other (270 deg) direction it decreases (S cones are presumed not to contribute to luminance, thus luminance remains constant despite variation in S-cone activity). The stimuli represented by 0, 180, 90, and 270 deg should be ones that selectively excite one of the four geniculate opponent cell types (De Valois et al., 1966; Derrington et al., 1984).

In addition to stimuli at each end of these geniculate axes, we presented colors at each end of three intermediate axes between 0 and 90 deg, and also at the ends of three axes between 90 and 180 deg, for a total of 16 isoluminant colors, see Fig. 1. The intermediate colors were chosen to be approximately equally spaced perceptually around the circle. We also made some measurements with an alternate set of 16 isoluminant colors that lay along vectors in between those of the 16 standard colors. The CIE coordinates of the standard stimuli are given in Table 1.

The angles by which the intermediate axes are denoted, and the lengths of the chromatic vectors, depend on how one (arbitrarily) weights the 0–180 deg axis vs the 90–270 deg axis. Following the convention used by Derrington et al. (1984) we set the stimuli at the ends of each of these orthogonal 0–180 deg and 90–270 deg axes for the maximum excursion possible with our color monitor, given equal cone activations in the two opposite directions around the Illuminant C center point. These axes were then treated as unit vectors in specifying the intermediate angles and vector lengths, e.g. the 45 deg vector was specified as a vector having equal (√2/2) contributions from the 0 and 90 deg vectors.

In Fig. 2 we show how the cone contrasts for the L, M, and S cones vary as a function of the color vector. [The cone contrast for a particular cone type is defined as its change in activation by the chromatic stimulus divided by its activation at the mean (Illuminant C), e.g. $C_L = \Delta L/L_{mean}$] Note that the L and M cone contrasts are maximum at 0 and 180 deg, and zero at 90 and 270 deg, while the S cone contrasts are just the reverse. Since these are all isoluminant stimuli, the L and M cone contrasts are always opposite in sign and in a fixed 1.91/1 $C_M/C_L$ ratio, reflecting the relative 1.91 L/M cone activations at Illuminant C. The S cone contrasts are much higher than those for the L and M cones (note that they are plotted in Fig. 2 at half-amplitude). Cone activations were calculated using the Smith and Pokorny (1975) cone fundamentals and the assumptions regarding cone populations described by Wyszecki and Stiles (1982).

In addition to these isoluminant colors, we used four non-isoluminant, cone-isolating colors, presented as shifts from the same Illuminant C background. These stimuli increased or decreased, respectively, the activation of only the L or of only the M cones. (The 90 and 270 deg isoluminant stimuli were of course also cone-isolating, for the S cones.) We thus had six cone-isolating stimuli, which respectively were increments or decrements for each of the three cone types.

Procedure. In a procedure much like that used by previous investigators (e.g. Boynton & Gordon, 1965; Abramov et al., 1990), the observer scaled the color presented in terms of one or more of four hue names: red, yellow, green, and blue. The hue scaling was signaled to the computer, which controlled the experiment and tabulated the results, by the use of four correspondingly color-coded response buttons. The observer specified the color perceived by making five button presses, in any combination and order. A pure green would thus be signaled with five green responses (GGGGG); one seen as mainly green but with a little yellow would be GGGGY; a still more yellowish green would be GGYYY; and then GYYY and GYYY to a pure yellow, YYYY. [In preliminary trials, we found that observers preferred, and differentially used, a scale finer than the three-level scale, e.g. GGG, GGY, GYY, YYYY, etc., used by Boynton & Gordon (1965), but did not require a 100-point scale as used by Abramov et al. (1990).] Although we did not restrict their responses, the observers, not surprisingly, never used more than two buttons to specify a given stimulus on a given trial, i.e. they never called a color BGGYY, although they might on one trial call it GGGGY and on another GGGGB. The stimuli were presented in random order, each stimulus being presented five times in the course of a run. The computer totaled the number of times each of the four colors was called in a trial, and each observer was presented with 100 trials.

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buttons was pressed in response to each stimulus color. Each observer participated in 5–10 sessions, with the individual sessions being dispersed over periods of days, among trials on other experiments and trials using the alternate colors. This minimized the extent to which the observer could remember the individual stimuli and how s/he had described them previously.

