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What covariance mechanisms underlie green/red equiluminance, luminance contrast sensitivity and chromatic (green/red) contrast sensitivity?

Karen R. Dobkins *, Karen L. Gunther, David H. Peterzell

Department of Psychology, University of California, San Diego, La Jolla, CA 92093, USA

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Abstract

In order to investigate the mechanisms underlying green/red equiluminance matches in human observers and their relationship to mechanisms subserving luminance and/or chromatic (green/red) contrast sensitivity, we tested 21 human subjects along these dimensions at 16 different spatial and temporal frequencies (spatial frequency, 0.25–2 c/deg; temporal frequency, 2–16 Hz) and applied factor analysis to extract mechanisms underlying the data set. The results from our factor analysis revealed separate sources of variability for green/red equiluminance, luminance sensitivity and chromatic sensitivity, thus suggesting separate mechanisms underlying each of the three main conditions. When factor analysis was applied separately to green/red equiluminance data, two temporally-tuned factors were revealed (factor 1, 2–4 Hz; factor 2, 8–16 Hz), suggesting the existence of separate mechanisms underlying equiluminance settings at low versus high temporal frequencies. In addition, although the three main conditions remained separate in our factor analysis of the entire data set, our correlation matrix nonetheless revealed systematic correlations between equiluminance settings and luminance sensitivity at high temporal frequencies, and between equiluminance settings and chromatic sensitivity at low temporal frequencies. Taken together, these data suggest that the high temporal frequency factor underlying green/red equiluminance is governed predominantly by luminance mechanisms, while the low temporal frequency factor receives contribution from chromatic mechanisms.

Keywords: Green–red equiluminance; Chromatic; Luminance; Individual differences; Factor analysis; Magnocellular and parvocellular pathways; Temporal and spatial contrast sensitivity

1. Introduction

Theories of color vision typically posit three post-receptoral 'channels', which are derived from the sums and differences of the three cone types. One channel, the 'luminance' channel, signals a weighted sum of long-wavelength-selective (L) and medium-wavelength-selective (M) cones, i.e. $L+M$ (with some debate regarding the contribution of short-wavelength-selective (S) cones). Two 'chromatic' channels signal weighted sums and differences of the cones. The *green/red* chromatic channel signals differences between L- and M-cones (i.e. $L-M$). The *tritan* chromatic channel signals differences between S-cones and the sum of L- and M-cones (i.e. $S-(L+M)$). Here, we focus on only two of the three channels, the 'luminance' and 'green/red chromatic' channels.

Many psychophysical and neurophysiological studies have investigated the degree to which these color signals remain separate and independent throughout the visual pathway. In experiments using adaptation (e.g. Krauskopf, Williams & Heeley, 1982; Bradley, Switkes & De Valois, 1988), masking (e.g. Gegenfurtner & Kiper, 1992; Mullen & Losada, 1994, 1999; Sankeralli & Mullen, 1997; Giulianini & Eskew, 1998; but cf. Switkes, Bradley & De Valois, 1988) and summation (e.g. Cole, Stromeyer & Kronauer, 1990; Chaparro, Stromeyer, Kronauer & Eskew, 1994; Mullen, Cropper & Losada, 1997; Mullen & Sankeralli, 1999, but cf. Gur & Akri, 1992) paradigms, the detection of chromatic (green/red) stimuli at contrast threshold is neither im-

* Corresponding author. Tel.: +1-858-534-5434.
E-mail address: kdobkins@ucsd.edu (K.R. Dobkins)

paired nor facilitated by the presence of luminance contrast, or vice versa. Thus, at least for experiments that measure contrast thresholds, the general consensus is that the mechanisms underlying detection of luminance contrast ($L+M$) and green/red chromatic contrast ($L-M$) are independent.

In addition to its putative role in luminance contrast sensitivity, the $L+M$ mechanism is also thought to underlie the perceptual ability to make luminance matches between two different colors. In theory, two colors will be perceived as equally luminous — or *equiluminant* — when the sum of L- and M-cone excitation produced by one color equals the sum of L- and M-cone excitation produced by the other color. Typically, equiluminance is measured using *heterochromatic flicker photometry* (HFP), which involves adjusting the relative intensities of two temporally alternating colors (often at ~15 Hz) until they 'fuse', or the sensation of flicker is minimal. At the point of fusion, alternation between the two colors is hypothesized to produce a 'silent substitution' in the luminance ($L+M$) pathway. The existence of an $L+M$ computation is supported by the observation that the human luminosity efficiency function (V_λ), which is derived primarily from HFP data, can be modeled by a weighted sum of the L- and M-cone fundamentals, with the weighting factor thought to represent the L:M cone ratio in the eye (see Lennie, Pokorny & Smith, 1993 for discussion).

Despite the suggestion that $L+M$ mechanisms underlie equiluminance judgments, there exists evidence to suggest that chromatic ($L-M$) mechanisms may also contribute under certain circumstances. For example, tasks that involve *directly* assessing and matching the brightness of two stationary colors (e.g. *heterochromatic brightness matching*, HBM) are thought to rely on signals from *both* $L+M$ and $L-M$ mechanisms. This is in contrast to HFP, which can be modeled solely by $L+M$ signals. Thus, as might be expected, two colors set to be equally bright (in an HBM task) are often not perceived as equiluminant (in an HFP task) (e.g. Wagner & Boynton, 1972; Guth & Lodge, 1973; Bauer & Roehler, 1977; Burns, Smith, Pokorny & Elsner, 1982; Yaguchi & Ikeda, 1983). One explanation for the discrepancy between the two measures concerns the possibility that different *tasks* (HFP vs HBM) tap into different ($L+M$ vs $L-M$) neural pathways (e.g. Ingling & Tsou, 1988; Webster & Mollon, 1993, and see Lennie et al., 1993). Alternatively, or in addition to this possibility, differences may arise because *stimulus* conditions differ between the two tasks, which in turn may affect the relative responsiveness of $L+M$ versus $L-M$ mechanisms. That is, the high temporal frequency stimuli employed in HFP may invoke relatively greater activity in $L+M$ as compared to $L-M$ mechanisms. Conversely, the stationary (or low temporal frequency) stimuli employed in brightness matching may invoke relatively greater activity in $L-M$ mechanisms. Thus, even in a 'minimal flicker' paradigm like HFP, we might expect responses in the $L-M$ pathway to be relatively strong (and hence contribute) when stimuli are presented at sufficiently low temporal frequencies. In sum, while $L+M$ mechanisms might dominate HFP equiluminance settings at high temporal frequencies, $L-M$ mechanisms might also be expected to contribute at low temporal frequencies.

In order to investigate the mechanisms underlying green/red equiluminance in human observers (as determined by HFP) and the degree to which these mechanisms overlap with luminance ($L+M$) or chromatic ($L-M$) mechanisms, we used a factor analysis approach. The methods and theories underlying this approach have been described in detail elsewhere (e.g. Sekuler, Wilson & Owsley, 1984; Peterzell, Kaplan & Werner, 1993, and see Peterzell & Teller, 1996 for a non-technical and historical overview of the topic). This technique uses individual differences across subjects as a way of revealing the number of visual mechanisms underlying performance across a range of stimulus conditions. Specifically, when performance under different stimulus conditions is controlled by a single visual mechanism, subject differences observed under one condition are expected to correlate with subject differences in the other conditions. By contrast, when performance under the different conditions is controlled by *separate* mechanisms, no such correlation is expected. When factor analysis is then applied to the correlations in the data obtained across a variety of stimulus conditions, the number and nature of underlying visual mechanisms can be estimated. The terms 'covariance channels' or 'factors' are used to describe the visual mechanisms estimated from this procedure, to differentiate them from visual mechanisms/channels derived from other methods.

