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Individual differences in chromatic (red/green) contrast sensitivity are constrained by the relative number of L- versus M-cones in the eye

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Abstract

Many previous studies have shown that the relative number of long-wavelength-selective (L) versus medium-wavelength-selective (M) cones in the eye influences spectral sensitivity revealed perceptually. Here, we hypothesize that the L:M cone ratio should also influence red/green chromatic contrast sensitivity. To test this, in each subject we derived an estimate of L:M ratio based on her red/green equiluminance settings (obtained with heterochromatic flicker photometry), and measured both red/green chromatic and luminance contrast sensitivity at different spatial and temporal frequencies. Factor analysis was applied to the data in order to reveal covariance between conditions. As expected, chromatic and luminance contrast sensitivity were found to be independent of one another, and no relationship was observed between L:M ratio and luminance contrast sensitivity. However, a significant relationship was observed between L:M ratio and chromatic contrast sensitivity, wherein subjects possessing the most symmetrical L:M cone ratios (i.e., near 1:1) appear to possess the relatively greatest chromatic contrast sensitivity. This relationship can be accounted for by a simple model based on the notion of random L- and M-cone inputs to the center and surround receptive fields of chromatic (L–M) mechanisms.

Keywords: Chromatic; Luminance; Contrast sensitivity; Cone opponency; L/M ratio

1. Introduction

Several lines of retinally based evidence have shown that the relative number of long-wavelength-selective (L)- to medium-wavelength-selective (M)-cones in the eye varies across individuals, with a mean L:M ratio of approximately 2:1 (e.g., Rushton & Baker, 1964; Dartnall, Bowmaker, & Mollon, 1983; Hagstrom, Neitz, & Neitz, 1997; Yamaguchi, Motulsky, & Deeb, 1997; Roorda & Williams, 1999). Long before methodologies were developed to allow direct sampling of cone types in the eye, the relative number of L- versus M-cones was estimated by modeling the psychophysically derived spectral sensitivity function (also referred to as the "luminous efficiency function" or "V_λ function") as a weighted sum of activity in L- and M-cones, with the weighting factor thought to represent the L:M cone ratio (e.g., Smith & Pokorny, 1975; Kremers et al., 2000, see also Jacobs & Neitz, 1993; Brainard et al., 2000; Kremers et al., 2000 for similar derivations based on data from electroretinogram flicker photometry). That is, when sensitivity for two colors is equated, referred to as *equiluminance*, the weighted sum of L- and M-cone excitation produced by one color ought to be equal to the weighted sum of L- and M-cone excitation produced by the other color. This model thus supposes that "luminance" is encoded by neural mechanisms that receive a weighted L+M cone input (see Lennie, Pokorny, & Smith, 1993 for review). And, implicit in this model is that the relative number of L- versus M-cones in the eye has direct consequences for spectral sensitivity revealed perceptually, a notion that has been supported by recent studies demonstrating a close correspondence between retinally based and spectral sensitivity-derived L:M ratios within individual subjects (Vimal, Pokorny, Smith, & Shevell, 1989; Wesner, Pokorny, Shevell, & Smith, 1991; Brainard et al., 2000; Kremers et al., 2000).

While the connection between L:M cone ratio and spectral sensitivity has received much attention, the possibility that the relative number of L- versus M-cones may influence red/green chromatic contrast sensitivity has been largely unexplored (but see Lennie, Haake,

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& Williams, 1991; Lennie, 2000). Here we hypothesize such a relationship, whereby individuals with symmetrical numbers of L- versus M-cones should possess relatively high chromatic contrast sensitivity. (Note that *L:M asymmetry* is distinguishable from *L:M ratio*, in that the former refers to the overall imbalance of L- versus M-cones, without regard for which cone type is in higher proportion.)

The logic behind this prediction is as follows. It is generally believed that red/green chromatic contrast sensitivity is mediated by midget ganglion cells in the eye, which are known to receive chromatically opponent (i.e., L–M) cone input (e.g., Lee, Martin, & Valberg, 1989; Lee, Pokorny, Smith, Martin, & Valberg, 1990; Smith, Pokorny, Davis, & Yeh, 1995). Within the central 5–10° of the retina, midget ganglion cells have small receptive fields, receiving single cone input to the center and multiple cone input to the surround (e.g., Kolb & Dekorver, 1991; Dacey, 1993; Goodchild, Ghosh, & Martin, 1996; McMahon, Lankheet, Lennie, & Williams, 2000). Although there is debate as to whether the surround input is selective or indiscriminant (see Lennie et al., 1991; Dacey, 1996; Lee, 1999; Lennie, 2000), it is the difference in spectral sensitivity between the center and surround that renders these cells chromatically opponent, thus allowing them to signal chromatic contrast.

Based on a model by Mullen and Kingdom (1996), which assumes indiscriminant cone inputs to the L–M mechanism, the predicted amount of cone opponency across a population of midget ganglion cells (referred to as the "average cone opponency purity") can be calculated from the L:M cone ratio and the number of cones inputting to the center and surround, as follows:

$$\sum_{j=0}^{N_c}\sum_{k=0}^{N_s} 0.5CS|[(N_c-2j)/N_c]-[(N_s-2k)/N_s]|$$

where N_c is the number of cones in the receptive field center; N_s, the number of cones in the receptive field surround, which is set to $6(N_c)$; j and k are the number of L-cones in each permutation of center and surround, respectively; p, the proportion of L-cones; C, the probability of selecting j out of N_c L-cones in the center $= [N_c!(p^j(1-p)^{N_c-j})]/[j!(N_c-j)!]$ and S, the probability of selecting k out of N_s L-cones in the surround $= [N_s!(p^k(1-p)^{N_s-k})]/[k!(N_s-k)!]$.

