Contrast salience across three-dimensional chromoluminance space

Eugene Switkes *

Department of Chemistry and Biochemistry, University of California, 1156 High Street, Santa Cruz, CA 95064, USA

ARTICLE INFO

ABSTRACT

We have extended previously studies of relative contrast salience [Switkes & Crognale, 1999. Comparison of color and luminance contrast: apples versus oranges? Vision Res. 39 (10), 1823–1831] to chromaticities intermediate to cardinal chromatic axes. We find that: (i) observers can reliably match the perceptual contrast of gratings differing in chromoluminance irrespective of whether they lie along canonical axes or intermediate axes; (ii) the relative perceptual contrast of gratings in the isoluminant plane correlates well with a metric based on an ideal observer but added luminance results in a perceptual contrast lower than would be predicted by this model; (iii) contrast matches in the isoluminant plane can be modeled by simple combinations of the cone contrasts for the LM and S pathways; (iv) unipolar, non-opponent, mechanisms may subserve the perception of contrast; and (v) the relative salience of suprathreshold chromatic gratings varies in accord with contrast thresholds but the low spatial frequency increase in luminance contrast threshold is not manifest in a reduced suprathreshold salience for luminance gratings.

1. Introduction

Over the past three decades, a variety of investigators have studied the ability of the human visual system to process form defined by spatial variations in chromaticity. Psychophysical studies have characterized detection thresholds, spatiochromatic masking and adaptation, suprathreshold appearance, and interactions among differing chromaticities in pattern perception. The question of whether purely chromatic contrast variations could subserve form detection was the focus of many of the earliest studies. Once this question was answered affirmatively, further experiments have addressed the role of color in higher level form processing [for a review see Regan, 2000].

Electrophysiological and functional imaging investigations that measure neural responses to purely chromatic patterns have complemented these psychophysical studies. Integrating results from psychophysics, electrophysiology, and functional imaging, the spatial and chromatic selectivity of mechanisms that are activated by chromatic patterns have been characterized. A picture has emerged that identifies at least three stages of color processing: an initial stage where selectivity is primarily mediated by the spectral responses of cone receptors; 'second-stage' cone-opponent mechanisms, mediated by retinal ganglion cells and neurons of the lateral geniculate nucleus; and a further 'third-stage' whose locus is presumably cortical and whose characteristics are a current topic of investigation. A variety of models have been proposed for chromatic processing at this third-stage: (i) a set of mechanisms

that retain chromatic selectivity identical to those of the second-stage; (ii) a limited set of mechanisms that arise from specific linear combinations of second-stage processes and thus exhibit chromatic selectivity corresponding to rotations of the second-stage preferred chromatic axes; and (iii) third-stage mechanisms whose peak chromatic responses tile all of the directions of two-dimensional color space. Additionally, some models propose that the bipolar chromatic mechanisms, i.e. ones which are excited by stimuli with one chromaticity but are inhibited by the complementary chromaticity, found at earlier stages are transformed to independent unipolar mechanisms responding only with excitation to stimuli which have chromaticities near the preferred chromatic axes. Electrophysiological experiments also have shown that groups of cells having distinct and differing spatiochromatic response properties coexist in cortical visual areas V1 and V2. Thus various behavioral tasks could recruit various of these subpopulations; and, for example, the spatiochromatic processing of threshold pattern detection may differ from that of color appearance. Extended discussions of these multi-stage and multiplex models, and related experimental imperatives, can be found elsewhere and will not be repeated (see for example De Valois & De Valois, 1993; Engel, Zhang, & Wandell, 1997; Johnson, Hawken, & Shapley, 2001; Sankeralli & Mullen, 2001; Solomon & Lennie, 2007; Webster & Mollon, 1994).

In a previous study (Switkes & Crognale, 1999) we investigated the relative salience, i.e. perceived suprathreshold contrast, among patterns defined by chromatic or luminance variations that selectively activate differing second-stage mechanisms. Here we found that, even though chromaticities were chosen to activate independent first- and second-stage mechanisms and despite the distinctly

* Fax: +1 831 459 2935.
E-mail address: switkes@chemistry.ucsc.edu

differing appearance of patterns from variations along differing color axes, observers can: (i) reliably make such pairwise contrast matches; (ii) there is reasonable consistency of matching contrasts among observers; and (iii) pairwise contrast matches exhibit the properties of homogeneity and transitivity. From these data we proposed that, for experiments which compare form perception among patterns with chromatic contours along differing chromatic axes, equating perceptual contrast by pairwise contrast matching provides a robust empirical metric and thus a 'level playing field' for specifying pattern strength. The current study extends these contrast comparisons to sinusoidal gratings whose chromaticities lie along axes intermediate to these canonical axes. Such stimuli activate multiple second-stage mechanisms.

2. Experimental methods

Inasmuch as the color space specification, the experimental procedures, and the data reduction are almost identical to those used in our earlier study (Switkes & Crognale, 1999), only a summary is presented here. In describing our stimuli we follow Chen, Foley, & Brainard (2000a, 2000b) in applying the term 'chromoluminance' to indicate the chromatic and luminance content of our stimuli in terms of a direction or point in MBDKL color space (Derrington, Krauskopf, & Lennie, 1984; MacLeod & Boynton, 1979). With an Illuminant C centerpoint, chromaticities were specified by an azimuthal angle ϕ ($\phi = 0° \leftrightarrow 180°$, LM-only variation; $\phi = 90° \leftrightarrow 270°$, S-only variation; intermediate ϕ's, other chromaticities) and an angle of elevation angle θ ($\theta = 0°$ isoluminant plane; $\theta = +90° \leftrightarrow -90°$, white–black achromatic luminance variation; intermediate θs an admixture of color and luminance). For each observer, the color space was specified with respect to their individual isoluminant plane as determined by motion null (Anstis & Cavanagh, 1983; Carney, Shadlen, & Switkes, 1987). In Experiments 1–4 chromaticity varied symmetrically (sinusoidally) around Illuminant C so that the mean chromaticity was constant.