Using this approach, we investigated the inter-dependency of green/red equiluminance, luminance contrast sensitivity and chromatic contrast sensitivity in human psychophysical observers. (Note that we use the term 'equiluminance' in an operationally-defined manner, without attributing the underlying basis to a luminance, i.e. $L+M$, mechanism.) We predicted that luminance and chromatic sensitivity would be governed by separate sources of variability, and thus modeled by separate covariance channels. In addition, we thought equiluminance measures might covary with luminance sensitivity at some, but not all, spatial-temporal frequencies. Similarly, if chromatic mechanisms contribute to equiluminance settings under certain conditions, we expected that equiluminance measures might also covary with chromatic contrast sensitivity under a different range of spatial-temporal frequencies. To test this hypothesis, we obtained data from 21 subjects, each of whom provided green/red equiluminance settings, lumi-

nance contrast sensitivity values and chromatic contrast sensitivity values at 16 different spatial-temporal frequencies. Factor analysis was then applied to the data to investigate the number and tuning of covariance channels underlying the results.

2. Methods

2.1. Subjects

Twenty-two subjects (including the three authors) participated in these experiments. All subjects had normal or corrected-to-normal vision, and normal green-red color vision (as assessed by the Ishihara Test for color deficiency). Subject age ranged from 18 to 41 years (mean, 23 years; S.D., 6.5 years). One subject was unable to provide reliable green/red equiluminance settings, and thus his data were excluded from our analyses. Data from 21 subjects were retained.

2.2. Apparatus

Visual stimuli were generated on a Nanao F2-21 monitor (21 in. display, 1024 × 768 pixels, 105 Hz) driven by a Cambridge Research Systems (CRS) Video Board. The 15-bit video board allowed for 32 768 discrete luminance levels. The CIE (x, y) coordinates for the monitor primaries were: red (0.625, 0.340), green (0.285, 0.605), and blue (0.150, 0.065). 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 ('OptiCal 265M', purchased from 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 (green/red) and luminance (white/black) sinusoidal gratings, counterphase-reversed (temporal sinusoidal) at 16 different combinations of spatial and temporal frequencies (SF = 0.25, 0.5, 1, and 2 c/deg; TF = 2, 4, 8, and 16 Hz). We chose to go no higher in spatial frequency than 2 c/deg in order to avoid luminance artifacts produced by chromatic aberration (Flitcroft, 1989; Logothetis, Schiller, Charles & Hurlbert, 1990; Cavanagh & Anstis, 1991). 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 green and red) bars 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 (green/red) gratings were created to selectively modulate activity within L- and M-cones, while keeping the S-cone excitation constant (S-cone activation = approximately 1.0 units in MacLeod-Boynton chromaticity space, normalized to equal energy white, see Boynton, 1996). Chromatic gratings were employed for the purpose of obtaining: (1) green/red equiluminance settings; and (2) chromatic contrast sensitivities. Luminance (white/black) gratings were produced by sinusoidally modulating the luminance of the white background, and were employed for the purpose of obtaining luminance contrast sensitivities. The contrast of all gratings is described in terms of the root-mean-square (r.m.s.) cone contrast produced in L- and M-cones (described below). The benefit of a cone contrast metric is that it standardizes across apparati and laboratories, and allows for the expression of chromatic and luminance contrast in comparable units (e.g. Mullen, 1985; Lennie & D'Zmura, 1988; Chaparro, Stromeyer, Huang, Kronauer & Eskew, 1993).

2.3.1. Cone contrast calculations

Although our monitor calibration allowed us to specify any desired cone contrast, we nonetheless used the PR-650 SpectraColorimeter to confirm the L- and M-cone contrasts produced by our stimuli. For V_λ-equiluminant stimuli, L- and M-cone excitations produced by the 'green' peak ($L_{(g,V_\lambda)}$, $M_{(g,V_\lambda)}$) and 'red' peak ($L_{(r,V_\lambda)}$, $M_{(r,V_\lambda)}$) of the gratings were obtained by integrating the product of stimulus spectral output (readings taken in 4 nm intervals from 380 to 780 nm) with the Stockman, MacLeod and Johnson (1993) L- and M-cone fundamentals for 2° stimuli. For stimuli differing from V_λ equiluminance, we obtained L- and M-cone excitations produced by the green (L_g, M_g) and red (L_r, M_r) peaks of the stimulus, using the following formulas:

$$L_g = (G/G_{V_\lambda}) * L_{(g,V_\lambda)} \quad (1a)$$

$$M_g = (G/G_{V_\lambda}) * M_{(g,V_\lambda)} \quad (1b)$$

$$L_r = (R/R_{V_\lambda}) * L_{(r,V_\lambda)} \quad (1c)$$

$$M_r = (R/R_{V_\lambda}) * M_{(r,V_\lambda)} \quad (1d)$$

where $L_{(g,V_\lambda)}$, $M_{(g,V_\lambda)}$, $L_{(r,V_\lambda)}$ and $M_{(r,V_\lambda)}$ refer to the cone excitations produced by the green and red peaks in the V_λ-equiluminant stimulus (as determined above), G_{V_λ} and R_{V_λ} are the green and red luminances of those

V_λ-equiluminant stimuli (which are necessarily equal to one another), and G and R are the green and red luminances that are not V_λ-equiluminant. The use of this formula circumvented the need to measure the spectral output for different green/red pairs employed in these studies. The validity of these equations was verified empirically for several green/red stimulus pairs. Cone excitations were used to compute L- and M-cone contrasts (CC): $L_{CC} = (L_g - L_r)/(L_g + L_r)$, $M_{CC} = (M_g - M_r)/(M_g + M_r)$. From these values, root-mean-square cone contrasts (r.m.s. CC = sqrt[$(M_{CC}^2 + L_{CC}^2)/2$]) were determined. For luminance stimuli, r.m.s. cone contrasts directly correspond to conventional Michelson contrast: [(Luminance$_{max}$ − Luminance$_{min}$)/(Luminance$_{max}$ + Luminance$_{min}$)].

Note that our calculation of cone excitations relies on the use of cone fundamentals for the *'standard'* observer (as determined by Stockman et al., 1993). Because cone fundamentals are expected to differ somewhat across individuals (based on differences across subjects in λ_{max}, photopigment optical density, as well as lens and macular pigment), there will be some error in cone excitations derived from a standard set of cone fundamentals for all subjects (see Bieber, Kraft & Werner, 1998). In addition, because relative L- versus M-cone weights and phase-lags can vary with stimulus parameters such as spatial-temporal frequency and background chromaticity (e.g. Hamer & Tyler, 1992; Stromeyer, Chaparro, Tolias & Kronauer, 1997), using a standard set of cone fundamentals to determine the cone excitations elicited across a range of stimulus parameters can also introduce error into estimates. Although we cannot rule out such error, we expect it to be quite small since our equal energy white background is roughly metameric (in terms of the relative excitation of L- and M-cones) with a 570 nm light, a wavelength which reportedly does not produce variability in the responses of L- and M-cones as a function of spatial-temporal frequency (Stromeyer et al., 1997).

2.4. Paradigm

2.4.1. General

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 key-presses on a response box. No feedback was provided. Three main conditions were tested: (1) green/red equiluminance [G/R-EQUIL]; (2) luminance contrast sensitivity [LUM-CS]; and (3) chromatic contrast sensitivity [CHROM-CS]. Data for these three main conditions were obtained at each of 16 different spatial-temporal frequencies. Thus, for the entire experiment, each subject provided 48 data points (16 G/R-EQUIL, 16 LUM-CS and 16 CHROM-CS), derived from a total of at least 4000 trials. For each subject, 10–12 h were required to complete the entire experiment, with testing divided into 1–2 h blocks.