For a given neuron, a cone opponency purity value of zero indicates that the center and surround possess the same proportion of L- to M-cones, while a value of 1.0 indicates that cones of all one type input to the center and cones of all the other type input to the surround. The average cone opponency purity value combines all possible cone opponent purities with their associated probabilities. The resulting values are plotted as a function of L:M asymmetry in Fig. 1. For the case of a single cone center (*filled symbols*, *solid line*), which is representative of midget ganglion cells in the central 10°, the largest average cone opponency purity value (and thus the strongest overall opponency) is observed when the number of L- versus M-cones is perfectly symmetrical (i.e., L:M equal to 1:1), with values decreasing markedly as L:M asymmetry is increased. For example, an L:M of 1:1 yields a cone opponency purity of 0.50, while an L:M of 8:1 yields a value of 0.20; a difference of 2.5-fold. This model thus predicts that subjects with the most symmetrical L:M ratios should possess stronger chromatic opponency than those with asymmetrical L:M ratios, and, in turn, exhibit relatively greater chromatic contrast sensitivity.

For luminance stimuli, it is generally believed that contrast sensitivity is mediated by parasol ganglion cells, which receive additive (i.e., L+M) cone input (Lee et al., 1990; Shapley, 1990; Smith et al., 1995, but cf. Ingling & Martinez-Uriegas, 1983a; De Valois & De Valois, 1993; Billock, 1995 for discussion of possible mediation by L–M mechanisms). In comparison to midget ganglion cells, parasol ganglion cells have large receptive fields, receiving multiple L- and M-cone input to both their center and surround (e.g., Curcio & Allen, 1990; Goodchild et al., 1996). For these cells, differences in the proportion of L- versus M-cones should have no effect on responses to (and thus contrast sensitivity for) luminance stimuli. This is because the amount of modulation produced in the L- and M-cones will be equal to and in phase with the luminance contrast in the stimu-

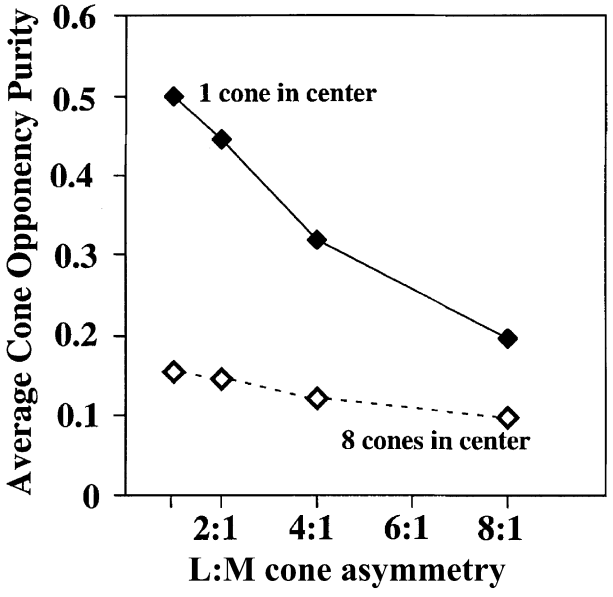

Fig. 1. Average cone opponency purity values calculated as a function of L:M cone asymmetry. For the case of a single cone in the center of the receptive field (*filled symbols*, *solid line*), which is representative of midget ganglion cells in the central 10°, there is a substantial effect of cone asymmetry. For a multiple-cone center (e.g., eight cones, *open symbols*, *dashed lines*), which is representative of midget ganglion cells in the far periphery, there is a negligible effect of cone asymmetry.

lus, and thus the signals carried by the L- and M-cones are effectively identical to one another. For this reason, an individual's L:M cone ratio is expected to have little or no influence on her luminance contrast sensitivity.

In the present study, we investigated the relationship between L:M asymmetry, red/green chromatic contrast sensitivity and luminance contrast sensitivity using a factor analysis approach. The methods and theories underlying this approach have been described in detail elsewhere (e.g., Sekuler, Wilson, & Owsley, 1984; Webster & MacLeod, 1988; Peterzell, Kaplan, & Werner, 1993; Peterzell & Teller, 1996). For each subject, an estimate of L:M asymmetry was derived from her red/green equiluminance settings obtained using heterochromatic flicker photometry (HFP). Data were analyzed from two separate groups of subjects. In the first ($n = 19$), nine women carriers of dichromacy were included, with the expectation that they would possess more extreme L:M values, thereby expanding the range of L:M asymmetries in our sample and thus potentially increasing the power of our analyses. In addition, we analyzed data from a second group of subjects ($n = 41$), which were obtained during the course of another experiment (Gunther & Dobkins, 2002). In line with our predictions based on the cone opponency model, the results from both subject groups suggest that more symmetrical L:M ratios are associated with higher chromatic contrast sensitivity. As expected, chromatic and luminance contrast sensitivity were found to be independent of one another, and no relationship was observed between L:M ratio and luminance contrast sensitivity.

2. Methods

2.1. Subjects

2.1.1. Subject group #1

Nineteen subjects participated in the main experiment (18 females, 1 male). All had normal or corrected-to-normal vision, and normal red/green color vision as assessed by the *Ishihara Tests for Color Deficiency*. Subject age ranged from 18 to 37 years (mean = 22.6 ± 6.8). Nine of these subjects were women carriers of dichromacy (determined by self-report of a dichromatic father), who were intentionally recruited in order to increase the range of L:M asymmetry values across our sample of subjects.

The logic behind exaggerated L:M asymmetries in women carriers of dichromacy is as follows. The genes for both the L- and M-cone pigments reside on both X chromosomes in women. However, due to "X inactivation", only one of the two X chromosomes is expressed per cone (Lyon, 1962). In *deutan* carriers, one X chromosome lacks the M-cone pigment gene, and thus, when this chromosome is activated, it can produce only the L-cone pigment. This results in an overall greater number of L-cones and thus a larger-than-average L:M ratio in such individuals. In *protan* carriers, the converse scenario occurs, resulting in an overall greater number of M-cones, and a lower-than-average L:M ratio. In terms of red/green spectral sensitivity, deutan carriers are expected to be relatively more sensitive to red, whereas protan carriers are expected to be relatively more sensitive to green, a prediction that has been borne out in several psychophysical studies (Crone, 1959; Adam, 1969; Swanson, 1991). Based on our nine carriers' relative red/green equiluminance settings (see Section 2.4), we estimate that seven were deutan carriers and two were protan carriers.