While fixating on the center of a video display, observers monocularly viewed two horizontally displaced circular patches on a gray background, each containing a horizontal grating. The observer's task was to indicate which of the two simultaneously presented sinusoidal gratings was of greater 'strength' or 'salience'. The circular patches subtended 10° and their centers were horizontally displaced by 6.5° from the fixation point. Stimuli were presented for 500 ms at the selected contrast levels with a 100-ms ramp-up and ramp-down from their zero contrast levels. The grating patches were presented on an achromatic background, Illuminant C at 18 cd/m². The observer's response initiated a subsequent presentation and the observer viewed the achromatic background in the interval between presentations In most experiments the circular patches contained 1 cycle-per-degree (cpd) sinusoidal gratings that had the same average chromaticity and luminance as the Illuminant C background. In Experiment 4, investigating the spatial frequency dependence of perceived contrast, gratings of 0.25, 0.5, 1.0, and 2.0 cpd were used. In Experiment 5, investigating unipolar contrast variations, the chromaticity of the gratings changed sinusoidally along the specified color axis, but now varied in chromaticity from that of the gray Illuminant C centerpoint to the chromaticity specified by the chosen color axis and the grating's unipolar chromatic contrast (saturation). At zero contrast the unipolar stimuli are identical to the background Illuminant C. However, as the contrast is ramped to the plateau level, the mean chromaticity of the grating patch differs somewhat from the background, as a function of the chosen unipolar chromatic axis and grating contrast. Observers report no difficulties arising from this difference in mean chromaticity of the two grating patches.

The experimental design and reduction of the contrast matching data were similar to that utilized in our previous study. For the pairwise contrast comparisons, the contrast of a grating in one chromatic direction was held at a reference point while the color contrast of the grating along a second direction was varied. The point of equal perceived contrast was determined as that contrast where the variable contrast grating was judged to have greater salience in 50% of the trials. For each pair of chromaticities, the procedure was repeated at four to six reference contrasts with the reference contrast alternating between the two chromaticities. In Experiment 1 we verify that, for the contrast range employed in these studies, the ratio of contrasts obtained for a pairwise match was independent of the absolute contrast of the reference. Thus for each pair of chromatic directions we report a single contrast salience value. For example, the relative salience of gratings along $\phi = 0°$ vs $\phi = 45°$ is the reported as the slope of a plot of (contrast)$_{\phi = 0°}$ vs (contrast)$_{\phi = 45°}$ for the perceptually matched contrasts.

The contrast thresholds reported In Experiment 4 were obtained by conventional methods previously reported (Switkes & Crognale, 1999). The threshold stimuli were presented in the same spatial configuration as were the contrast comparison stimuli.

The experimental apparatus was conventional: Sun–TAAC graphics display and SONY GDM monitor. Data analysis and modeling utilized programs written by the author using the Mathematica software system.

3. Results

Although, in both the earlier and current studies we gave the observers only limited instructions regarding criteria to apply in selecting the higher contrast or 'more salient' grating, we find consistent results for both within and among observer data. After completing the experiments, observers uniformly described their strategies as selecting the grating patch with 'greater strength as a whole' or the grating that 'popped out' during the short presentation interval. We believe that these reports indicate that the results presented here reflect a global process of salience estimation rather than local region-by-region brightness comparisons. Such a description of perceptual salience has been used by other investigators (Banks, Vlaskamp, Hillis, & Gardner, 2007) to describe a similar comparison among color and luminance patterns.

3.1. Experiment 1: Transitivity and homogeneity for intermediate color directions

Our previous studies indicated that pairwise contrast comparisons along canonical axes exhibited the properties of homogeneity and transitivity and thus a single scale factor could characterize the relative perceptual salience in each color direction. In series of pairwise comparisons among gratings at angles (ϕ) of 0°, 45°, 157°, and 170° in the isoluminant plane, we tested whether these observations held for gratings having chromaticities lying between the cardinal chromatic axes. To test homogeneity (i.e. if the contrast of one of two gratings is increased by a given factor, will the matching contrast for the grating along the second color axis be increased by the same factor), we measured relative salience at six reference contrasts for each of the six pairwise comparisons. Plots of relative perceived contrast for the two chromaticities (as in Fig. 2., Switkes & Crognale, 1999) were linear with average correlation coefficients of 0.991 for observer AE and 0.996 for observer JN. Thus, in the contrast regime tested (approximately a 3-fold variation in absolute contrast), the perceptual contrasts for each color scaled similarly with absolute contrast even for chromaticities along directions intermediate to the canonical axes.

If chromatic salience were a unitary sensation, independent of the specific pairwise comparison, one would expect to observe transitivity among the resulting relative contrast matches. For example one could predict the 45° vs 170° pairwise match from the matches observed for 45° vs 157° and for 157° vs 170°. From the six pairwise color matches directly measured in Experiment 1, application of transitivity yields 12 indirect predictions of relative perceptual contrast. The average error of the 12 indirectly derived contrast matches relative to the six directly measured values was 6.4% (observer AE) and 8.1% (observer JN). These results are similar to those observed along the cardinal directions and are consistent with a model where the observer's sensation of a chromatic salience is independent of the reference to which the contrast is compared.