2.4.2. Determining green/red equiluminance in individual subjects

Standard HFP was used to obtain equiluminance points in individual subjects. Chromatic (green/red) counterphase gratings were centered on the fixation cross, and the luminance ratio of the grating was adjusted with a key press. Luminance ratio is defined as G/R, where '$G/R = 1.0$' denotes V_λ equiluminance, '$G/R > 1.0$' denotes green more luminous than red, and '$G/R < 1.0$' denotes red more luminous than green. On each trial, subjects adjusted the G/R luminance ratio (interval step = 1.2% change in G/R ratio) of the grating until the percept of flicker was least salient. The chromatic gratings employed for determining equiluminance produced 7.10% r.m.s. cone contrast in L- and M-cones (at V_λ equiluminance). This cone contrast value was 5.1 × the mean chromatic contrast threshold (averaged across all spatial-temporal frequency conditions), and ranged from 1.4 × threshold for high frequency (i.e. 16 Hz, 2 c/deg) gratings to 8.7 × threshold for low frequency (i.e. 2 Hz, 0.25 c/deg) gratings.

For each subject, equiluminance points were determined from the mean of 20 trials, separately at each of the 16 different spatial-temporal frequency conditions ('outlier' trials were excluded if they were greater than 2.5 S.D. from a subject's mean on a particular condition). Mean equiluminance values obtained in this manner were used to set the G/R luminance ratio for each subject when tested in the *CHROM-CS* condition (see below).

2.4.3. Contrast sensitivity paradigm

Contrast sensitivity was determined for both luminance and chromatic stimuli, at each of the 16 different spatial-temporal frequencies. To this end, a Best-PEST staircase procedure (Lieberman & Pentland, 1982) was employed 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. Stimuli were presented for 300 ms, with contrast ramped on and off in a cosine fashion within the first and last 100 ms. The staircase procedure continued until the subject had completed at least 120 trials for each stimulus condition. Contrast sensitivity measurements were divided into four different blocks. Each block contained four chromatic stimuli (chosen randomly out of the 16 different spatial-temporal frequencies) and four luminance stimuli (also chosen randomly out of the 16 spatial-temporal frequencies), for a total of eight stimulus conditions per block.

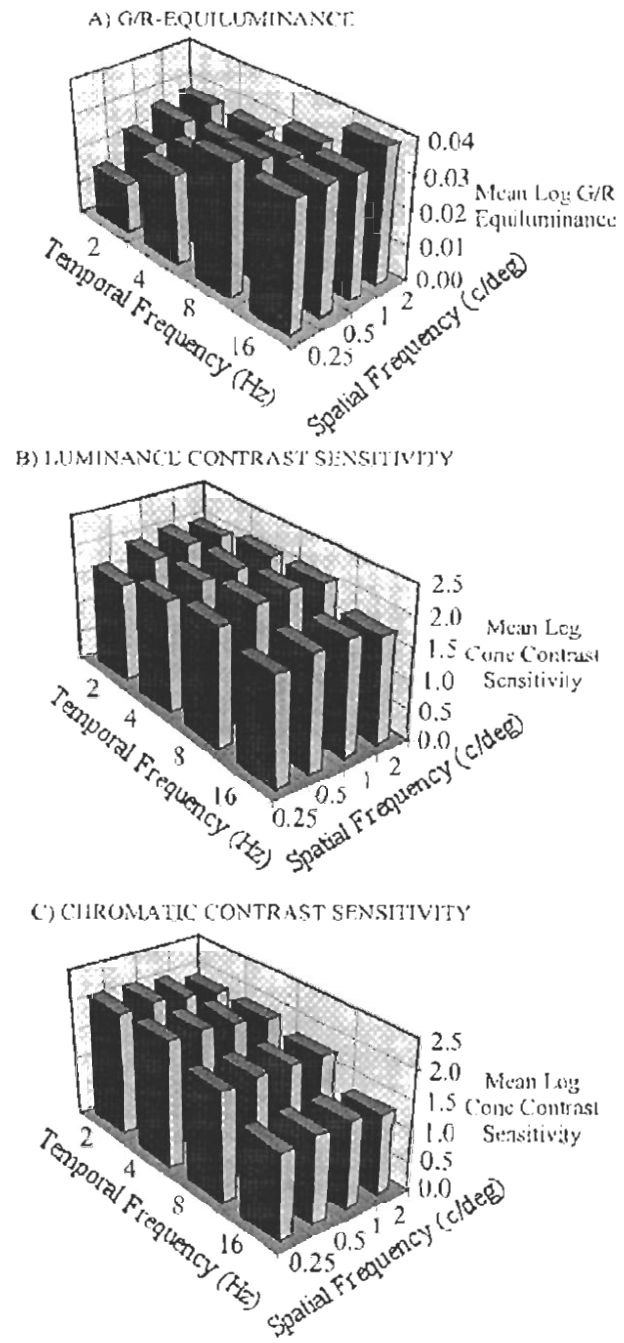

Fig. 1. Geometric means obtained from 21 subjects tested at each of 16 spatial-temporal frequencies, for three different stimulus conditions. (A) Green:red equiluminance. Here, a log $G:R$ ratio of zero denotes V_λ equiluminance. Across all conditions, subjects tended to require more green to match the red, as evidenced by mean log $G:R$ ratios greater than zero. We do not attribute any significance to this, but rather believe it is a simple consequence of the particular stimulus parameters used in our experiments (i.e. size and placement of stimuli, background chromaticity, etc.). (B) Luminance contrast sensitivity. (C) Chromatic contrast sensitivity. In order to facilitate comparison between spatial-temporal frequency conditions, standard deviations are not plotted. Standard deviations were, on average, 0.02 log units for the equiluminance data, 0.13 log units for luminance data, and 0.15 log units for chromatic data.

2.5 Correlational and 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) to determine the degree of dependence versus independence of green/red equiluminance, luminance sensitivity and chromatic sensitivity, as well as the tuning of spatial and temporal channels within the three main conditions. Because frequency histograms of subject data conformed to normal distributions when log-transformed, all analyses were performed on log values.

As a first step in our factor analysis, a principal component analysis (PCA) was performed on the correlational data. Scree tests, χ^2 statistics, and visual inspection were used to determine the minimum number of statistically-significant components (i.e. with eigenvalues greater than 1.0). A chosen number of orthogonal components were then rotated to 'simple structure' using the Varimax criterion (Gorsuch, 1983), which maximizes the number of zero factor loadings. Factor analyses were performed (using identical statistical procedures) on the following: (1) the entire data set; (2) G/R-EQUIL data alone; (3) CHROM-CS data alone; and (4) LUM-CS data alone. In addition, in order to determine the effects of *age*, this parameter was also included in some of our analyses.

3. Results

3.1. Means

Geometric mean data from 21 subjects are presented in Fig. 1, separately for G/R-EQUIL, LUM-CS and CHROM-CS, with values plotted as a function of both spatial and temporal frequency. For the G/R-EQUIL condition (Fig. 1a), equiluminance settings varied across the different spatial-temporal frequency combinations, in accordance with results from previous studies (e.g. Cushman & Levinson, 1983; Cavanagh, MacLeod & Anstis, 1987; Livingstone & Hubel, 1987; Logothetis & Charles, 1990; Dobkins & Albright, 1993). Specifically, equiluminance settings varied significantly with temporal frequency ($F(3,60) = 7.6$, $P < 0.001$), with more green required to match the red as temporal frequency was increased. In addition, while there was not a significant main effect of spatial frequency, there was a significant interaction between spatial and temporal frequency ($F(9,180) = 4.169$, $P < 0.001$), due to a significant effect of spatial frequency on equiluminance settings at 2 Hz. We return to a potential explanation for the effects of spatial-temporal frequency on equiluminance settings in Section 4.