2.1.2. Subject group #2

In addition to the data from the 19 subjects described above, data were analyzed from another group of 41 subjects (age range = 17–30 years, mean = 20.6 ± 2.6 years, 31 females, 10 males). These data were obtained during the course of another study, which used factor analysis to investigate the independence of cardinal and non-cardinal mechanisms in color vision (Gunther & Dobkins, 2002). Although not intentionally recruited as such, two of the women subjects in this experiment were carriers of dichromacy. Subject group #2 was tested over a slightly different range of spatial/temporal frequencies than was subject group #1 (see below), and thus data from the two groups could not be combined.

2.2. Apparatus

For all experiments, visual stimuli were generated on a Sony Trinitron 500PS monitor (21 in. display, 1024 × 768 pixels, 100 Hz refresh) driven by a Cambridge Research Systems (CRS) VSG 2/3 video board. The 15-bit board allowed for 32,768 discrete luminance levels. The maximum output for the monitor was calibrated to equal energy white (CIE chromaticity coordinates = 0.333, 0.333), and the voltage/luminance relationship was linearized independently for each of the three guns in the display, using a Gamma Correction System and an OptiCAL 256M (CRS). A PR-650 SpectraColorimeter (PhotoResearch) was used for spectroradiometric and photometric measurements of our stimuli.

2.3. Stimuli

Stimuli consisted of horizontally oriented, chromatic (red/green) and luminance (black/white) sinusoidal gratings, counterphase-reversed (temporal sinusoidal) at different spatial and temporal frequencies. For subject group #1, four combinations were tested: two spatial frequencies (0.25 and 2 c/deg) and two temporal

frequencies (4 and 16 Hz). For subject group #2, three different spatial frequencies (0.25, 0.5 and 1 c/deg) at a single temporal frequency (4 Hz) were tested. Note that we chose to go no higher in spatial frequency than 2 c/deg in order to avoid luminance artifacts produced by chromatic aberration in red/green gratings (Flitcroft, 1989; Cavanagh & Anstis, 1991; Bradley, Zhang, & Thibos, 1992). Gratings subtended 5.4° of visual angle, and were convolved with a Gaussian circular envelope (Gabor standard deviation = 2.7°) to eliminate spatial edges. Gratings were presented with the zero-crossing positioned in the center of the stimulus to ensure equal number of light and dark (or red and green) stripes in the stimulus. Note that because stimulus size was held constant across all conditions, the total number of cycles necessarily varied across different spatial frequencies.

All gratings (chromatic and luminance) were modulated through equal energy white (CIE = 0.333, 0.333) at 28 cd/m^2, and were of the same mean chromaticity and luminance as the background. Chromatic gratings were created to selectively modulate activity within L- and M-cones, while keeping the S-cone excitation constant. Luminance gratings were produced by sinusoidally modulating the luminance of the gray background. The contrast of all stimuli was defined in terms of the root-mean-square (r.m.s.) cone contrast produced in L- and M-cones. For chromatic gratings, these values were computed by determining the L- and M-cone excitations produced by the peaks of the red and green phases of our chromatic gratings. These excitations were obtained by integrating the cross-product of stimulus spectral output of these stimuli (measured with the PR-650 in 4 nm intervals from 400 to 700 nm) by the Stockman, MacLeod, and Johnson (1993) cone fundamentals (see Dobkins, Gunther, & Peterzell, 2000 for details). R.m.s. cone contrast for chromatic stimuli was calculated as follows:

$$\sqrt{\frac{[(L_r - L_g)/(L_r + L_g)]^2 + [(M_r - M_g)/(M_r + M_g)]^2}{2}}$$

where L_r and M_r refer to the L- and M-cone excitations, respectively, produced by the red peak, and L_g and M_g refer to the cone excitations produced by the green peak. For luminance gratings, r.m.s. cone contrast directly corresponds to conventional Michelson contrast: $(\text{Luminance}_{max} - \text{Luminance}_{min})/(\text{Luminance}_{max} + \text{Luminance}_{min})$.

2.4. Procedure

For all portions of these experiments, subjects were tested in a dark room and viewed the video display binocularly from a chin rest situated 57 cm away. Subjects were instructed to maintain fixation on a small central cross, and provide perceptual reports via keypresses on a response box. For each spatio/temporal frequency tested, three types of data were obtained: (1) red/green equiluminance, (2) red/green chromatic contrast sensitivity and (3) luminance contrast sensitivity.

For each subject, red/green equiluminance was determined via heterochromatic flicker photometry (HFP). On each trial, the red/green grating appeared centered on the fixation cross, and the subject adjusted the relative luminance between the red and the green phases until the percept of flicker was least salient. At V_λ equiluminance, the chromatic gratings produced 12.1% r.m.s. cone contrast in L- and M-cones, which was approximately 20 times the mean chromatic contrast threshold. The equiluminance point was determined from the mean setting across 20 trials (see Dobkins et al., 2000 for further details). For subject group #1, HFP was performed separately for each of the four stimulus conditions (20 trials per condition). These equiluminance settings were used to: (1) set the red/green luminance ratio for each subject when tested in the chromatic contrast sensitivity condition and (2) derive estimates of L:M cone ratios for each subject (see below). For subject group #2, HFP was performed only for the 0.5 c/deg, 4 Hz condition, and the resulting value was used to set red/green equiluminance for all three spatial frequencies, including 0.25 and 1 c/deg. Our reason for using this one setting is based both on previous studies (e.g., Cavanagh, MacLeod, & Anstis, 1987; Mullen, 1991; Dobkins et al., 2000; Dobkins, Thiele, & Albright, 2000) and on our findings from subject group #1 ($F(1, 18) = 0.94$, $p = 0.35$) that spatial frequency has negligible effects on equiluminance settings.

Chromatic and luminance contrast sensitivities were determined using a Best-PEST staircase procedure (Lieberman & Pentland, 1982) in a spatial two-alternative forced-choice paradigm. On each trial, the stimulus appeared centered 2.5° to the left or right of fixation, and the subject reported its location via a key press on a response box. No feedback was provided. Stimuli were presented for 300 ms, with contrast ramped on and off in a cosine manner within the first and last 100 ms. The staircase procedure continued until the subject had completed 125 trials for each stimulus condition. Chromatic and luminance stimuli, as well as the different spatial and temporal frequencies, were randomized across trials. Approximately 2.5–6 h were required to complete the experiment, with testing divided into 1- to 2-h blocks.