3.2. Experiment 2: Variation of chromaticity within the isoluminant plane

In the majority of experiments, the chromatic salience of a grating along a selected direction was compared to that of a grating having a chromaticity along the LM-axis. Fig. 1 plots the results of these comparisons for various directions in the MBDKL isoluminant plane. In these polar plots the radial coordinate indicates the ratio of the contrasts of the grating at the specified angle ϕ to that of a grating at $\phi = 0°$ (LM direction) at equal perceived contrast [data with radii > 1 indicate a greater matching contrast was required for the grating at ϕ relative to that at $\phi = 0$]. In Fig. 1(a) the data are computed as the ratios of the cone contrasts along
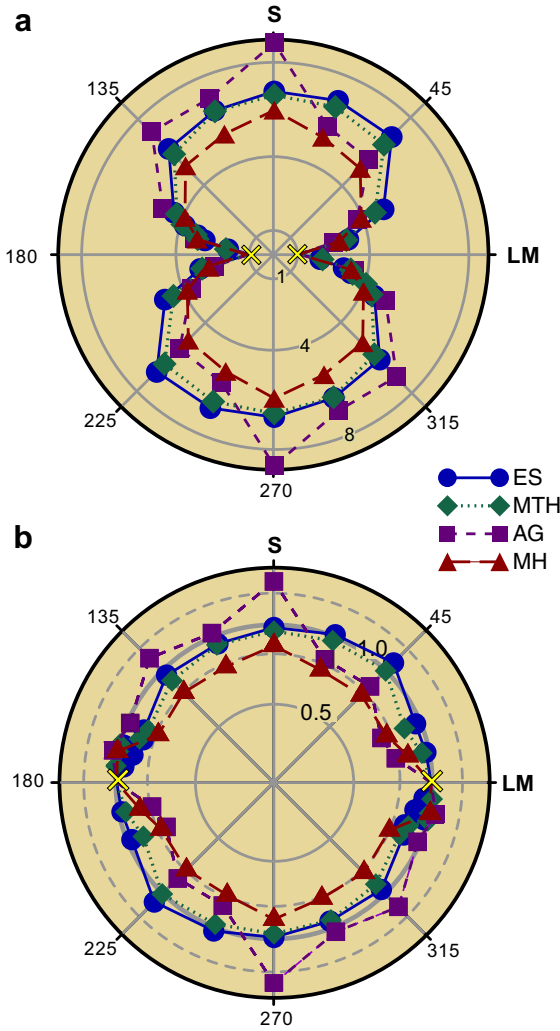
Fig. 1. Contrast salience of isoluminant gratings. (xs indicate LM reference chromaticity). (a) ϕ/LM contrast matching ratios in terms of cone contrast and (b) ϕ/LM contrast matching ratios in terms of ideal observer equivalent contrast.

Fig. 2. Contrast salience of grating consisting of color-luminance mixtures. (xs indicate LM reference chromaticity). (a) θ/LM contrast matching ratios in terms of cone contrast and (b) θ/LM contrast matching ratios in terms of ideal observer equivalent contrast.

the two directions (cone contrast being defined as $\sqrt{\left(\frac{\Delta L}{L}\right)^2 + \left(\frac{\Delta M}{M}\right)^2 + \left(\frac{\Delta S}{S}\right)^2}$; noting that for luminance gratings this gives a cone contrast 1.73 times the standard Michelson contrast). Results from the four observers are similar and, along the LM and S directions, are consistent with the contrast salience ratios previously reported.
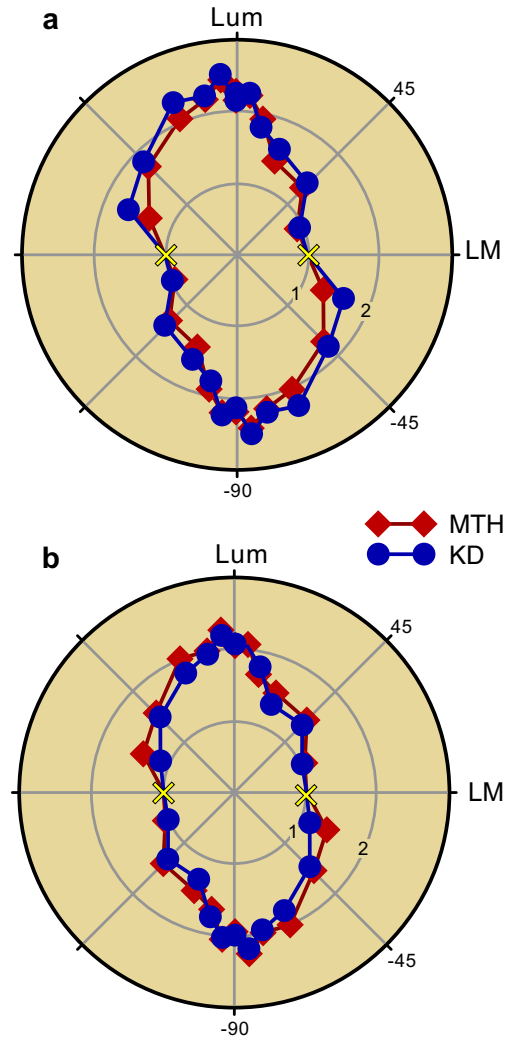
In Fig. 1(b) the ratios are replotted using an equivalent contrast metric based on the visibility of color contrast to an ideal observer (Geisler, 1989; Jordan, Geisler, & Bovik, 1990; Scharff & Geisler, 1992). Our application of this metric is given by the formula (see footnote 2, (Switkes & Crognale, 1999):

$$C^{equiv} = \varsigma^{equiv} C^{cone}$$

$$= \left\{ \frac{(\bar{L}c_L d_L + \bar{M}c_M d_M + \bar{S}c_S d_S)}{\left(\bar{L}d_L^2 + \bar{M}d_M^2 + \bar{S}d_S^2\right)^{\frac{1}{2}}(\bar{L}^2 + \bar{M}^2 + \bar{S}^2)} \frac{\sqrt{3}}{\sqrt{c_L^2 + c_M^2 + c_S^2}} \right\} C^{cone}$$

where $c_L = \left|\frac{\Delta L}{\bar{L}}\right|$, $d_L = \ln\left[\frac{1+c_L}{1-c_L}\right]$, etc.