Data were collected from two of the experimenters and two naïve observers. All have normal color vision as measured by the Farnsworth-Munsell 100-hue test, Ishihara plates, and settings on a Nagel anomaloscope. The main features of these results have been confirmed on several other observers who were tested less extensively, and whose data we do not present here.

Results

Models of color vision based solely on the characteristics of geniculate cells make quite precise predictions about what colors one should see with the various stimuli we presented. A common version of such models has two opponent-color channels, corresponding to the two main types of geniculate opponent cells: a red–green opponent channel that differences the outputs of the L and M cones, and a yellow–blue opponent channel that differences the S and the (L + M) cone outputs. The L–M stimulus (0 deg) should thus be seen as red, M–L (180 deg) as green, S–LM (90 deg) as blue, and LM–S (270 deg) as yellow, see Discussion. (In the figures we abbreviate S–LM as +S, and LM–S as −S.)

What we found was quite different. Figure 3 shows the results from each of our four observers for their hue scaling of the various isoluminant colors around the circle. On the x-axis are the various color directions (or color vectors) given by the angle $\phi$. On the y-axis is the percentage of all responses in which a given hue name was used to describe the stimulus at each color vector. The data are partially repeated (for $\phi \geq 360$ deg) so that one can see the red (R) function as a whole. The vertical lines mark the locations of each of the geniculate opponent-cell vectors, those that Krauskopf et al.
FIGURE 3. Hue scaling of isoluminant spots for each of the four observers. Plotted for each color vector is the percentage of times that that stimulus was called each of the four permissible color names (R, Y, G, or B). Spline-fit curves join the points for each color name. In order to show the red function as a whole rather than as two separate parts, the values from 0–90 deg have been repeated at right (0 = 360 deg, etc.). The vertical lines show the locations of the geniculate opponent-cell vectors [the cardinal axes of Krauskopf et al. (1982)]; 90 deg = +S–LM; 180 deg = M–L, etc. It can be seen that the dominant directions in color space identified by the four color names do not coincide with the geniculate axes for any of the observers. Note also that blue is shifted more from the tritan axis than is yellow, and green is shifted more from the LM-varying axis than is red.

(1982) refer to as the cardinal axes. It can be seen that the data for the different observers are generally quite similar, the only considerable individual differences being in the R function. For comparison with models, the averaged data for these four observers were used and are presented in the Discussion, see Fig. 8.

There are two points of particular interest in these data. First, the different color regions and unique hues are not centered either on the 0–180 deg axis or on the 90–270 deg axis, as predicted from simple geniculate-based models, but are in each case shifted away from these axes by various amounts. Secondly, there are distinct asymmetries in the extent to which the opposite ends of what are supposedly unitary opponent-color axes are shifted away from the geniculate axes, and there are also asymmetries in the angular extents of the opponent color regions.

**RG/YB color diamond.** To further examine how the perceptual scaling is related to geniculate axes, the same data are presented in a different way in Fig. 4. This is in effect a quantitative version of the traditional color circle, although as we formulate it, it is a color diamond, not a circle. This representation is similar to the uniform appearance diagram of Abramov et al. (1990). The vertical axis represents the percentage of times the stimulus was called red minus the percentage of times it was called green (%R–%G); the horizontal axis indicates %Y–%B. Thus a color that was called red 100% of the time would be plotted at 0 on the YB axis and 100 on the RG axis; a color called blue 100% of the time would be −100 on the YB axis and 0 on the RG axis; one called red 50% of the time and blue 50% of the time would be plotted half way down the top left diagonal, at 50 RG and −50 YB, etc. If the particular set of stimuli used included the unique hues for that observer, and if the observer never used both opponent color names for a given stimulus (e.g., never specified a particular color as being yellow with a little red, and another time yellow with a little green), the data for that observer would all lie along diagonal lines with the corners at the unique hue axes. While this type of presentation loses some information about the actual color-scale values given to individual stimuli, it provides a convenient summary of the data and also allows comparison with the presentation in the same format of our cone-specific stimuli data (see below).

In Fig. 4 the four geniculate opponent-cell vectors 0,
90, 180 and 270 deg are also shown. Both of the points made with respect to the data in Fig. 3 can also be seen in this representation. The perceptual color vectors (B, G, Y, R) do not coincide with the geniculate opponent-cell vectors, but deviate from them to various degrees. Secondly, the opposite ends of what have been considered unitary color axes deviate by different amounts, respectively, from the geniculate axes (0–180 deg, and 90–270 deg).