2.5. Determining L:M cone ratio asymmetries from red/green equiluminance settings

Estimates of L:M cone ratios were derived from HFP equiluminance settings in the following manner. We first determined the L- and M-cone excitations produced by the peaks of the red and green phases of chromatic

gratings (as described above) set to be equiluminant. These values were calculated separately for each subject and for each stimulus condition (see Dobkins et al., 2000 for details). As addressed in Section 1, at equiluminance, the weighted sum of L- and M-cone excitation produced by the red peak of the chromatic grating is expected to equal the weighted sum of L- and M-cone excitation produced by the green peak. The weighting factors are thought to represent the relative proportion of L-cones (P_L) versus M-cones (P_M). The equation describing this is as follows:

$$P_L L_r + P_M M_r = P_L L_g + P_M M_g$$

where L_r and M_r refer to the cone excitations produced by the red peak, and L_g and M_g refer to the cone excitations produced by the green peak. Thus, P_L/P_M (which represents the L:M ratio) is calculated as

$$P_L/P_M = (M_g - M_r)/(L_r - L_g) = \text{L : M ratio}$$

For subject group #1, we used each subject's mean L:M ratio derived from 16 Hz stimuli (i.e., averaged across the 0.25 and 0.5 c/deg conditions). Our reason for using the data from only the 16 Hz condition is based on the notion that the luminance (i.e., L+M) mechanism is isolated at high temporal frequencies (e.g., Kelly & van Norren, 1977; Varner, Piantanida, & Baker, 1997) and because studies using HFP and electroretinography to derive L:M ratios typically use high temporal frequencies (e.g., Smith & Pokorny, 1975; Kremers et al., 2000). However, we also analyzed our data using 4 Hz-derived L:M ratios, in order to compare the results to those obtained from 16 Hz-derived estimates. For subject group #2, equiluminance was obtained only for the 0.5 c/deg, 4 Hz condition, and thus this sole condition was used for estimating each subject's L:M ratio.

After determining an L:M ratio for each subject, this value was transformed into an L:M *asymmetry* value. This latter metric was chosen because it tests our hypothesis that imbalances in the number of L- versus M-cones, regardless of which is in higher proportion, may influence chromatic contrast sensitivity. Thus, any estimated L:M ratio that was <1.0 was converted to the *inverse* ratio (e.g., an L:M ratio of 0.2 was converted to an asymmetry of 5.0).

It is important to emphasize that our estimates of L:M asymmetry assume that P_L/P_M represents the relative *proportion* of L- versus M-cones, as opposed to some post-receptoral synaptic *weighting* of L- versus M-cones. We believe this is a reasonable assumption since there exists empirical evidence, within individual human subjects, demonstrating that spectral sensitivity is closely tied to the relative proportion of L- versus M-cones (e.g., Vimal et al., 1989; Wesner et al., 1991; Brainard et al., 2000; Kremers et al., 2000). Note also that our L:M asymmetry estimates rely on cone fundamentals for the "standard" observer (as determined by Stockman et al. (1993)) to compute L- and M-cone excitations. Because cone fundamentals are expected to differ somewhat across individuals (based on differences across subjects in photopigment λ_{max}, photopigment optical density, as well as lens and macular pigment), there will be some error in L:M derivations associated with using a standard set of cone fundamentals for all subjects (see Bieber, Kraft, & Werner, 1998 for further discussion). However, this type of error, albeit likely present in our estimates, cannot account for the results of our factor analyses (see Section 3).

2.6. Factor analyses

Covariance analyses of individual differences (i.e., factor analyses) were performed on the correlations from the data (as previously described, e.g., Peterzell, Kaplan, & Werner, 1995; Peterzell & Teller, 1996; Dobkins et al., 2000) to determine the degree of dependence versus independence between L:M asymmetry, chromatic contrast sensitivity and luminance contrast sensitivity. Because subject data conformed to normal distributions when log-transformed, all analyses were performed on log values, and all mean data are presented here as geometric means (i.e., the linear equivalents of the log means).

As a first step in our factor analysis, a principal component analysis (PCA) was performed on the correlational data. Eigenvalues reflect the proportion of variance explained by a given factor, with 1.0 being the value expected by chance alone. Hence, an eigenvalue greater than one was used as the criterion for statistical significance of the components (Guttman, 1954; Gorsuch, 1983). In order to maximize the number of zero or near zero factor loadings, these orthogonal principle components, or factors, were rotated to 'simple structure' using the Varimax criterion (Kaiser, 1958) and then further rotated obliquely.

3. Results

3.1. Sample L:M ratios

A frequency histogram of L:M ratios derived from red/green equiluminance settings in all 60 subjects is shown in Fig. 2. Data from each subject group are shown separately for color-normal subjects (solid bars) and carriers of dichromacy (bars with white diagonal lines). For subject group #1 ($n = 19$, black bars), the geometric mean L:M ratio for color-normal subjects ($n = 10$) was 1.41 (based on 16 Hz equiluminance data). For subjects presumed to be deutan carriers ($n = 7$, based on their relatively greater sensitivity to red) and protan carriers ($n = 2$, based on their relatively greater sensitivity to green), the mean L:M ratios were 3.33 and

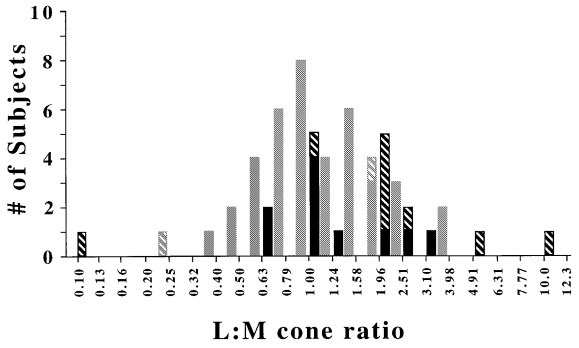

Fig. 2. Frequency histogram of L:M ratios derived from red/green equiluminance points for all 60 subjects. Data from subject groups #1 and #2 are presented as black and gray bars, respectively. For both groups, color-normal subjects are represented by solid bars, and carriers of dichromacy by striped bars. Bins are of equal log divisions, yet linear L:M cone ratios are presented for ease of interpretation.