The relative salience along each color direction is well represented by this metric. In MBDKL space (e.g. Fig. 1) the major effect of the transformation is to weight the contribution of S-cone contrast relative to that of L-cone and M-cone contrast via $\bar{L}$, $\bar{M}$, and $\bar{S}$

in the numerator. We have used relative weightings $\bar{L}:\bar{M}:\bar{S}$ (32:16:1) from Wyszecki & Stiles (1982) It has been elegantly demonstrated that, even in color normal observers, the ratio of cone types can vary significantly among individuals (Roorda & Williams, 1999) We find that for the average luminance utilized in Fig. 2 raising the relative S-cone weighting by a factor of 2 will raise $\frac{\varsigma_S^{equiv}}{\varsigma_{LM}^{equiv}}$ by 30%, a figure consistent with the deviations of individual observers in Fig. 1. Although unique hue studies have indicate perceptual compensation among observers with varying L:M cone ratios (Brainard, Roorda, Yamauchi, Calderone, Metha, Neitz, Neitz, Williams & Jacobs, 2000), determining contrast salience matches for individuals with markedly differing cone populations and for color anomalous observers would be an interesting extension of the current study.

3.3. Experiment 3: Salience for mixed chromatic luminance variations

In a MBDKL color space a color axis with angle of elevation $\theta \neq 0°$ corresponds to a mixture of luminance and chromatic components. In Experiment 3A observers obtained contrast matches between isoluminant LM gratings ($\theta = 0°$, $\phi = 0°$) and sinusoidal gratings having $\phi = 0°$ and various values of $\theta \neq 0°$ (i.e. admixtures
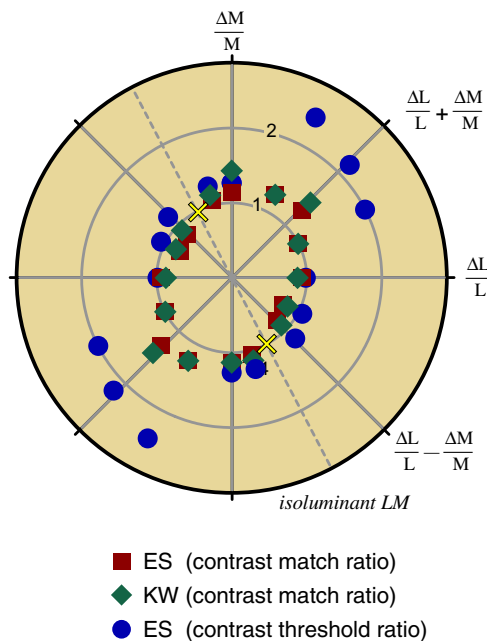
of a black-white grating and an isoluminant LM grating). Here $\theta > 0°$ corresponded to a luminance increment in phase with +L and luminance decrement in phase with +M, and vice versa for $\theta < 0°$. The results are in Fig. 2.

Plots of contrast matches in terms of cone contrast (Fig. 2a) and equivalent contrast (Fig. 2b) indicate that, in these metrics, luminance variations are less effective in producing perceptual salience than are chromatic variations. Such effects have been noted for contrast thresholds (Chaparro, Stromeyer, Huang, Kronauer, & Eskew, 1993; Mullen, 1985; Valberg, 2005). The slight tilt of the contours indicates that the addition of luminance increment in the +L−M (reddish) phase produces a higher perceptual salience than in the +M−L (greenish) phase.

Contrast thresholds, measured in a cone contrast color space, provide one of the most direct demonstrations of chromoluminance processing by second-stage opponent mechanisms (Chaparro et al., 1993; Cole, Hine, & McIlhagga, 1993). In Experiment 3B we measured contrast thresholds and contrast salience in the $\left(\frac{\Delta L}{L}, \frac{\Delta M}{M}\right)$ plane. In Fig. 3 we plot contrast thresholds and suprathreshold contrast salience relative to the threshold or matching contrast of a grating in the isoluminant LM direction. The threshold measurements follow the classical pattern, i.e. a roughly rectangular contour with higher thresholds occurring along the $\left(\frac{\Delta L}{L} + \frac{\Delta M}{M}\right)$ direction (Chaparro et al., 1993; Cole et al., 1993). However, the contrast matching contours show only slight elongation in this direction (note that the $\left(\frac{\Delta L}{L} + \frac{\Delta M}{M}\right)$ direction in Fig. 3 corresponds to a somewhat different chromoluminance than along the achromatic luminance axis, $\theta = \pm 90°$, in Fig. 2; in Fig. 2 the cone contrast for the achromatic axis contains an additional $\frac{\Delta S}{S}$ contribution, increasing the computed contrast without a concomitant increase in salience).