**Rotation of color axes.** The fact that the geniculate cells that difference the S cones from some combination of the longer-wave cone types have a chromatic response axis different from the blue–yellow perceptual color axis was noted by Krauskopf et al. (1982); Derrington et al. (1984); Drum (1989), Abramov and Gordon (1994) and others. The data shown in Fig. 3 are in accordance with that: the blue and yellow peaks do not occur at +S–LM and −S + LM (90 and 270 deg, respectively), but are shifted away from that axis. Our data show that the same is also true for the red–green perceptual directions, as discussed by Abramov and Gordon (1994), but contrary to the conclusion of Krauskopf et al. (1982). The red and especially the green perceptual peaks deviate from the corresponding geniculate axes (0 and 180 deg, respectively).

**Asymmetries.** An important finding of this experiment is that of significant asymmetries between the two halves of what have long been treated as unitary, mirror-image opponent-color systems. It is explicit in geniculate-based models, as well as in such alternatives as the recent theory of Guth (1991), that there are three chromatic systems: a red–green system, a yellow–blue system, and a black–white system. Each of these is treated as a single (mirror-image) system, e.g. L–M and M–L for the red–green system in geniculate-based models or, in Guth’s 1991 model \[0.388(0.8845L - 0.7258M) + (-0.077L +

**FIGURE 4.** RG/YB color diamond. The data shown in Fig. 3 were transformed into % R–% G and % Y–% B and plotted as in the traditional color circle. For each stimulus, the percentage of time it was called G was subtracted from the percentage of time it was called R to determine the y-axis coordinate for that stimulus. The percentage of time it was called B was subtracted from the percentage it was called Y to determine the x-axis coordinate. White, in such a diagram, should be at the center (0% red or green, 0% yellow or blue), although we did not make saturation measurements. Also shown on this diagram are the geniculate opponent-cell vectors. It can be seen in this color-appearance diagram that the hue vectors do not coincide with the geniculate opponent-cell vectors, and that there are asymmetries between the amounts of deviation in opposite chromatic directions.
0.013M + 0.091S]) for red vs the opposite for green. We find, however, that for all of our subjects, the shift of the perceptual red vector from the L–M, M–L geniculate axis is less than that of the green. It can be seen in Fig. 3, for instance, that the L–M stimulus (0 and 360 deg) was called red most of the time by all observers, but the M–L stimulus (180 deg) was seen as blue almost as frequently as green. Similarly, our observers find blue to be shifted from the S–LM vector to a greater degree than yellow is from the LM–S vector.

The unique hues are traditionally defined by exclusion: e.g., unique yellow is that yellow which is seen as containing neither any green nor any red (Hurvich & Jameson, 1955). The directions in color space from white that produce the unique hues, then, are those at which, for a given observer, the G–R and the Y–B functions, as computed in Fig. 4, cross zero. That is, unique yellow and blue lie on those chromatic vectors at which the R–G function is zero (thus these colors are seen as having no red or green); and the unique green and red vectors are correspondingly at those points at which the Y–B function crosses zero. It can be seen in Fig. 4 that with the exception of red (for at least two of the observers), the unique hue points do not correspond to the LGN axes.

**Cone-isolating stimuli.** In addition to having observers scale the various isoluminant stimuli, we examined hue scaling of (non-isoluminant) stimuli that activated just the L or just the M cones, relative to the white background. The data for cone-isolating stimuli are most clearly presented in the RG–YB color diamond. The data for the individual observers are shown in Fig. 5(A), and the results averaged across observers in Fig. 5(B). The results from the S-cone isolating stimuli (90 and 270 deg in MacLeod–Boynton space) are also shown in Fig. 5(A and B).

It can be seen that, in general, S-cone increments were described as reddish blue (purple), and S-cone decrements as greenish-yellow (chartreuse), as noted earlier. L-cone increments were called yellowish-red (orange) and L-cone decrements, blue-green (cyan). M-cone changes came closest to corresponding to single unique hue categories: M-cone increments were named a slightly bluish-green, and M-cone decrements a slightly bluish-red.

Note that these data from the single-cone-activating stimuli clearly show the same asymmetry seen in the isoluminant data. Shifts towards long wavelengths (+L and −M) are seen as closer to red than shifts in the opposite direction (+M and −L) are to green. This agrees with the results from isoluminant stimuli that show perceptual red to be close to the L–M vector, but green about halfway between the +S and the M–L vectors.