0.32, respectively. For subject group #2 ($n = 41$, gray bars), the geometric mean L:M ratio for color-normal subjects ($n = 39$) was 1.03 (based on 4 Hz equiluminance data), which was not significantly different from the color-normal subjects in the first group ($t(47) = 1.61$, $p = 0.11$). The presumed deutan carrier and protan carrier in this subject group had estimated L:M ratios of 1.60 and 0.22, respectively.

3.2. Factor analysis of subject group #1

The results from our factor analysis based on the data from the first group of subjects ($n = 19$) are presented in Fig. 3. Shown are the factor loadings for a two-factor solution, based on nine data points (four chromatic sensitivities, four luminance sensitivities and one derived L:M value). Note that a two-factor solution was chosen based on our hypothesis that L:M asymmetries should correlate with chromatic contrast sensitivity but not luminance contrast sensitivity, and because only two factors were found to be significant based on their eigenvalues (see Section 2). As has been used previously (e.g., Peterzell et al., 1995; Peterzell & Teller, 1996; Dobkins et al., 2000), our criterion for factor loading significance was a factor loading of ± 0.4. Thus, factor loadings with values greater than or equal to $|0.4|$ are plotted for each of the data points. The correlation matrix underlying the factor analysis for subject group #1 is provided in Appendix A.

In accordance with previous findings from factor analysis (Dobkins et al., 2000; Peterzell & Teller, 2000), chromatic and luminance contrast sensitivity were found to load onto separate factors. Specifically, chromatic contrast sensitivity loaded onto Factor 1, accounting for 48.3% of the overall variance, while luminance contrast sensitivity loaded onto Factor 2, accounting for 25.8% of the variance. (Note that a single chromatic stimulus at 2 c/deg, 16 Hz also loaded onto Factor 2, although

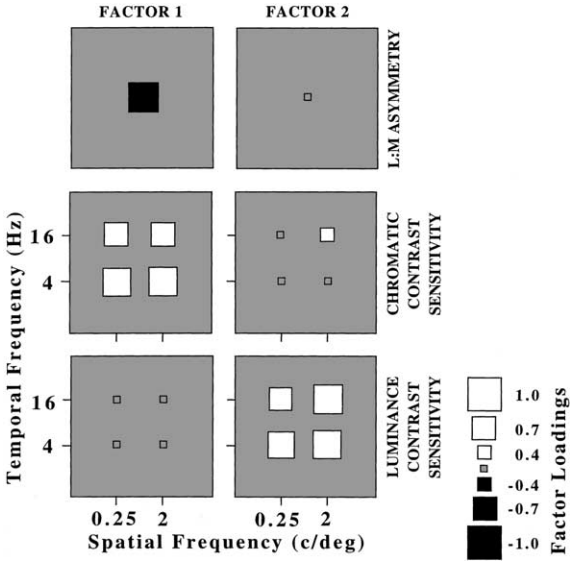

Fig. 3. Factor analysis for subject group #1. Factor loadings, which represent the correlation between each of the 9 measures (one L:M estimate, four chromatic contrast sensitivities and four luminance contrast sensitivities) and the factor, are shown for a two-factor solution. White and black squares represent positive and negative factor loadings, respectively. Squares are scaled in size according to their value. Small gray squares represent factor loadings that fell below the criterion for significance (absolute value of factor loading <0.4). Note that chromatic and luminance contrast sensitivity load separately onto Factors 1 and 2, respectively. In addition, note that chromatic contrast sensitivity and L:M asymmetry co-load *inversely* onto Factor 1 (i.e., positive loadings for chromatic sensitivity and negative loading for L:M asymmetry), indicating that more symmetrical L:M cone ratios are associated with greater chromatic contrast sensitivity. The L:M asymmetry values in this analysis were calculated from 16 Hz data collapsed over the 0.25 and 2.0 c/deg conditions (see Section 2).

the factor loading for this point just barely surpassed our criterion loading.) Thus, in line with previous studies employing paradigms such as adaptation, masking and summation-near-threshold (e.g., Krauskopf, Williams, & Heeley, 1982; Barbur, Harlow, & Plant, 1994; Mullen & Losada, 1994, 1999; Mullen & Sankeralli, 1999; Gunther & Dobkins, 2002), this factor analysis result implies the existence of independent mechanisms underlying red/green chromatic and luminance contrast sensitivity. Most relevant to our predictions, in addition to chromatic contrast sensitivity loading onto Factor 1, L:M asymmetry also loaded onto this factor, but *negatively*. This result suggests that *higher* chromatic contrast sensitivity is associated with *lower* L:M asymmetry (i.e., more equal numbers of L- and M-cones). And, conversely, higher L:M asymmetry is associated with lower chromatic contrast sensitivity. As expected, L:M asymmetry did not co-load with luminance contrast sensitivity values.

It is perhaps important to point out that this set of results is not an artifact of choosing a two-factor solution, as the two factors are completely unconstrained in the analysis. Although only the first two factors yielded

significant eigenvalues, we nonetheless investigated the effects of requesting three- and four-factor solutions. For both, spatial frequency tuning was revealed. Specifically, in the three-factor solution, separate luminance contrast sensitivity factors emerged for 0.25 versus 2 c/deg. In the four-factor solution, both luminance and chromatic contrast sensitivity split into spatial frequency factors. However, this did not affect our main pattern of results, i.e., the separation between chromatic and luminance contrast sensitivity and the negative relationship between chromatic contrast sensitivity and L:M asymmetry were maintained.

The above-presented factor analysis for subject group #1 was conducted using L:M estimates derived solely from 16 Hz data. To determine whether these results depend on the use of 16 Hz data, and to compare more directly results from subject group #1 with those of group #2 (whose L:M estimates were based on 4 Hz data), we also conducted an analysis on data from subject group #1 using L:M estimates derived from 4 Hz data. The results of this analysis were nearly identical to those obtained using 16 Hz data. Specifically, chromatic contrast sensitivity loaded positively and L:M asymmetry loaded negatively onto Factor 1, accounting for 48.1% of the variance, while luminance contrast sensitivity alone loaded onto Factor 2, accounting for 24.7% of the variance. This result is perhaps not surprising given that our 16 Hz-derived L:M estimates were highly correlated with those derived from 4 Hz data ($r = 0.97$, $p < 0.001$, slope of regression = 1.03).