3.4. Experiment 4: Salience as a function of spatial frequency

Although the spatial frequency dependence of suprathreshold contrast appearance has been previously investigated for lumi-

nance and for color gratings individually (Georgeson & Sullivan, 1975; Poirson & Wandell, 1996; Vimal, 2000), the current study compares contrast salience between color and luminance patterns. Fig. 4(a) displays contrast sensitivity curves for luminance-varying, LM-varying, and S-varying gratings in the 0.25–2.0 cycle-per-degree range. These data reproduce the distinctive features of the threshold CSF for color versus that for luminance, i.e. the pronounced low spatial frequency attenuation in sensitivity for luminance gratings and the more rapid fall-off for chromatic gratings with increasing spatial frequency (Mullen, 1985; Valberg, 2005).
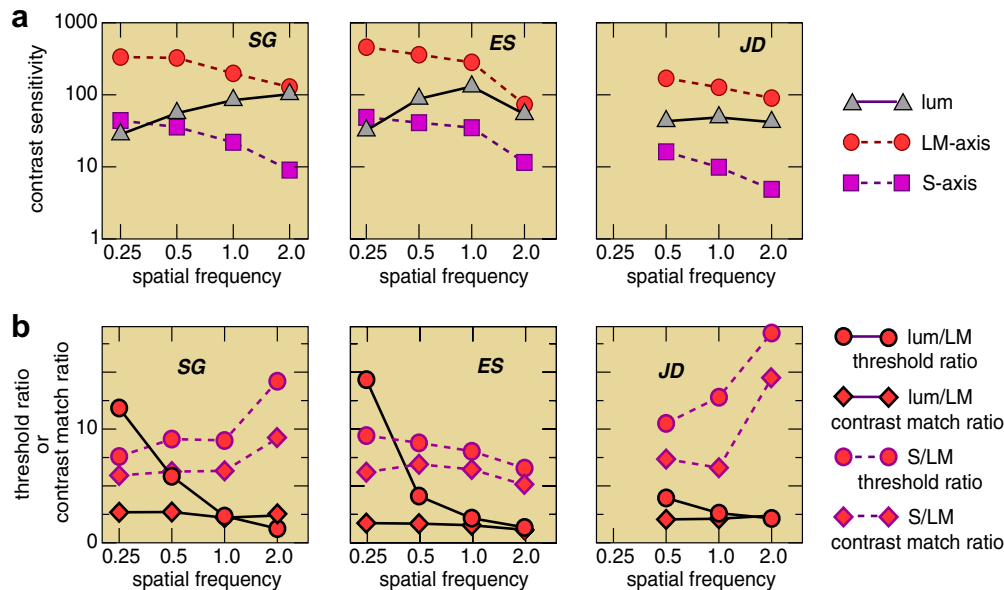
Fig. 4(b) reports the results of contrast matching experiments. Contrast matches between a luminance or an S-axis grating and a LM-varying grating of the same spatial frequency were obtained for spatial frequencies of 0.25, 0.5, 1.0, and 2.0 cpd. For luminance versus LM, the contrast match ratios (diamonds, solid line) were constant and thus did not exhibit the low frequency luminance attenuation evident in the ratio of luminance/LM contrast thresholds (circles, solid line). However, for S-axis versus LM-axis contrast matches, the data do follow the relative contrast thresholds for the individual observers. For SG and JD the relative higher S/LM contrast threshold ratios at 2 cpd versus 1 cpd (circles, dashed line) are accompanied by increased S/LM contrast matching ratios (diamonds, dashed line). However, for observer ES, who exhibits approximately equal for S/LM threshold ratios at 1 cpd and 2 cpd, the S/LM contrast match ratios are also comparable at these spatial frequencies.

3.5. Experiment 5: Salience for unidirectional chromatic excursions

Several studies have investigated whether mid-level chromatic and luminance processing is subserved by traditional bipolar opponent mechanisms or by mechanisms that selectively respond to unipolar chromatic excursions from an achromatic background (Beer & MacLeod, 2000; Gegenfurtner & Kiper, 1992; Sankeralli & Mullen, 2001; Smith & Pokorny, 1996). Both simple rectification of the responses of second-stage opponent mechanisms and further reorganization of cone-input weightings, accompanied by rectification, have been proposed as models for this third-stage (and fourth-stage) processing (De Valois & De Valois, 1993; Smith & Pokorny, 1996). In Experiment 5 observers matched the salience of isoluminant patterns where the chromaticity of one pattern varied sinusoidally from gray (Illuminant C) to a specified contrast along one chromatic direction and the second from gray along the complementary chromatic direction. For example, if one of the gratings varied along the +L−M direction ($\phi = 0°$) a contrast match was obtained with a grating varying along the +M−L direction ($\phi = 180°$) or a unipolar grating with $\phi = 45°$ was matched in contrast with one having a unipolar chromaticity $\phi = 225°$. For these displays the mean chromaticity within each of the two comparison unipolar patches differed somewhat depending on the color directions and contrasts. For example with a background at CIE [.310, .316] the average chromaticity the grating region varied from [.317, .312] to [.330, .306], for low to high contrast +L−M ($\phi = 0°$) unipolar sinusoids. For the matching +M−L ($\phi = 180°$) unipolar gratings the mean chromaticity varied from [.301, .320] to [.282, .329]. However, observers did not find this to be a confounding factor. The achromatic background (identical in chromaticity to the gray stripes in each unipolar grating patch), the short duration of the grating presentations, the balanced presentations of each unipolar chromaticity to the left and right of fixation, and the gray screen viewed between presentations insured adaptation to the Illuminant C mean.

The results of these contrast matches are plotted in Fig. 5. For each angle ϕ, we plot the ratio of the cone contrasts (calculated relative to the achromatic background) required to produce equal perceptual salience for a unipolar grating with chromaticity ϕ

Fig. 3. Contrast thresholds and contrast matches in the L-cone contrast vs M-cone contrast plane cont with threshold. (x's indicate LM reference chromaticity). Circles are contrast thresholds for ES; squares and diamonds (for ES and KW) are ratios of cone contrasts for perceptual matches of gratings along various axes to isoluminant LM-varying gratings.