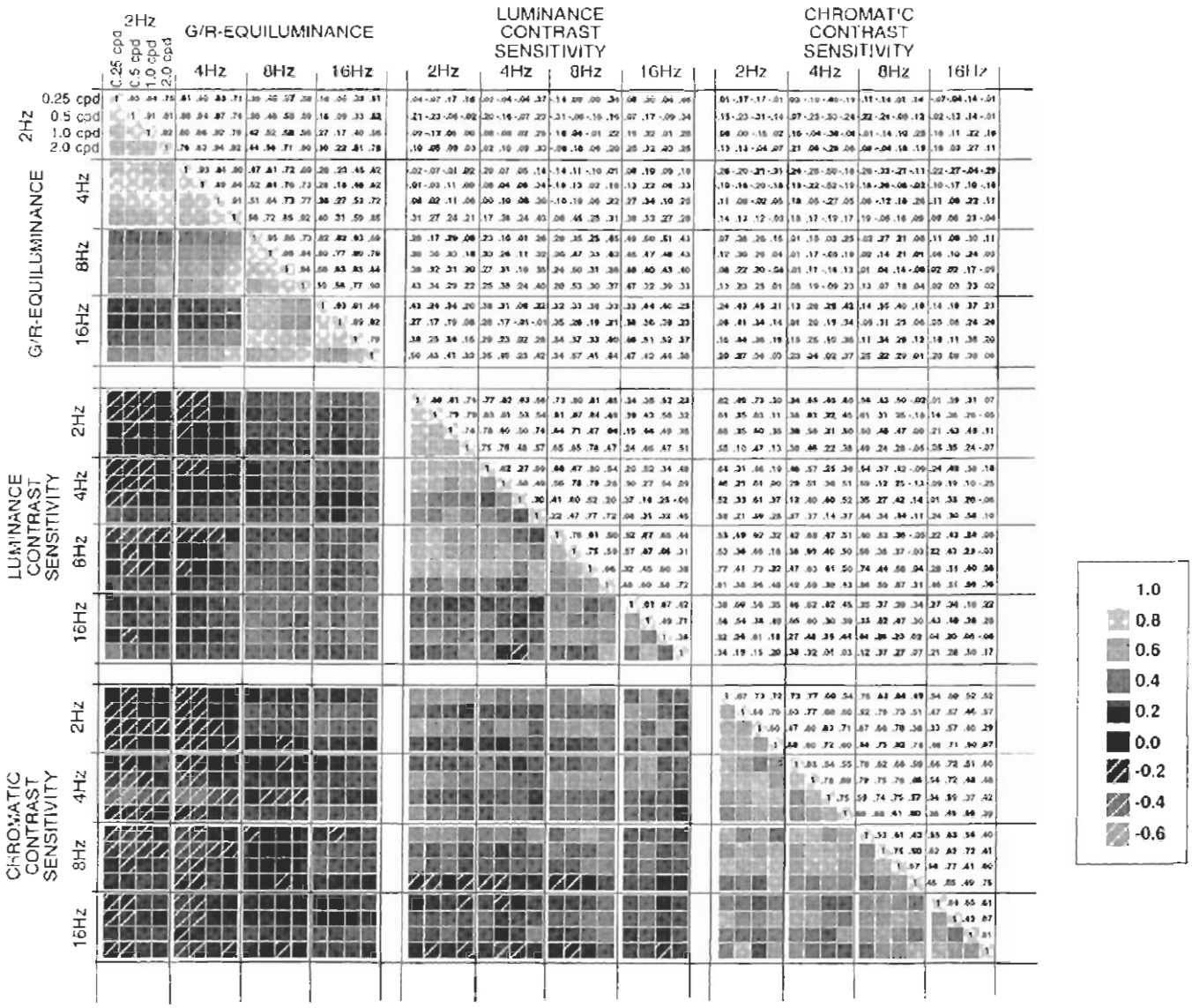

Fig. 2. Correlation matrix for the entire data set (three main conditions by 16 spatial-temporal frequencies). *Upper-right triangle*: Pearson *r* values. *Lower-left triangle*: correlation matrix coded by gray scale. (Negative correlations are distinguished by the addition of white diagonal lines).

Mean contrast sensitivities for LUM-CS and CHROM-CS data are shown in Fig. 1b and c, respectively. As expected from previous studies (e.g. Robson, 1966; Kelly, 1971; Burr & Ross, 1982; Mullen, 1985; Mullen & Boulton, 1992; Derrington & Henning, 1993; Gegenfurtner & Hawken, 1995; Dobkins, Lia & Teller, 1997; Peterzell & Teller, 2000), luminance contrast sensitivity exhibited bandpass tuning with sensitivity peaking at intermediate spatial and temporal frequencies, while chromatic contrast sensitivity exhibited lowpass tuning for both spatial and temporal frequency.

3.2. Correlation matrix

As a first step in our factor analysis, we calculated correlations across the 21 subjects for the 48 different data points (i.e. three main conditions by 16 spatial-temporal frequencies). The values in this matrix also allowed us to visualize consistent trends in the correlations prior to conducting the factor analysis. The resulting correlation matrix is presented in Fig. 2, with the values partitioned for the three main conditions. The upper-right portion of the matrix provides the numerical Pearson *r* values, while the lower-left portion presents these values coded by intensity. A high correlation value between two stimulus conditions indicates that subject data obtained for one stimulus condition were highly correlated with (i.e. predictive of) data obtained for the other stimulus condition. This could be in the form of a *positive* correlation (i.e. higher values in one condition predicted higher values in the other) or a *negative* correlation (i.e. higher values in one condition

predicted *lower* values in the other). Low (near zero) values indicate that there was little correlation between conditions.

As can be observed in the correlation matrix, the highest correlations were found *within* each of the three main conditions (i.e. G/R-EQUIL, LUM-CS, CHROM-CS). For example, correlations were positive and uniformly high within the CHROM-CS condition, indicating that a subject who was more sensitive than others at one spatial-temporal frequency was typically more sensitive at all spatial-temporal frequencies. A generally similar pattern was observed for the LUM-CS condition, although relatively low correlations were observed between high (i.e. 16 Hz) and low (i.e. 2–4 Hz) temporal frequencies. This pattern suggests the existence of separate temporally-tuned mechanisms for LUM-CS, which is supported by the results of our factor analyses (below). For G/R-EQUIL data, this effect of temporal frequency was even more pronounced. Here, high positive correlations were found separately at low (i.e. 2–4 Hz) and at high (i.e. 8–16 Hz) temporal frequencies, yet correlations between the two temporal frequency ranges were quite low. This pattern in the correlation data indicates that a subject's equiluminance point at 2 Hz could be used to predict her equiluminance point at 4 Hz, but not at 8 or 16 Hz (or vice versa).

Compared to the correlations observed *within* conditions, correlations *across* the three main conditions were typically much lower, indicating that performance in one condition (e.g. LUM-CS) was not, in general, a good predictor of performance in the other two conditions (e.g. G/R-EQUIL or CHROM-CS). Noted exceptions to this can be found, however. For example, G/R-EQUIL data at higher temporal frequencies (8 and 16 Hz) correlated moderately with LUM-CS at these same temporal frequencies (which can be observed by the relatively higher numbers and lighter squares in the high temporal frequency region of the G/R-EQUIL vs LUM-CS matrix). This indicates that a subject who, relative to others, required more green to match the red also tended to exhibit higher luminance contrast sensitivity. In addition, there existed moderate and systematic *negative* correlations between G/R-EQUIL and CHROM-CS at lower temporal (i.e. 2 and 4 Hz) and lower spatial (i.e. 0.25 and 0.5 c/deg) frequencies. This indicates that a subject who required green more luminous than red (relative to others) tended to exhibit *lower*-than-average chromatic contrast sensitivity under these spatial-temporal conditions. We return to the potential significance of these correlations across the three main conditions in Section 4. (Also note that there were negative correlations between G/R-EQUIL and LUM-CS, although these values were smaller and less consistent. In addition, note that positive correlations between LUM-CS and CHROM-CS were generally low and not systematic.)

In sum, these results demonstrate that the highest correlations exist *within* the three main conditions, although some systematic correlations do appear to exist across conditions. To investigate these relationships further, we turn to the results of factor analysis, a procedure that investigates statistically the covariance structure of the data.