3.3. Factor analysis of subject group #2

The results from our factor analysis based on the data from the second group of subjects ($n = 41$) are presented in Fig. 4. Shown are the factor loadings, based on seven data points (three chromatic sensitivities, three luminance sensitivities and one derived L:M value). Mirroring the results observed in the first group of subjects, chromatic contrast sensitivity loaded positively and L:M asymmetry loaded negatively onto Factor 1, accounting for 58.0% of the variance. Luminance contrast sensitivity alone loaded onto Factor 2, accounting for 20.1% of the variance. As for the first group of subjects, L:M asymmetry did not co-load with luminance contrast sensitivity. In sum, the results for subject group #2 provide a replication of the effects observed for subject group #1. This is despite the fact that, unlike subject group #1, group #2 included an extreme minority of women carriers of dichromacy (two of the 41 subjects). This suggests that an exaggerated range of L:M asymmetries is not, in fact, required to see this pattern of results. Most likely, the ability to observe this effect in group #2 is a result of the greater number of subjects in this analysis (twice as many as in group #1), yielding more statistical power. The correlation matrix underlying the factor analysis for subject group #2 is provided in Appendix B.

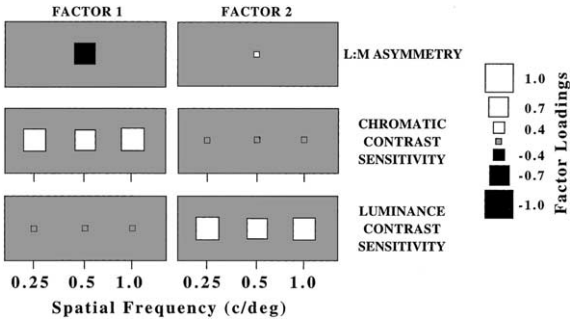

Fig. 4. Factor analysis for subject group #2. Data are presented as in Fig. 2. As for subject group #1, chromatic and luminance contrast sensitivity load onto separate factors. And, chromatic contrast sensitivity and L:M asymmetry co-load inversely onto Factor 1, indicating that more symmetrical L:M cone ratios are associated with greater chromatic sensitivity. The L:M asymmetry values in this analysis were calculated from 0.5 c/deg, 4 Hz data (see Section 2).

3.4. Effects of age

Due to the yellowing of the lens with age, older subjects are expected to be relatively less sensitive to green as compared to younger subjects (e.g., Said & Weale, 1959; Ruddock, 1965; Fiorentini, Porciatti, Morrone, & Burr, 1996 and see Werner, Peterzell, & Scheetz, 1990 for a review). However, this factor should not have affected our results since these effects are thought to be minimal within our subject age range of 18–37 years (e.g., Ruddock, 1965; Knoblauch, Vital-Durand, & Barbur, 2001). Nonetheless, if a tendency existed for our older subjects to be less green sensitive as a consequence of lens yellowing, derived L:M ratios (and consequently L:M asymmetries) would have been artificially high in these individuals. If these older subjects were also less sensitive to chromatic contrast than the younger subjects (as previous research suggests they might be, e.g., Fiorentini et al., 1996; Knoblauch et al., 2001, and see Werner et al., 1990 for a review), this could potentially drive the negative relationship between L:M asymmetry and chromatic contrast sensitivity observed in our factor analyses.

To investigate whether age could account for our results, we included subject age as a dimension in our factor analyses. As before, we requested a two-factor solution, because if age underlies variations in both L:M asymmetry and chromatic contrast sensitivity, it would be expected to co-load with both of these measures (but not with luminance contrast sensitivity). The results of this factor analysis produced a pattern that was essentially identical to that observed in the main analyses (see Figs. 3 and 4), with age not loading (absolute values of factor loadings were all <0.4) onto either Factor 1 or 2.

Specifically, chromatic contrast sensitivity and L:M asymmetry loaded onto Factor 1 (43.8% of the variance in subject group #1; 50.8% of the variance in subject group #2), while luminance contrast sensitivity loaded onto Factor 2 (23.3% of the variance in subject group #1, which also included the 2 c/deg, 16 Hz, chromatic data point; 17.6% of the variance in subject group #2). Based on these results, we believe that age cannot account for the relationship observed between L:M asymmetry and chromatic contrast sensitivity.

3.5. Effects of cone fundamentals used to derive L:M ratios

Our derived L:M asymmetry values relied on cone fundamentals provided by Stockman et al. (1993) for 2° stimuli (see Section 2), where the λ_{max} for the L- and M-cone fundamentals are at 568 and 540 nm, respectively. However, cone fundamental values are known to vary somewhat across studies, on the order of approximately 5 nm (Vos & Walraven, 1971; Smith & Pokorny, 1975; Stockman et al., 1993). Because derived L:M ratios have been shown to be dependent on the particular λ_{max} employed for L-cones (although only small effects are seen for λ_{max} of M-cones), different cone fundamentals are likely to produce different values of L:M ratios (see Bieber et al., 1998). For example, the mean L:M ratio for our 49 color-normal subjects (subject groups #1 and #2, combined) was 1.10 when using a 568 nm λ_{max} for the L-cone fundamental. However, when the L-cone λ_{max} was shifted by +4 nm (to 572 nm), the mean L:M ratio for this sample decreased to 0.79. A −4 nm shift (to 564 nm) increased the mean to 1.88. In accordance with Bieber et al. (1998), much smaller changes were observed for variations in M-cone λ_{max}, i.e., L:M ratios of 0.90 and 1.26 for M-cone λ_{max}'s of 544 nm (+4 nm) and 536 nm (−4 nm), respectively.