**EXPERIMENT 2: HUE SCALING FROM A DIFFERENT “WHITE” POINT**

The data in Experiment 1 were collected using stimuli presented as shifts from a background of Illuminant C. The question arises whether these results, which show large discrepancies from what geniculate-based models would predict and also asymmetries within the opponent-color systems, were just due to the particular white point used. We therefore collected additional hue scaling data with isoluminant stimuli on a different “white” background. These data also bear on the question of the extent to which something like von Kries adaptation is operative.

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**FIGURE 5.** Hue scaling of cone-isolating stimuli, presented in a RG/YB color diamond plot. Plotted here are the hues reported when the photon catch for each of the cone types in turn is either increased or decreased, without any change in activation of the other cone types. In (A) are the data for each observer; in (B) the data are averaged across observers. It can be seen that unique hue vectors do not correspond to the activation of single cone types. Note also that either increasing or decreasing the activation of M cones leads to a percept of some amount of blue.
Methods

We examined the hue scaling of isoluminant and cone-specific stimuli from two different white points: Illuminant C, as before, and Illuminant B (CIE coordinates: $x = 0.3485$, $y = 0.3517$). In Experiment 1 we had used the maximum balanced excursions in cone activation around Illuminant C for the 0–180 and 90–270 deg axes that were possible with our monitor. It is not possible to produce balanced excursions of this size from each of two different center points. Therefore, to produce identical cone contrasts for the Illuminant C and Illuminant B tests in Experiment 2, we reduced the excursions from white slightly (and thus the saturation of the stimuli), and collected data from two naive observers for excursions from Illuminant C as well as from Illuminant B with these new stimulus sets. The CIE coordinates of the stimuli are shown in Fig. 6. Note that shifts in each of the isoluminant color directions from these two different center points resulted in chromatic stimuli which had the same cone contrasts, but which differed from each other in their spectral loci, and in their dominant wavelengths. We used a newer and slightly brighter version of the Sony monitor used in Experiment 1, at a mean luminance of 28 cd/m².

Results

Figure 7 presents the results for isoluminant shifts along the various chromatic vectors from Illuminant B (dashed lines and open symbols) compared with those from Illuminant C (solid lines and filled symbols), for each of the two observers. The results are essentially identical for these two different conditions. Thus the main conclusions from Experiment 1 were supported by the data from these two additional observers, and this experiment shows that our earlier conclusions are not limited to isoluminant stimuli along various vectors around Illuminant C. The different hue regions again failed to coincide with the geniculate opponent-cell axes but rather fell in between them, as in Experiment 1 and as predicted by our color model.

Note that for a given color vector ($\phi$), the stimuli in the Illuminant C vs B tests had quite different chromaticities, as shown in Fig. 6, but the cone contrasts for the two comparable stimuli in each case were the same. Note also that the stimuli on the Illuminant B background are not
simply rigid translations in CIE space of the ones centered on Illuminant C.

A question could be raised as to whether these results might be accounted for on the basis of the dominant wavelength of the stimuli. However, the color vectors around Illuminant C and B corresponding to the same dominant wavelength differ by as much as 13 deg (e.g. a color vector of 155 deg with respect to Illuminant B has the same dominant wavelength as 168 deg with respect to Illuminant C), and they deviate systematically from each other. Consequently, there should be systematic shifts of up to 10 deg or more between the two sets of hue scaling curves, shifts that we did not find, as can be seen in Fig. 7. The fact that the observers reported the two different stimuli along each particular color vector to be the same hue indicates that cone contrast relative to the white background, not absolute chromaticity or dominant wavelength, is the crucial variable under these circumstances. This is what would be expected if virtually complete von Kries (receptor-specific) adaptation occurred with the shift from Illuminant C to Illuminant B. The results might well be different with more extreme chromatic adaptation, outside the range of lights seen with adaptation as white, such as the red and green backgrounds studied by Stromeyer et al. (1985).