3.3. Factor analyses

3.3.1. Factor analysis of entire data set

The results from our factor analysis of the entire data set are presented in Fig. 3. Shown are the factor loadings obtained for a *three*-factor solution, which was chosen because it yielded systematic and highly interpretable results. As in previous analyses (e.g. Gorsuch, 1983; Peterzell et al., 1995; Peterzell & Teller, 1996), our criterion for 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 48 data points (three main conditions by 16 spatial-temporal frequencies). The results of this analysis yielded separate factors for each of the three main conditions of the experiment. Specifically, Factor 1, which accounted for 37% of the overall variance, loaded primarily onto LUM-CS values at all but four spatial-temporal frequencies, yet explained almost no variability in the two other conditions (with the exception of a few scattered points in the CHROM-CS condition). Factor 2 accounted for an additional 22% of the variance, and loaded exclusively onto the G/R-EQUIL condition at all spatial-temporal frequencies. Likewise, Factor 3, which accounted for 11% of the variance, loaded onto all spatial-temporal frequencies in the CHROM-CS condition.

In sum, this pattern of results suggests the existence of separate neural mechanisms underlying each of the three conditions — G/R-EQUIL, LUM-CS and CHROM-CS. It is important to point out that this separability is not an artifact of choosing a three-factor solution, as the three factors are completely unconstrained in the analysis. Moreover, choosing a *greater* than three-factor solution had no effect on our findings; when we allowed a four-, five- or six-factor solution to emerge (all of which were significant based on our scree plots), frequency-tuning began to emerge within a condition, yet the three main conditions continued to remain separate. We should also point out that the absence of cross-condition factors (i.e. between the three main conditions) should not be attributed to an overall failure of our factor analysis approach, since strong and systematic factors were observed *within* each of the three main task conditions. This positive result, we believe, clearly demonstrates that our methods are strong enough to reveal covariance factors.

3.3.2. Factor analyses for each condition

To investigate the potential for spatial-temporal tuning, factor analyses were conducted *separately* for each of the three main conditions. The results are plotted in Fig. 4. When factor analysis was performed on G/R-EQUIL data, two significant temporally-tuned factors were found (Fig. 4, top panel). Factor 1, accounting for 68% of the variance, loaded onto low temporal frequencies (2–4 Hz), whereas Factor 2 (20% of the variance) covered high temporal frequencies (i.e. 8–16 Hz). In an earlier pilot study employing slightly different stimulus conditions (i.e. relatively larger stimuli, a yellow background, SF range = 0.3–2.2 c/deg, TF range = 1–19 Hz, Gunther, Peterzell & Dobkins, 1997) we also found frequency-tuned factors underlying green/red equiluminance, which were quite consistent with the ones observed in the present study. Thus, these now replicated findings suggest the existence of multiple temporally-tuned mechanisms underlying green/red equiluminance settings.

Similar to the case for G/R-EQUIL data, our factor analysis conducted on LUM-CS data revealed two temporally-tuned factors. Factor 1 covered lower temporal frequencies (2–8 Hz, 59% of the variance), while Factor 2 covered higher temporal frequencies (8–16 Hz, 13% of the variance), with overlap between factors at 0.25 c/deg, 8 Hz. For the CHROM-CS condition, a single factor (accounting for 64% of the variance) loaded onto all spatial-temporal frequencies.

3.3.3. Effects of age

When subject age was included in our analyses, we found a fairly strong positive correlation between age and G/R-EQUIL data at high temporal frequencies (8–16 Hz: mean correlation = 0.47), but essentially no correlation at low temporal frequencies (2–4 Hz: mean

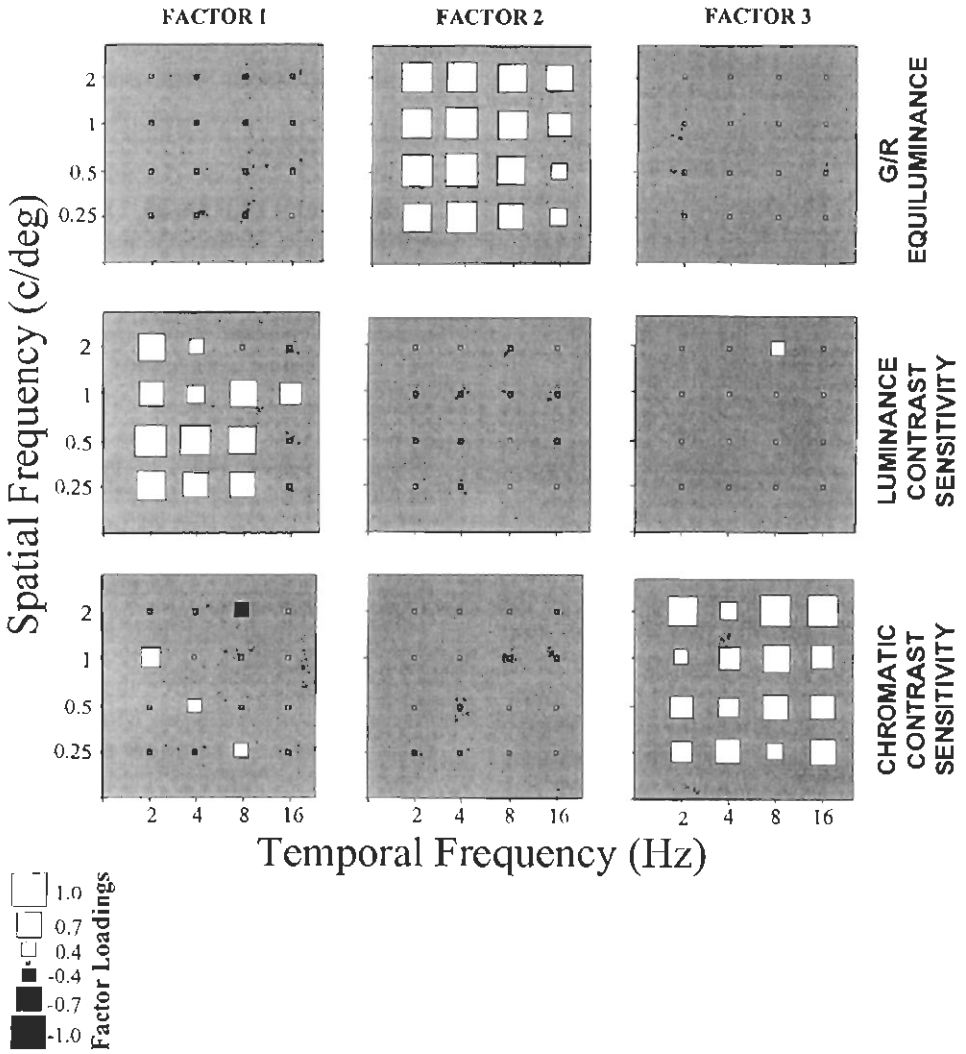

Fig. 3. Factor loadings from a three-factor solution using Principal Component Analysis (with factors rotated to simple structure) on the entire data set. White and black squares represent positive and negative factor loadings, respectively. Squares are scaled in size according to their value. Small gray squares represent factor loadings that fell below the criterion for significance (factor loading < |0.4|). Note that separate factors were obtained for each of the three main conditions (see text for further details).

intercorrelated channels that reveal their individual identities in adaptation studies (see Peterzell & Teller, 1996 for further discussion). This could occur if all channels are manufactured from common inputs, for example, from common subcortical inputs to different classes of frequency-tuned cortical cells, and adaptation occurs at the cortical level only. In order to more directly test this possibility, it will be important to systematically evaluate results obtained under different paradigms (e.g. the factor analysis approach vs an adaptation paradigm), being careful to use identical stimulus conditions and subjects across studies.

4.3. Relationship between green/red equiluminance, luminance contrast sensitivity and chromatic contrast sensitivity

When our factor analysis was performed on the entire data set, we found three main factors, each loading separately onto one of the three main conditions: green/red equiluminance, luminance contrast sensitivity and chromatic contrast sensitivity (Fig. 3). The independence between luminance contrast sensitivity and chromatic (green/red) sensitivity observed in our data set confirms reports from previous psychophysical studies that have employed adaptation, masking or summation paradigms (Krauskopf et al., 1982; Bradley et al., 1988; Cole et al., 1990; Gegenfurtner & Kiper, 1992; Chaparro et al., 1994; Mullen & Losada, 1994, 1999; Mullen et al., 1997; Sankeralli & Mullen, 1997; Giulianini & Eskew, 1998; Mullen & Sankeralli, 1999). In addition, recent studies employing the factor analysis approach have also observed separability between luminance and chromatic contrast sensitivity for static grating stimuli (Peterzell, Chang & Teller, 2000; Peterzell & Teller, 2000), and for steady-state sweep-VEP contrast sensitivity obtained with counterphase gratings (Peterzell et al., 1996, 1997). In sum, the results across diverse studies strongly support the existence of separate mechanisms underlying the detection of luminance and green/red chromatic contrast.