In order to determine the effects of variations in λ_{max} on our results, we conducted additional factor analyses using L:M estimates derived from ±4 nm shifted cone fundamentals. When the value of the L-cone λ_{max} was shifted 4 nm in either direction, the pattern of factor loadings was identical to those obtained for the non-shifted values reported above, for both subject groups. The only exception to this, a minor one, was the reversal of Factors 1 and 2 for the −4 nm shift in subject group #1. Here, chromatic contrast sensitivity and L:M asymmetry loaded onto Factor 2, while luminance contrast sensitivity (and chromatic contrast sensitivity at 16 Hz, 2 c/deg) loaded onto Factor 1. Shifting the λ_{max} of the M-cone by ±4 nm also had no effect on our results, for either subject group. Thus, the results of these additional analyses suggest that the observed relationship between L:M asymmetry and chromatic contrast sensitivity is not an artifact of the particular cone fundamental λ_{max}'s employed.

In addition to variation in cone fundamental λ_{max} across studies, λ_{max} is also known to vary across *individuals* (by as much as ±1 to 3 nm, e.g., Eisner & MacLeod, 1981; Kraft, Neitz, & Neitz, 1998; Sharpe, Stockman, Jaegle, Knau, & Nathans, 1999), due to individual differences in photopigment λ_{max}, photopigment optical density, and lens and macular pigment. Because we employed a "standard" set of cone fundamentals for all of our subjects, the derived L:M values for some subjects will necessarily be slightly erroneous. In addition to errors in L:M values, the use of a single set of cone fundamentals will, of necessity, result in somewhat erroneous estimates of chromatic contrast sensitivity for some subjects (see Section 2 for details on these calculations). Consequently, we can expect varying degrees of error in both derived L:M values and chromatic contrast sensitivity across our sample of subjects. If such errors tended to artificially elevate a given individual's L:M estimate while simultaneously lowering her estimate of chromatic contrast sensitivity (or vice versa), this could potentially drive the negative relationship between L:M asymmetry and chromatic contrast sensitivity.

To address this possibility, we simulated the effects of an erroneous λ_{max} on both L:M asymmetry and chromatic contrast sensitivity values. This was performed only for the L-cone fundamental, since variations in the M-cone λ_{max} produce only small changes in L:M values (see above). To this end, we recalculated L:M values and chromatic sensitivities for a representative subject (whose L:M asymmetry and chromatic contrast sensitivity were both close to the mean across subjects) using an L-cone λ_{max} shifted by ±4 nm. For this subject, a λ_{max} of 568 nm (used in our original analysis) yielded an L:M asymmetry of 1.28 and a chromatic contrast sensitivity of 157. When λ_{max} was shifted −4 nm to 564 nm, both the L:M asymmetry (2.09) and chromatic contrast sensitivity (169) for this individual were elevated. Conversely, when λ_{max} was shifted +4 nm to 572 nm, both the L:M asymmetry (1.09) and chromatic contrast sensitivity (142) for this individual were decreased. Thus, had our use of a 568 nm λ_{max} been erroneously high (or low) for a given subject, both the derived L:M asymmetry and chromatic contrast sensitivity for that subject would have been underestimated (or overestimated). Because such errors are expected to be in the same direction, this, if anything, would tend to create a *positive* relationship between L:M asymmetry and chromatic contrast sensitivity. Since this effect is opposite to that observed in the present study, we feel confident that errors in cone fundamentals cannot account for our results.

4. Discussion

The results of these studies suggest that symmetry in the number of L- versus M-cones creates an advantage

for chromatic (red/green) contrast sensitivity, yet has negligible effects on luminance contrast sensitivity. As addressed in Section 1, this relationship between L:M asymmetry and chromatic contrast sensitivity can be accounted for by a model of indiscriminant L- and M-cone inputs to chromatic (L–M) mechanisms, whereby the most symmetrical L:M ratios produce the strongest chromatic opponency, and, in turn, the greatest chromatic contrast sensitivity. By this account, variations in chromatic contrast sensitivity across subjects appear to be influenced by variations across subjects in the relative number of L- versus M-cones inputting to the L–M mechanism.

Although this hypothesis is tenable, it appears inconsistent with the popular notion that inputs to the L–M mechanism are normalized to ~1:1 (L:M), regardless of the actual L:M cone ratio in the eye. Evidence for this idea is based largely on the finding that unique yellow settings, which are thought to rely on the L–M mechanism, vary much less than do L:M cone ratios, and are roughly consistent with an L:M input ratio of 1:1 (Ingling & Martinez-Uriegas, 1983b; Pokorny, Smith, & Wesner, 1991; Miyahara, Pokorny, Smith, Baron, & Baron, 1998; Brainard et al., 2000). Recently, Yamauchi, Williams, Carroll, Neitz, and Neitz (2001) provided evidence that this normalization process arises from environmental factors, by demonstrating that unique yellow settings shift in a systematic fashion after prolonged (4–20 h) experience in red or green environments (e.g., through the wearing of colored contact lenses). It is perhaps important to point out, however, that not all studies support the notion of normalized 1:1 input to L–M mechanisms. Cicerone and colleagues have reported that subjects who possess relatively higher L:M ratios set unique yellow to relatively lower wavelengths, and vice versa (Cicerone, 1990; Gowdy & Cicerone, 1998; Otake & Cicerone, 2000). Thus, both the chromatic contrast sensitivity measure of the present experiment and the unique yellow results of Cicerone and colleagues suggest that the L–M mechanism is influenced by the relative number of L- versus M-cones in the eye.

In another recent study, Kremers et al. (2000) investigated the issue of L:M input to the L–M mechanism by deriving L:M ratios from cone modulation thresholds obtained across a wide range of temporal frequencies (1–30 Hz). Their approach was based on the assumption that lower frequencies (1–4 Hz) enhance the contribution from the L–M mechanism, while higher frequencies (15–30 Hz) enhance the contribution from the L+M mechanism. At high temporal frequencies, they observed substantial subject variation in derived L:M ratios (with a mean near 2:1), which correlated extremely well ($r = 0.93$) with direct L:M estimates they obtained using retinal densitometry. By contrast, at low temporal frequencies, they observed little variability in derived L:M ratios, with a mean near 1:1. These results were taken as evidence that L:M input to the L–M, but not the L+M, mechanism is normalized to 1:1 L:M, regardless of the actual number of L- versus M-cones in the eye.