■ ES (contrast match ratio)
◆ KW (contrast match ratio)
● ES (contrast threshold ratio)

Fig. 4. Spatial frequency dependence of contrast salience: (a) contrast thresholds for luminance-varying (triangles), LM-varying (circles), and *S*-varying (squares) gratings at four spatial frequencies and (b) ratio of contrast thresholds (filled circles lum/LM; open circles *S*/LM) and contrast matches (filled diamonds lum/LM; open diamonds *S*/LM) at four spatial frequencies.

versus one with chromaticity $\phi + 180°$ (the data plotted at opposite poles are redundant, i.e. the reciprocal of one another). The curves are best fitting hemi-ellipses calculated for points where the contrast ratio was $\geqslant 1$ and the reciprocal of the ellipse for angles where the contrast ratio was $\leqslant 1$. Lines indicate the axis of maximum asymmetry. All of the observers show asymmetric matches with maximum asymmetries of at least ±20% (dotted circles correspond to contrast ratios of 1.2 and 0.8). For the four observers, the angle of maximum asymmetry ranged from $\phi = (130°$ vs $310°)$ to $\phi = (157°$ vs $337°)$. The bluish unipolar direction ($\phi = 130°$–$157°$) required a greater cone contrast to appear of equal salience to the yellowish ($\phi = 310°$–$337°$) unipolar grating. For each observer the relative luminance of the opposing color poles had been empirically matched by the motion null technique thus providing an empirical control against experimental artifact due to calibration errors.

4. Discussion

The aims of this study were to extend contrast salience comparisons to chromoluminances intermediate to first- and second-stage cardinal axes and to investigate the relationship between perceived contrast and mechanisms of color processing. Our new data generalize several aspects of our previous study. Specifically: (i) observers can make reliable pairwise contrast matches of differing chromaticities irrespective of direction in 3D color space; (ii) pairwise contrast matches are transitive along both cardinal and intermediate color directions; (iii) for a pair of differing chromaticities, the ratio of perceived contrast is constant throughout the contrast range employed in the study; and (iv) trends in the perceived salience of differing chromaticities are similar for various observers. These qualities recommend empirically measured salience as an appropriate starting point for equating contrast in studies that compare visual performance for stimuli of differing chromaticities (Banks et al., 2007; Frome, Buck, & Boynton, 1981; Wilson, 1999; Wilson & Switkes, 2005). Although relative salience is roughly related to relative contrast detection thresholds (Switkes & Crognale, 1999), we find that measuring perceived suprathreshold contrast for a given contrast range and a given stimulus spatial configura-

tion to be a more robust, and perhaps more relevant, method than using a times threshold metric for equating suprathreshold contrasts.

The current study also reveals additional properties of chromoluminance contrast perception. The relative salience for luminance-, LM-, and *S*-gratings at various spatial frequencies generally correlates with relative threshold contrast sensitivity, even on an observer-by-observer basis. However, the low spatial frequency (0.25 cpd) rise in contrast threshold for luminance gratings is not accompanied by a reduction in perceived suprathreshold salience. Inhibitory mechanisms usually implicated in the low spatial frequency fall-off in luminance threshold contrast sensitivity do not appear to be a determinant in the suprathreshold appearance of low frequency luminance gratings.

Providing insights on the relationship of perception and physiological mechanism is an obvious goal of experiments such those in the current study. Experiment 5 reveals an asymmetry between the cone contrasts required to produce equal salience for complementary directions in color space. For all four observers the maximum asymmetry lies along the in the perceptual yellow–blue direction with blue being less salient than yellow. Smaller deviations are found along the LM-axis, with +LM reddish chromaticities being somewhat more salient than +*ML* greenish chromaticities. Such asymmetries would arise from individual unipolar mechanisms that have differing sensitivities, each responding to one of the complementary chromaticities.

Psychophysical adaptation and masking studies provide experimental evidence for such separable mechanisms (Beer & MacLeod, 2000; Gegenfurtner & Kiper, 1992; Sankeralli & Mullen, 2001; Smith & Pokorny, 1996). In the De Valois and De Valois model (De Valois & De Valois, 1993) unipolar "R", "G", "B", and "Y" mechanisms, obtained as rectified rotations of opponent axes, comprise a 'fourth-stage' of chromatic processing. Although this model proposes equal (but opposite) cone weighting for complementary unipolar mechanisms (e.g. the Yellow vs Blue channels), such symmetry is not a necessary feature. In our data the axis of maximal asymmetry corresponds to isoluminant excursions where, for given cone contrasts, the bluish-white grating $[-\Delta L, +\Delta M, +\Delta S; \sim 135°]$ color appears less salient than the yellowish-white $[+\Delta L,$
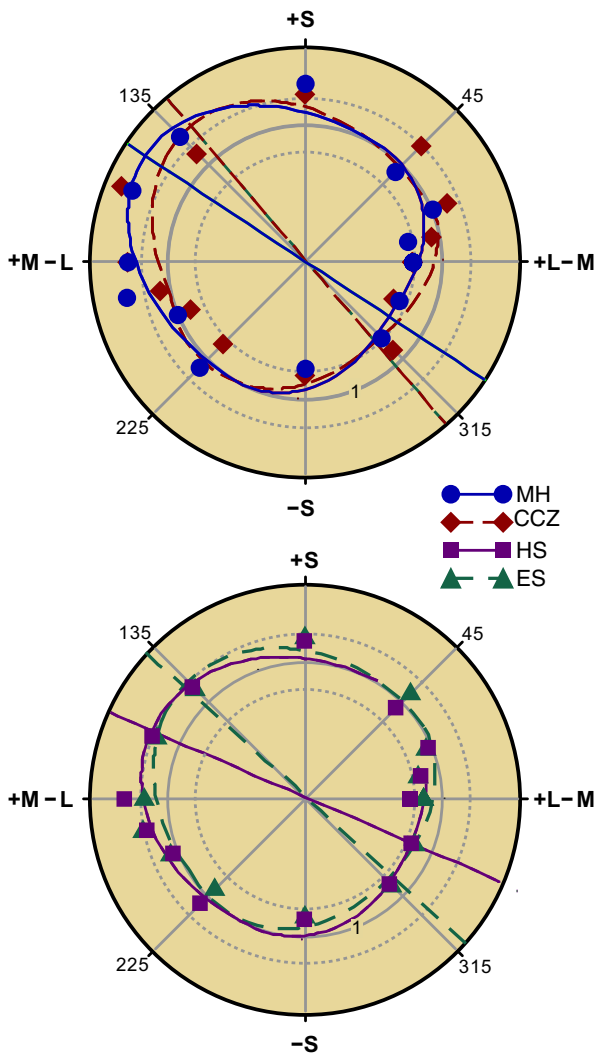
Fig. 5. Contrast salience of unipolar chromatic gratings along complementary chromatic axes. Data are the ratio of the cone contrast at ϕ and the cone contrast at $\phi + 180°$ that give equal salience. The data for ϕ and $\phi + 180°$ are redundant (reciprocals). The curves are hemi-ellipses fit to the data points with matching ratio > 1 and the straight lines give the major axis of the hemi-ellipses.