At first glance, the finding of separability between contrast sensitivity and green/red equiluminance settings in our factor analysis may seem somewhat surprising, since we expected that green/red equiluminance would at least be served by a luminance (i.e. $L+M$) mechanism, if not by both a luminance and chromatic (i.e. $L-M$) mechanism. There are two main possibilities why our factor analysis may not have extracted a common factor between green/red equiluminance and (luminance or chromatic) contrast sensitivity. One, the signals underlying the different perceptual phenomena may be processed within a common neural pathway, yet be extracted at different *levels* of visual processing. For example, green/red equiluminance may be determined very early in visual processing, by the inputs of L- and M-cones to retinal ganglion cells. Contrast sensitivity, on the other hand, may be largely determined at the *cortical* level, by gain control mechanisms (e.g. Ohzawa, Sclar & Freeman, 1985), temporal filtering of signals (e.g. Lee, Pokorny, Smith, Martin & Valberg, 1990) or the variability of firing rate (e.g. Tolhurst, Movshon & Dean, 1983). If this were the case, the mechanisms underlying equiluminance and contrast sensitivity might be limited by separate sources of variability. This, in turn, might allow the measures to remain separate in our factor analyses.

Alternatively, a relationship may exist between the measures, yet not at a statistically significant level as would be required to be pulled out by our factor analysis. We tend to believe this second alternative, because the correlation matrix revealed interpretable results, with systematic positive and negative correlations between green/red equiluminance and contrast sensitivity (see Fig. 2). Specifically, at high temporal frequencies, higher-than-average G/R ratios were correlated with higher-than-average luminance contrast sensitivity. At low temporal frequencies, higher G/R ratios were correlated with *lower*-than-average chromatic contrast sensitivity. Although one could argue that these cross-condition correlations were moderate at best (i.e. mean positive correlation = ~ 0.35, mean negative correlation = ~ -0.20), it is the *pattern* of correlations (as opposed to the absolute numbers) that is revealing.

Interestingly, similar to the way in which these cross-condition correlations were observed separately at low vs. high temporal frequencies, the results from our analyses of green/red equiluminance data also revealed separate mechanisms underlying performance at low (2–4 Hz) vs. high (8–16 Hz) temporal frequencies (seen in the correlation matrix of Fig. 2 and the factor loadings of Fig. 4, top panel). Taken together, these findings suggest that the high temporal frequency mechanism underlying green/red equiluminance settings is related to luminance sensitivity, while the low temporal frequency mechanism is related to chromatic sensitivity. This pattern of results is consistent with the finding that the V_λ function (derived mainly from HFP data obtained at high temporal frequencies, i.e. ~ 15 Hz) can be modeled by a simple weighted sum of L- and M-cone signals. Likewise, the possibility that chromatic ($L-M$) mechanisms contribute to the low temporal frequency factor underlying equiluminance data is consistent with the observation that matches made between two stationary colors (in a *heterochromatic brightness matching* task) can be modeled by contributions from both $L-M$ and $L+M$ mechanisms. Our results are also consistent with a study by Webster and Mollon (1993) demonstrating that chromatic adaptation alters equiluminance settings at low, but not high, temporal frequencies. Like the present study, their findings support the existence of separate mechanisms (presumably

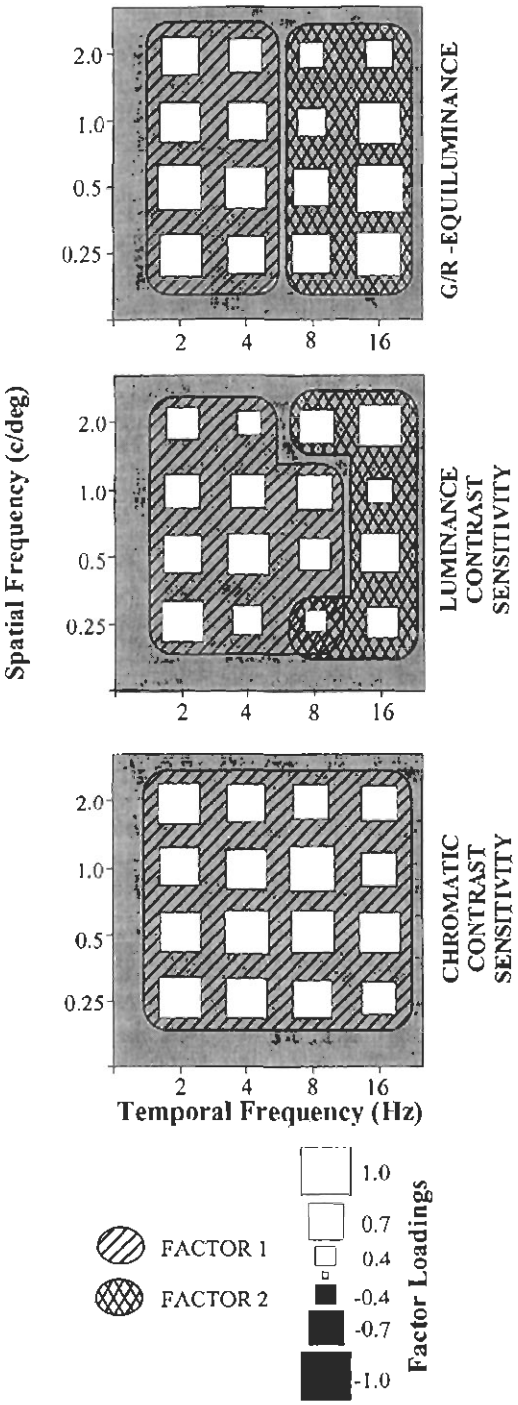

Fig. 4. Factor loadings obtained from analysis of each condition alone (see text for details). Factor loadings are represented as in Fig. 3. Unlike Fig. 3, separate factors are grouped by different patterns, separately within each main condition.

correlation = 0.07). Thus, as expected based on the yellowing of the lens with age (e.g. van Norren & Voss, 1974; Werner, Peterzell & Scheetz, 1990), older subjects required relatively more green to match the red than did younger subjects (at least for high temporal frequencies). With respect to the LUM-CS condition, we found no evidence for age affecting performance, as correlations between age and LUM-CS were extremely low under all conditions (2–4 Hz: mean correlation = 0.10, 8–16 Hz: mean correlation = 0.04, overall mean = 0.07). We did, however, find a moderate positive correlation between age and CHROM-CS that was fairly consistent across all spatial-temporal frequencies (mean correlation = 0.21), suggesting that older subjects tended to be *more* sensitive than younger subjects. This result is a bit surprising because contrast sensitivity has been shown to worsen with age (e.g. Tyler, 1989; Mayer, Dougherty & Hu, 1995; Knoblauch, Barbur & Vital-Durand, 1995, and see Werner et al., 1990 for a review).

In summary, the results from our analysis of age show moderate effects on performance, with the strongest (and least surprising) effects of age seen for G/R-EQUIL data. The fact that age affects G/R-EQUIL, but not LUM-CS, data indicates that age cannot account for the moderate positive correlations seen between these two conditions (see correlation matrix, Fig. 2). Likewise, age cannot account for the moderate *negative* correlations seen between G/R-EQUIL and CHROM-CS data (see Fig. 2), since this effect is opposite to that which would be predicted based on the *positive* correlation observed for both age versus G/R-EQUIL and age versus CHROM-CS. In addition, when age was included in the factor analysis of the entire data set and four factors were allowed to emerge, the first three factors were identical to the factors in our original three-factor solution (with each factor covering one of the three main conditions), and the fourth factor loaded exclusively onto age (with a factor loading of 0.62). When we attempted a *three*-factor solution with age included in the analysis, age did not load significantly onto any factor (i.e. no factor loadings $> |0.4|$). Based on these results, we believe that age cannot account for the relationships observed between the three main conditions.