However, we would argue that, at least for their 4 Hz data (which matches one of the temporal frequencies employed in the present study), the variability in Kremers et al.'s derived L:M ratios, although reported to be small (~0.13 log units), was in fact much larger than would be expected if (1) their 4 Hz estimates relied *exclusively* on the L–M mechanism and (2) the L–M mechanism receives normalized 1:1 L:M cone input. To illustrate this point, we compared the variability in their L:M ratios to known variations in unique yellow settings, under the assumption that unique yellow settings are based on normalized 1:1 input of L:M cones to the L–M mechanism. Using the equations of Cicerone (1990), and the parameters used by Brainard et al. (2000), we calculate that the Kremers et al. 4 Hz data predict a standard deviation of approximately 17 nm in unique yellow settings, which is substantially higher than known standard deviations in unique yellow (typically on the order of 2–5 nm, e.g., Miyahara et al., 1998). Some of the unexplained variability in the 4 Hz-derived L:M estimates of Kremers et al. could be due to noise arising from individual variability across subjects in cone fundamentals. In addition to this possibility, the variability is likely to reflect partial contribution from the L+M mechanism (see Ingling & Tsou, 1988; Lennie et al., 1993; Webster & Mollon, 1993; Dobkins et al., 2000 for further discussion) and/or incomplete 1:1 normalization of L- and M-cone input to the L–M mechanism.

Although the weighting of the L:M input to the L–M mechanism is still somewhat controversial, there are two ways to reconcile a 1:1 normalization (which suggests a lack of dependence on L:M value) with the chromatic contrast sensitivity results of the present study (which suggest a dependence on L:M value). The first is to propose that the normalization to 1:1 is not perfect, leaving enough variability across subjects to reveal correlations between L:M ratio and chromatic contrast sensitivity (as in the present study) and between L:M ratios and unique yellow (as in the studies by Cicerone and colleagues). The second possibility is that the normalization process in the L–M pathway simply occurs *after* the site that underlies chromatic contrast sensitivity. This latter scenario could also account for the residual variability in the Kremers et al. low temporal frequency data. That is, the cone modulation thresholds they used to estimate L:M ratios may isolate the L–M mechanism, yet at a level prior to the point of normalization.

Although further experiments will be required to distinguish these possibilities, the results of the present experiment suggest that chromatic contrast sensitivity is related to the relative number of L- versus M-cones in the eye. Such findings are consistent with a model of indiscriminant L- and M-cone inputs to single cone

center midget ganglion cells of the central retina, whereby the most symmetrical L:M ratios result in the overall greatest chromatic opponency, and in turn, the highest chromatic contrast sensitivity. If this model is correct, then a different set of results would be predicted for chromatic contrast sensitivity in the *periphery*, where midget ganglion cells are known to receive multiple cone inputs to the center and surround (Dacey, 1993; Goodchild et al., 1996). To illustrate this point, in Fig. 1 we have plotted the predicted average cone opponency purity value as a function of L:M asymmetry for the case of eight cones in the center (*open symbols*, *dashed line*). As for the case of a single cone center, the overall strongest chromatic opponency occurs when the number of L- versus M-cones is symmetrical (L:M ratio of 1:1), while the weakest opponency occurs when there is a large asymmetry. However, owing to the summing of inputs in both the center and surround, the influence of L:M asymmetry is far weaker than for the case of a single cone center. For example, with eight cones in the center, the cone opponency purity value varies from 0.15 for an L:M asymmetry of 1:1 to 0.10 for an L:M asymmetry of 8:1; a difference of only 1.5-fold (down from 2.5-fold for single-center cones, see Section 1). Thus, as compared to chromatic contrast sensitivity in central vision, peripheral sensitivity should be far less affected by variations in L:M asymmetry. Testing this hypothesis in future experiments will provide an important step in understanding how chromatic contrast sensitivity might be constrained by the relative number of L- versus M-cones in the eye.

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Appendix A

Correlation matrix underlying factor analysis for subject group #1.

	RG 4 Hz 0.25 cpd	RG 16 Hz 0.25 cpd	RG 4 Hz 2 cpd	RG 16 Hz 2 cpd	LUM 4Hz0.25 cpd	LUM 16 Hz 0.25 cpd	LUM 4 Hz 2 cpd	LUM 16 Hz 2 cpd	LM ASYM
RG 4 Hz 0.25 cpd	1.00								
RG 16 Hz 0.25 cpd	0.717	1.00							
RG 4 Hz 2 cpd	0.587	0.552	1.00						
RG 16 Hz 2 cpd	0.576	0.628	0.781	1.00					
LUM 4 Hz 0.25 cpd	0.163	0.185	0.076	0.554	1.00				
LUM 16 Hz 0.25 cpd	0.437	0.426	0.409	0.608	0.741	1.00			
LUM 4 Hz 2 cpd	0.025	0.195	0.232	0.387	0.531	0.431	1.00		
LUM 16 Hz 2 cpd	0.116	0.351	0.217	0.382	0.484	0.574	0.825	1.00	
LM ASYM	−0.634	−0.448	−0.784	−0.566	0.020	−0.270	0.150	0.219	1.00

Pearson *r* values are presented. RG = red/green chromatic contrast sensitivity, LUM = luminance contrast sensitivity, LM ASYM = L:M cone asymmetry, cpd = cycles/degree.

Appendix B

Correlation matrix underlying factor analysis for subject group #2.

	RG 0.25 cpd	RG 0.5 cpd	RG 1 cpd	LUM 0.25 cpd	LUM 0.5 cpd	LUM 1 cpd	LM ASYM
RG 0.25 cpd	1.00						
RG 0.5 cpd	0.721	1.00					
RG 1 cpd	0.848	0.799	1.00				
LUM 0.25 cpd	0.290	0.308	0.359	1.00			
LUM 0.5 cpd	0.500	0.438	0.566	0.665	1.00		
LUM 1 cpd	0.269	0.427	0.420	0.611	0.710	1.00	
LM ASYM	−0.552	−0.544	−0.702	−0.194	−0.344	−0.255	1.00

Format as in Appendix A.

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