$-\Delta M$, $-\Delta S$; $\sim325°$]. Vector models of brightness at isoluminance (Guth, Massof, & Benzschawel, 1980), based on activation of bipolar or symmetric second-stage mechanisms, would not predict asymmetries for complementary MBDKL directions. Recent anatomical and electrophysiological evidence for multiple S-cone pathways at the level of the retina and LGN (Dacey & Packer, 2003; Klug, Herr, Ngo, Sterling, & Schein, 2003; Solomon & Lennie, 2005) suggests distinct mechanisms for the B^+Y^- and Y^+B^- polarities. However, the direction of the perceptual asymmetry we observe is not consistent with the reports that in the LGN $S+$ cells are more responsive than $S-$ cells (Solomon & Lennie, 2005), implying the perception of the salience of blue vs yellow may be mediated by mechanisms at some higher processing stage (De Valois & De Valois, 1993). This lower salience of the unipolar blue-white gratings at equal cone contrast may simply further reflect deficiencies in utilizing unscaled S-cone contrast as a relative measure of chromatic strength, i.e. S-cone contrast increments overestimate excitatory inputs to blue (135°) mechanisms relative to that of S-cone contrast decrements as excitatory inputs to the yellow (315°) detecting mechanisms.

If observers were making brightness matches between the chromatic peaks of the unipolar sinusoids, a comparison of our results

to classical heterochromatic brightness matching (HBM) data is relevant. Although HMB studies typically use simple bipartite fields (Comerford & Kaiser, 1975; Kaiser & Comerford, 1975), Yaguchi (1987) has measured brightness matching with checkerboards composed of white squares alternating with those of a specified chromaticity. In this study observers varied the luminance of the chromatic squares to match the brightness of the reference white squares. Both checkerboards with adjacent squares and those with squares separated by a dark gap were tested. Yaguchi's experimental conditions closest to those of our most asymmetric unipolar results (135° vs 315°) were for 1 cpd checkerboards with blue and white squares and 1 cpd checkerboards with yellow and white squares. Yaguchi found that at 1 cpd the data followed the traditional HBM results, i.e. blue squares of lower luminance match the brightness of reference white squares while for yellow vs white brightness matches were achieved with comparable chromatic and achromatic luminances. The effects were accentuated when comparison regions were separated by a black gap and were greatly reduced at 2 cpd. Thus (assuming transitivity) at the reference luminance blue appears brighter than yellow. This would appear to be consistent with electrophysiological suggestion that 'blue increments are more amplified than blue decrements' and appear contrary to our '$\phi = 315°$ unipolar gratings are more salient than those at $\phi = 135°$' results. However, in comparing our unipolar contrast salience measurements with HMB results several important differences in the two paradigms must be noted. First the HMB study used highly saturated chromaticities and equated brightness by varying the luminance of the chromatic vs achromatic squares. Our unipolar study uses relatively desaturated chromaticities and equates salience by varying saturation (MBDKL contrast) in the isoluminant plane rather than by luminance variation. Second, the HMB study did not involve direct comparison of blue–white patterns versus yellow–white patterns. Cone contrasts estimated for Yaguchi's 1 cpd checkerboards at equal brightness indicates somewhat higher blue–white cone contrast than for yellow–white (approximately 1.07 times greater, assuming a non-achromatic mean adaptation level; see discussion below). Additionally our observers report making comparisons on the basis of an overall salience rather than a brightness comparison between local chromatic regions in the two grating patches.

An alternative explanation of the observed asymmetry is possible. The data displayed in Fig. 5 utilize the background Illuminant C chromaticity as the reference for calculating respective unipolar cone contrasts. We previously cite the experimental conditions which argue that this chromaticity is appropriate to the observer's average adaptation level. Furthermore, salience matches ratios based on the background chromaticity show consistent and homogenous variation with unipolar contrast, as do other matches where mean (reference) chromaticity is not ambiguous. We have also recast the data using cone contrasts based on the average chromaticity across each unipolar grating patch; these differ from the background chromaticity as a function of the unipolar contrast. With this metric, the relative matching contrasts depend strongly on the contrast regime, i.e. do not exhibit homogeneity. However, the data based on this local chromaticity do give results in a direction that resolve the 'weak $+S$ response' quandary addressed above. For example, in Fig. 5 subject MH shows a matching ratio of 1.28 in the 135° vs 315° directions (ratios of 1.27, 1.27, 1.37, and 1.28 as reference grating contrast increases). However, recalculating cone contrasts relative to the unipolar grating patch mean chromaticities gives matching contrast ratios of 1.05, 1.04, .89, and .61 as absolute reference grating contrast increases. Thus one cannot rule out that a scheme which takes into account the various adaptation, background, and local chromaticities in calculating a reference for cone contrasts will yield symmetric unipolar matching contrasts.