4. Discussion

These results are discussed in several contexts. First, we address the potential effects of chromatic aberration. Second, we discuss spatial and temporal factors underlying the data, and relate our findings to those of previous studies. Third, we discuss the relationship between our three main conditions (green/red equiluminance, luminance contrast sensitivity and chromatic contrast sensitivity), as revealed by our factor analyses and correlation data. Fourth, we discuss potential underlying neural substrates for our results, with a particular focus on contribution from parvocellular and magnocellular pathways. On a final note, we discuss the evidence for the possibility that $L{:}M$ ratios (which are directly related to green/red equiluminance settings)

may place constraints on both luminance and chromatic contrast detection.

4.1. Chromatic aberration

Although our use of spatial frequencies ≤2 c/deg should preclude the existence of luminance artifacts arising from chromatic aberration of the eye (Flitcroft, 1989; Logothetis et al., 1990; Cavanagh & Anstis, 1991), we nonetheless address the potential effects of this phenomenon had it existed. First, because our stimuli were presented near the fovea, the effects of transverse (i.e. lateral) chromatic aberration are expected to be negligible. Longitudinal chromatic aberration, on the other hand, can produce luminance contrast on the retina if a subject accommodates to one of the two endpoint colors of the grating instead of to the midpoint/background color. For example, accommodating to the red peak of the chromatic grating will cause the green portion to be de-focused and thus attenuated in contrast. It is important to remember, however, that subjects were required to set the green/red grating to be equiluminant (using HFP). Thus, if differential accommodation occurred (for example, to red), the equiluminance procedure would allow the subject to compensate by increasing the luminance of the green. This resulting green/red value would then be appropriately used in the chromatic contrast sensitivity condition. Moreover, had subjects been using luminance contrast (as a result of chromatic aberration) to detect the green/red gratings, we would have expected systematic correlations between luminance and chromatic contrast sensitivity at high spatial frequencies, a pattern that is not seen in the correlation matrix or factor analyses. For these reasons, we feel confident that, even had chromatic aberration existed, it did not contribute to our results.

4.2. Temporal and spatial channels underlying contrast detection

Several previous studies have demonstrated temporal and spatial channels underlying contrast detection of luminance and chromatic contrast. With respect to *temporal channels for luminance detection*, results from masking, summation and temporal frequency discrimination paradigms point to the existence of two to four temporal-frequency-tuned channels (King-Smith & Kulikowski, 1975; Tyler, 1975; Mandler & Makous, 1984; Moulden, Renshaw & Mather, 1984; Anderson & Burr, 1985; Lehky, 1985; Tyler, 1989; Hammett & Smith, 1992; Hess & Snowden, 1992; Metha & Mullen, 1996). In addition, results from previous studies employing factor analyses on luminance contrast sensitivity data also suggest the existence of two to three temporal channels (Mayer et al., 1995; Billock & Harding, 1996; Peterzell, Dougherty & Billock, 1996a; Peterzell, Kelly, Chang, Gordon, Omaljev & Teller, 1996b; Peterzell, Chang, Kelly, Hartzler & Teller, 1997a; Peterzell, Dougherty & Mayer, 1997b). In the present study, our factor analyses revealed two temporal factors underlying luminance contrast detection (one loading onto 2–8 Hz, the other loading onto 8–16 Hz, see Fig. 4, middle panel), thus supporting the general consensus that at least two mechanisms underlie temporal sensitivity for luminance stimuli.

For *chromatic* stimuli, the number of temporal channels underlying contrast detection has been relatively less explored. In one recent study employing temporal frequency detection and discrimination techniques, two temporal channels (one lowpass, one bandpass) appeared to underlie chromatic (green/red) sensitivity (Metha & Mullen, 1996). By contrast, our factor analyses revealed only a *single* temporal factor underlying chromatic contrast sensitivity (Fig. 4, bottom panel). Clearly, more studies in the chromatic domain will be required to resolve this issue.

With respect to *spatial* channels, the results of our factor analyses were somewhat surprising because they yielded no spatial factors for either luminance or chromatic contrast sensitivity data across the range of spatial frequencies tested (0.25–2 c/deg). These results are at odds with the sizeable literature obtained from masking, summation and adaptation paradigms, which supports at least two spatial channels below 2 c/deg for both luminance (e.g. Tolhurst, 1973; Greenlee, Magnussen & Norby, 1988) and chromatic (e.g. Losada & Mullen, 1994; Mullen & Losada, 1994) stimuli, and for both stationary and counterphase-reversing gratings (see Graham, 1989 for a review). Previous factor analytic studies using *stationary* luminance-modulated gratings have reported multiple factors consistent with the masking, summation and adaptation literature (Sekuler et al., 1984; Peterzell & Teller, 1996, 2000). By contrast, studies that have applied factor analysis to data obtained for *counterphase* luminance-modulated gratings report only a single spatial covariance channel below 2 c/deg (Billock & Harding, 1996, data re-analyzed by Peterzell et al., 1996), as is the case in the present factor analysis. For chromatic stimuli, results from the factor analyses of Peterzell and Teller (1996, 2000) agree with our findings of a single spatial covariance channel below 2 c/deg. As such, the factor analytic results for both stationary and counterphase chromatic gratings, although consistent with each other, are inconsistent with results obtained using more traditional methods.

It should also be pointed out that the factor analysis approach may yield fewer factors than do other methods (e.g. adaptation) if the channels revealed by these other techniques are, in fact, correlated. That is, a single covariance channel may represent a *group* of

$L-M$ vs $L+M$) dominating equiluminance settings at low versus high temporal frequencies (also see Lennie et al., 1993).

We should emphasize here that the task in our experiment (i.e. to minimize flicker in the stimulus) was constant across all spatial-temporal frequency conditions. Thus, the contribution of separate mechanisms to equiluminance settings is expected to be due to different temporal frequencies differentially affecting the relative activations of $L-M$ vs $L+M$ pathways, as opposed to task demands differentially tapping into one pathway versus the other (see Shioiri & Cavanagh, 1992 for a similar argument). This change in the relative activations of $L-M$ versus $L+M$ pathways could explain why equiluminance settings tend to vary with temporal frequency (as observed in the present and previous studies). In addition to this possibility, the effect of temporal frequency on equiluminance settings may be due to phase-lags and/or relative cone weights between L- and M-cones that vary with temporal frequency (see Hamer & Tyler, 1992; Smith, Lee, Pokorny, Martin & Valberg, 1992; Stromeyer et al., 1997). As mentioned earlier in Section 2, the use of an equal energy white background in our experiments is expected to produce small (if not negligible) variability in phase-lags or cone weights. Nonetheless, we cannot rule out the possibility that this factor contributed to the observed effects of temporal frequency on equiluminance settings.