**DISCUSSION**

There have been several previous investigations of hue scaling using monochromatic lights (e.g. Boynton &

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**FIGURE 7.** Comparison of hue scaling of isoluminant stimuli of the same cone contrast vectors, but from a background white of Illuminant C (solid lines and symbols) in one case and from Illuminant B (dashed lines and open symbols) in the other. The data are quite similar to each other (and to those presented in Fig. 3 for larger excursions around Illuminant C). Thus our results showing a deviation of color regions from the geniculate axes do not depend on the particular white used in Experiment 1. They also show that the critical variable determining the color seen under these circumstances is the cone contrast, not the absolute chromaticity or the dominant wavelength.
monochromatic rather than color luminance. Jameson (1965; Abramov et al., 1990). These are superficially similar to our study, but there are certain important differences. One was that we did not use monochromatic increments of different wavelength, but rather isoluminant color changes from white. This simplifies the interpretation of the results, by leaving just color changes as opposed to combined color and luminance changes. Another important difference between this study and earlier hue scaling studies is that we examined hue scaling in many directions from the white points, including the roughly one-quarter of the color vectors that are in extraspectral directions. This is of particular importance in looking at the relations between opponent colors since, for most observers, perceptually unique red is extraspectral. By examining hue scaling in all color directions from white we could examine the whole perceptual red function to see how it relates to the green function.

It is also of obvious importance for understanding the physiological underpinning of color perception to determine as precisely as possible how color appearance is related to the activity of the receptors and of neurons at different levels in the visual system. This is difficult to do when the physiological and perceptual experiments to be compared are conducted under quite different experimental conditions. One aim of these experiments was to examine hue scaling of stimuli under very similar conditions to those used in the geniculate recording experiments of Derrington et al. (1984), and under conditions identical to those in our ongoing repetition and extension of those LGN recording studies.

If there were no color processing past the geniculate, and if the red–green perceptual system were based on cells that difference the output of the L and M cones, the red and green perceptual maxima should be at 0 and 180 deg, respectively, and the crosspoints of the LM cells at 90 and 270 deg, should coincide with unique blue and unique yellow. Correspondingly, if the yellow–blue system were just based on differencing the outputs of the S cones from the L+M cones, the yellow and blue perceptual maxima should be at 270 and 90 deg, and unique red and unique green should be at the crosspoints of these cells, at 0 and 180 deg, respectively. The discrepancies between these predictions and the data shown in Figs 3 and 7 are quite obvious. The actual colors seen with various isoluminant stimuli do not agree with the geniculate cell axes. The point that the yellow–blue perceptual axis is rotated with respect to the S–LM geniculate axis was made by Krauskopf et al. (1982) and others and is widely accepted. Our data directly confirm this. But our data also show that a rotation of similar magnitude occurs with respect to the red–green function, contrary to the statement of Krauskopf et al. (1982). There has long been considerable evidence for an S-cone contribution to the red mechanism (e.g. Hurvich & Jameson, 1955; Ingling, 1977; Wooten & Werner, 1979), accounting for the reddish appearance of short wavelength lights. This is consistent with the small shift in the red peak to color vectors above 0 deg that we see in our data. However, our data show that the principal deviation of red–green from the LM axis is at the green end of the red–green function. It is in fact this larger rotation of the green end which produces the large red–green asymmetry we discuss below.

There is a long and unfortunate history, decreasingly followed recently by visual psychophysicists but still very common among visual anatomists and physiologists, of referring to “blue cones”, “green cones”, and “red cones”. Calling cones by color names effectively perpetuates the idea that color, as opposed to, say, form and motion, is totally determined at the receptor level, and does not involve any significant later neural processing. The results we present here, as well as many other lines of evidence, show that that is not the case: clearly, in addition to cone-opponent processing in the retina, at least one later cortical stage is required to account for even the most basic color organization.

As discussed further below, the model we (De Valois & De Valois, 1993) recently suggested comes somewhat closer to predicting correctly the colors seen along various chromatic vectors than does a geniculate-based model. In our model, we dissociate the perceptual color axes from the geniculate axes, postulating a third processing stage at which the geniculate information is combined in various ways that lead to the perceptual color space. Specifically, we postulate that the outputs of the (relatively few, scattered) S–LM opponent cells (which we term S, cells, for short) are added to or subtracted from the outputs of the more common geniculate cells that difference the two longer-wavelength cone types (the +L, −L, +M, and −M, cells, respectively) to form the four perceptual hue systems. This modulation of the various LM opponent cells by the S, cells would produce the observed effect of rotating the perceptual color axes with respect to the geniculate cell axes. Thus, for instance, the subtraction of the outputs of +S–LM cells from that of +M–L cells to form the green mechanism shifts the green peak from the M–L axis of 180 deg to about 215 deg. Our model thus predicts that none of the perceptual hue peaks would coincide with the geniculate axes, but rather would lie in between the geniculate axes, as they in general do.