4.4. Contributions from magnocellular versus parvocellular pathways

In order to elucidate potential neural substrates underlying our psychophysical results, we turn to the known response properties of neurons in the macaque visual system. Comparisons between macaque and humans are justified based on the known similarities between the visual systems of the two primates (e.g. De Valois, Morgan, Polson, Mead & Hull, 1974a; De Valois, Morgan & Snodderly, 1974b). In particular, we focus on the properties of two distinct subcortical pathways — parvocellular and magnocellular — which originate in the retina and remain segregated up through layer 4C of area V1 (see Merigan & Maunsell, 1993 or Dobkins & Albright, 1998 for a review). (There also exists a third pathway, the 'koniocellular' (K) pathway, which is less studied and appears to respond selectively to stimuli that modulate the S-cones, e.g. Irvin, Casagrande & Norton, 1993; Martin, White, Goodchild, Wilder & Sefton, 1997. This pathway is not relevant to this discussion.) Although there exists substantial evidence to suggest that the magnocellular pathway receives additive (i.e. $L+M$) cone input while the parvocellular pathway receives chromatically-opponent (i.e. $L-M$) cone input, the notion of complete dichotomy of function has been called into question on several grounds. First, both cell types are known to respond to both chromatic (green/red) and luminance stimuli (e.g. Lee et al., 1990), suggesting that neural pathways for chromatic and luminance processing are not completely segregated. Second, stimulus parameters (such as spatial-temporal frequency and background chromaticity) can produce phase-lags between L- and M-cones and/or between center and surround mechanisms, which in turn can alter the additive or subtractive nature of L- and M-cone input to the two cell types (e.g. Gouras & Zrenner, 1979; Derrington, Krauskopf & Lennie, 1984; Smith et al., 1992 and see Stromeyer et al., 1997).

Given these complications, it is perhaps surprising that psychophysical evidence supports *independence* between chromatic and luminance contrast detection. One way this apparent discrepancy has been reconciled rests on the fact that magnocellular cells are far more sensitive to luminance contrast than are parvocellular cells, while parvocellular cells are much more sensitive to chromatic contrast than are magnocellular cells (e.g. Hicks, Lee & Vidyasagar, 1983; Derrington & Lennie, 1984; Lee et al., 1990). Thus, since the most sensitive system presumably underlies contrast detection *at threshold*, it is reasonable to assume that magnocellular and parvocellular pathways provide the neural substrate for luminance and chromatic contrast sensitivity, respectively (see Lee et al., 1990; Smith, Pokorny, Davis & Yeh, 1995; Dobkins, Anderson & Lia, 1999). This notion is not universally accepted, however. An opposing point of view proposes that the parvocellular subdivision subserves both chromatic and luminance detection, with the signals for the two types of contrast 'de-multiplexed' at the level of visual cortex (e.g. Ingling & Martinez-Uriegas, 1983; Lennie & D'Zmura, 1988; De Valois & De Valois, 1993; Billock, 1995; Mullen et al., 1997). Note that this idea rests on the assumption that, despite the superior luminance sensitivity of single magnocellular cells, the far more numerous parvocellular cells (outweighing magnocellular cells in number by eight-fold) could, as a *population*, govern luminance sensitivity revealed perceptually. The parvocellular pathway's role in luminance sensitivity is partially supported by the results of lesion studies in macaques, which show impaired luminance contrast sensitivity for low temporal frequencies/high spatial frequencies after parvocellular lesions. By contrast, magnocellular lesions produce large impairments for high temporal frequencies/low spatial frequency stimuli (e.g. Merigan & Maunsell, 1990; Merigan, Katz & Maunsell, 1991). Given the controversy surrounding this issue, it is currently unclear whether the independence of luminance and chromatic contrast sensitivity can be mapped neatly onto magnocellular and parvocellular substrates, respectively.

With regard to the neural substrates for green/red equiluminance settings, results from several neurophysiological studies have shown that magnocellular, but not parvocellular, cells exhibit minimal responses when the luminance ratio between two colors is near human V_λ equiluminance (Lee, Martin & Valberg, 1988; Kaiser, Lee, Martin & Valberg, 1990; Logothetis et al., 1990; Valberg, Lee, Kaiser & Kremers, 1992, and see Dobkins & Albright, 1995 for similar results obtained from the middle temporal area of visual cortex). Because magnocellular responses mirror the perceptual phenomenon of 'minimal saliency' at equiluminance, this pathway has been implicated as providing the neural substrate for equiluminance. (It is interesting to point out that the lack of correspondence between parvocellular and perceptual responses implies that parvocellular responses are either ignored or attenuated by filters at the cortical level, see Lee et al., 1990). Given the evidence from psychophysical studies for $L-M$ contribution (at low temporal frequencies), however, a total lack of parvocellular input to equiluminance settings would be surprising. This can perhaps be reconciled by proposing that previous neurophysiological studies missed a contribution from parvocellular ($L-M$) cells, either because they used relatively high temporal frequencies and/or because the parvocellular contribution is small and difficult to detect. Alternatively, parvocellular cells may not be required to account for the psychophysical results if magnocellular cells, in fact, respond in a chromatically-opponent ($L-M$) fashion at low temporal frequencies (e.g. Smith et al., 1992; Stromeyer et al., 1997).

4.5. Do L:M ratios place constraints on luminance and chromatic contrast sensitivity?

In theory, an individual who exhibits a relatively high G/R equiluminance ratio is predicted to have a relatively high number of L- to M-cones (i.e. L:M cone ratio) in the eye. This prediction is based on a simple $L+M$ model of green/red spectral sensitivity, i.e. two colors are expected to be equiluminant when the weighted sums of L- and M-cones signals produced by the two colors are equated. This weighting factor, which represents the L:M cone ratio in the eye, is thought to be approximately 2:1 in humans (see Lennie et al., 1993). The validity of this model has been supported by several studies demonstrating that, within individual human subjects, L:M cone ratios derived from green/red spectral sensitivity data correspond quite closely with those obtained using methods that directly 'count' cone types in the eye (e.g. Vimal, Pokorny, Smith & Shevell, 1989; Wesner, Pokorny, Shevell & Smith, 1991; Sharpe, Kremers, Knau, Berendschot & Usui, 1998; Brainard, Roorda, Yamauchi, Calderone, Metha, Neitz et al., 2000, and see Jacobs & Deegan, 1997; Dobkins, Thiele & Albright, 2000 for relevant experiments in macaques).

Given that green/red spectral sensitivity is, in fact, a reasonable indicator of L:M cone ratios (i.e. higher green/red equiluminance settings reflecting higher L:M ratios), we can address how L:M ratios might place constraints on both luminance and chromatic contrast sensitivity. In our correlation matrix (Fig. 2), we observed *positive* correlations between green/red equiluminance settings and luminance contrast sensitivity, yet *negative* correlations between green/red equiluminance settings and chromatic contrast sensitivity. This indicates that subjects with higher L:M cone ratios (relative to others) are at an advantage for detecting luminance contrast, yet at a disadvantage for detecting chromatic contrast. For chromatic (green/red) stimuli, sensitivity is thought to be implemented on the neuronal level by cells that receive chromatically-opponent (i.e. $L-M$) cone input. Whether or not this wiring arises as a consequence of selective or stochastic processes (e.g. Lennie, Haake & Williams, 1991; Reid & Shapley, 1992; Calkins & Sterling, 1996), an L:M ratio near 1:1 should be most advantageous for pairing L-cones with M-cones. Conversely, a high (and thus imbalanced) L:M ratio would yield the worst chances for chromatic opponency, and in turn, lower chromatic sensitivity. Thus, the correlation between higher G/R ratios (indicative of higher L:M ratios) and lower chromatic contrast sensitivity seen in our data may reflect variation in the degree of chromatic opponency across subjects, as dictated by L:M cone ratios.

By contrast, with regard to *luminance* contrast sensitivity, a greater degree of cone homogeneity (i.e. higher L:M cone ratios) might be considered more advantageous. Consider the case of a heterogeneous L- and M-cone mosaic. Due to differential spectral sensitivities across cone types, a homogeneous (i.e. zero-contrast) field might produce small differences in cone signals across a patch of retina, which would be confusable with signals arising from a low-contrast luminance stimulus. Here, the visual system must disambiguate differences in cone signals that are due to luminance variation in the stimulus from differences that are due to variation in spectral sensitivity across cone types. In theory, this could be achieved by 'normalizing' to the signal jitter produced by differential cone spectral sensitivities. By contrast, a homogenous cone mosaic would avoid the need to disambiguate the source of differential signals, and would consequently detect luminance variation more efficiently. Thus, the correlation between higher G/R ratios (indicative of higher L:M ratios) and higher luminance contrast sensitivity seen in our data may reflect this sort of phenomenon. Experiments in our laboratory are underway to investigate this issue further.

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