A second major conclusion from this experiment is that there are considerable asymmetries between the two halves of what modern color models treat as single, unitary opponent-color systems. That is, we find that the particular cone and geniculate cell combinations that lead to the percept of red are not the opposite of those that produce green. It is interesting that Abramov et al. (1991) have also found an asymmetry of a different sort between the supposed mirror-image color systems. They determined how large peripheral stimuli had to be to appear as saturated as small foveal stimuli, and found that green spots in the periphery needed to be much larger than red ones, and yellow bigger than blue, to match foveal spots of a fixed diameter. Burns et al. (1984), in a study of the Abney effect, also report a red–green asymmetry.

In our model (De Valois & De Valois, 1993), we
FIGURE 8. (A) The hue-scaling results expected if perceptual color space corresponded to the outputs of the geniculate cells. (B) The isoluminant hue-scaling data from Experiment 1, averaged across our four observers. In (C) (solid lines) are shown the predictions based on cone contrast with a weighting of cone inputs into the various color systems that corresponds to the third stage of the De Valois and De Valois (1993) model. The dashed lines and open symbols for the Y and R functions in (C) reflect our modified model, with S_y weightings of 3.5 for Y and 1 for R, instead of weights of 2 for S_y inputs to all systems as in the original model. One can see that the geniculate axes (A) do not predict accurately the location of different color regions (B) found in the data. The regions corresponding to the different hues are all shifted away from the geniculate axes. On the other hand, the De Valois and De Valois model (C), particularly with the modified weights for Y and R (dashed lines), comes quite close to predicting the actual hue-scaling data: it predicts reasonably well the regions seen as blue, green, yellow, and red, and also the cross-points from one color to another (the classic unique hue points). It does not, however, predict to lesser widths of the yellow and green regions.

postulated separate systems for red and green, and separate systems for yellow and blue, treating each of the four unique hue systems individually rather than as opposite ends of only two chromatic mechanisms. However, in that initial version of the model we postulated mirror-image inputs to the two halves of each opponent pair, which is not in accordance with the data from this experiment. It seems apparent that while the red
and green subsystems are tied together in a perceptual color-opponent organization, the particular combination of geniculate inputs that are put together to form red is not identical to that combination that produces green. The same is true for the yellow and blue subsystems.

**Modeling**

To look at some of these issues further, we have examined more quantitatively the predictions for hue scaling made by models of cone inputs to geniculate cell responses to perceptual color systems. An immediate issue in any such analysis is what cone-input metric to use. There are three obvious possibilities: absolute cone activation; change in cone activation from the white point (which we shall call Δ activation); and cone contrast (or Δ activation divided by the mean). Absolute cone activation is akin to the classical modeling of hue naming functions describing the appearance of incremental monochromatic lights presented on a dark background. Cone contrast and Δ activation are both metrics that depend upon the background illuminant, which is important when modeling responses to excursions from nonzero backgrounds. In our modeling using absolute and Δ cone-activation, the individual L-, M-, and S-cone activations were scaled as in our previous treatment (De Valois & De Valois, 1993). However, cone contrast, a ratio metric is invariant to such assumptions about relative scaling.

In comparing models to our data, three aspects are particularly salient: do the models generally predict the hues named along the different directions? Do the peaks of the hue scaling functions correspond to the maximal responses of the relevant mechanisms? And do the predictions match the data for the different white backgrounds (Illuminants B and C)? As might be expected, results using absolute cone activation fail in several respects. The resultant response curves (from the rectified third stage of the De Valois and De Valois model) are biased towards yellow, predicting that only a very limited region would be seen as blue, and give large shifts with a change from Illuminant C to B. The predictions using Δ activation and cone contrast as input metrics are somewhat similar to each other, but the smaller shift with different white backgrounds predicted using a cone contrast metric better matches the experimental observations. For these reasons, we have taken cone contrast as the relevant input metric in the following analysis.

For each of the 16 isoluminant color vectors used in the main experiment, we plotted the outputs of the RG and YB systems as predicted by an assumed identity between geniculate responses and perceived hues, and by the rectified third stage of the De Valois and De Valois (1993) model. In Fig. 8 we show the predictions from the two models along with the average hue scaling results from our four observers. It is clear that neither model fits the data perfectly, but the experimental results [Fig. 8(B)] are much closer to the De Valois and De Valois three-stage model [Fig. 8(C)] than they are to the geniculate model [Fig. 8(A)]. The different hue regions do not coincide with the geniculate axes, but instead lie between these axes (as predicted by the three-stage model, and by an amount close to that predicted by the three-stage model).

Since the stimuli presented as shifts from the Illuminant C and B backgrounds (Experiment 2) were selected to have virtually identical cone contrasts, the three-stage model using inputs based on cone contrasts would also predict virtually identical hue scaling curves for the two backgrounds, as we observed (Fig. 7).

While there is fairly good agreement between the data and the predictions from the three-stage model as shown in Fig. 8(B and C), there are certain discrepancies. First, the locations of the perceptual color axes with respect to the geniculate axes are not precisely those predicted by the model. Secondly, the model predicts symmetrical RG and YB functions while the data clearly show certain asymmetries between the separate red and green functions, and between the yellow and blue functions.

Our color model suggests that there is effectively only a single geniculate color axis, 0–180 deg, that of the predominant parvocellular-layer neurons that difference the L and M cones. We then postulate that at some cortical level the relatively few S$_o$ cells, doubled in weight are added to or subtracted from the LM cells to split and rotate this dominant geniculate axis in opposite directions, forming the four perceptual color channels. This interaction would produce red and green functions that are shifted clockwise (to larger angles) from the 0 and 180 deg vectors, respectively, and yellow and blue functions that are shifted counterclockwise (to smaller angles), respectively, from these same 0 and 180 deg vectors. The model predicts the rotations for green and blue quite well, but it predicts greater rotations than are observed for red, and smaller ones than are found for yellow. The initial model treated the opponent-color systems, red–green and yellow–blue, as mirror-images, in terms of their geniculate inputs. However, the hue-scaling data are better fit if the S$_o$ cells are given less weight when added to the red subsystem than to the green, and greater weight when added to the yellow than to the blue subsystem. In Fig. 8(C) we show in dotted lines the model revised to weight the S$_o$ cells by 1.0 for the red system and 3.5 for the yellow (rather than by 2 for both, as in the original model). The isoluminant regions seen as red, yellow, green, and blue, respectively, are more accurately captured by this modified (asymmetric) model.

The hue-scaling data show a second asymmetry between red and green, and between yellow and blue, that is not accounted for by our or any other color model of which we are aware. Specifically, red is seen over a greater range of color angles than is green, and blue over a greater range than yellow. To quantify this asymmetry, we fit a spline to each of the color regions using the averaged data, and computed the areas under the curves (as well as the centers of gravity). The areas, relative to the red, were R = 1; Y = 0.71, G = 0.75 and B = 1.03. We have not attempted to account for this asymmetry in our
model. Note that this is in the same direction as the asymmetry found by Abramov et al. (1991) in examining the color appearance of small stimuli in the periphery. They found that small peripheral blue and red stimuli appeared similar to foveal ones, but that small green and yellow stimuli were desaturated and had to be made much larger to appear as saturated as foveal spots. A similar loss in sensitivity to green as opposed to red in the periphery was also reported by Stromeyer et al. (1992). Thus there appear to be different amounts of spatial summation within the different halves of the supposed mirror-image opponent color systems, with more summation for maximal saturation being required for green than red, and more for yellow than blue. Perhaps the 2 deg foveal stimuli we used were not large enough to equalize these systems.

Many psychophysical studies and physiological investigations of LGN cells (e.g. Derrington et al., 1984), have used bidirectional gratings, e.g. gratings modulated in both the 0 and 180 deg directions around a mean white level. The use of such stimuli carries the implicit assumption that the two halves of the patterns are stimulating mirror-image systems. Given our evidence that such an assumption of symmetry does not hold for hue perception (at least), as well as other evidence for red–green as well as yellow–blue asymmetries (e.g. Abramov et al., 1991; Stromeyer et al., 1992; De Valois et al., 1994), we suggest that it might be useful in future studies to examine responses to unidirectional gratings or unidirectional Gabor patches as well as to bidirectional patterns.

REFERENCES


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