Although masking and adaptation studies (Bradley, Switkes, & De Valois, 1988; Chen et al., 2000a, 2000b; De Valois & Switkes, 1983; Gegenfurtner & Kiper, 1992; Mullen & Losada, 1994; Webster & Mollon, 1994) provide a more direct technique for investigating preferred chromatic axes and selectivity of cortical color mechanisms than does the current experimental paradigm, we have investigated decomposition of our data in terms of combinations of contributions from components along specific sets of axes. From our data it is clear that S-cone contrast overestimates the strength of relative perceived contrast for stimuli with chromaticities near the S-axis. The equivalent contrast metric, derived by Geisler and coworkers (Geisler, 1989; Jordan et al., 1990; Scharff & Geisler, 1992; Switkes & Crognale, 1999), takes into account the numerosity of each cone population as well as the respective cone contrasts. With no parameters adjusted fit to the contrast comparison data, this metric yields a mean absolute error of 10% for the averaged data for the four observers (data of Fig. 1(b), Table 1).

A transformation of data into a basis that optimizes the Minkowski length metric is often used to describe isovalue contours (in our study isosalience) as a function of preferred coordinates (Poirson & Wandell, 1990). Preferred axes in the transformed coordinate system can imply underlying separable mechanisms (Poirson & Wandell, 1990). We have investigated such transformations for our salience matches of isoluminant chromaticities. We model the psychophysical 'salience response', $r(cc_\phi)$, to a grating of cone contrast cc_ϕ as proportional to a scaled combination of the activation of two mechanisms, initially taken to be LM and S with component cone contrasts $cc_{\phi,\text{LM}}$ and $cc_{\phi,S}$:

$$r(cc_\phi) \propto cc_{\phi,\text{LM}}^\gamma + (k_S cc_{\phi,S})^\gamma.$$

Using this, one can calculate the cone contrast ratios, $\frac{cc_\phi}{cc_{\phi=0^\circ}}$, corresponding to gratings of equal salience, i.e. the data of Fig. 1(a). The exponent γ and scaling constant k_S were determined to best fit the data for each observer. The optimization converged to a distinct minimum of the error criterion $\frac{1}{n} \sum_{i \neq 0^\circ} \left| \frac{(\text{predicted}_i - \text{data}_i)}{\text{data}_i} \right|$. Table 1 gives the optimized parameter values and goodness-of-fit for each of the four observers. This two parameter fit gives an excellent representation of the data; for three of four observers the parameterized function matches the experimental points to within 3.7%. The values of k_S indicate that S-cone contrast activation is only about 15% as potent as that of LM-cone contrast. Ideally one would like to generalize this optimization by allowing the component mechanisms to have arbitrary cone weightings, rather than assume the LM and S cardinal axes above. However, in cases where $\gamma = 2$ the transformation to preferred axis, and thus identification of underlying mechanisms, is ambiguous (Poirson & Wandell, 1990); presumably values of γ near 2 give a poorly behaved optimization. To gain insight into possible rotations of preferred axis from the second-stage LM and S, we attempted such a more general optimization. Two additional parameters specified the linear combinations of LM- and S-cone contrasts in each of the two component mechanisms:

$$r(cc_\phi) \propto |(k_{1,\text{LM}} cc_{\phi,\text{LM}} + k_{1,S} cc_{\phi,S})|^\gamma + |(k_{2,\text{LM}} cc_{\phi,\text{LM}} + k_{2,S} cc_{\phi,S})|^\gamma$$

$$\text{with} \quad k_{2,\text{LM}} = (1 - k_{1,\text{LM}}^\gamma)^{\frac{1}{\gamma}}.$$

Table 1
Contrast salience in isoluminant plane power law fitting parameters

Observer	k_S	γ	Mean absolute error *power law*	Mean absolute error *equivalent contrast*
ES	0.146	1.52	0.037	0.055
MTH	0.154	1.62	0.029	0.050
MH	0.181	1.54	0.035	0.170
AG	0.116	0.937	0.111	0.139

Table 2
Contrast salience in LM vs lum plane power law fitting parameters

Observer	k_{lum}	γ	Mean absolute error *power law*	Mean absolute error *equivalent contrast*
MTH	0.443	1.36	0.086	0.401
KD	0.439	1.24	0.066	0.367

These additional degrees of freedom produced modest improvements in the goodness-of-fit to the experimental data (e.g. change in average error 3.1% vs 3.7% for ES and 2.1% vs 2.9% for MTH). However, we find multiple minima with very similar fitting errors. At the absolute minimum, for both MTH and ES, one finds the two mechanisms, roughly the weighted sum and difference of 85% LM and 15% S cone contrasts, and a relatively high exponent (γs of 2.8 for ES and 3.4 for MTH). For both MTH and ES one finds a secondary minimum (goodness-of-fits within .001% of absolute minima) that corresponded to mechanisms essentially along the LM and S axes with smaller exponent (γs of 1.31 and 1.39), similar to the two-parameter optimization in Table 1.

These results demonstrate that a power law summing the activation of two chromatic channels clearly can yield a very accurate description of our data. However, we do not suggest that this decomposition can be invoked further to make strong inferences about the underlying mechanisms of chromatic salience perception. In particular, it has not definitively answered whether two, or multiple, chromatic mechanisms participate and does not provide the specific chromatic signature of such mechanisms. Masking and adaptation studies provide a more direct paradigm for evaluating the nature of individual mechanisms that contribute to perception of chromaticity (Chen et al., 2000a; Webster & Mollon, 1994).

Figs. 2 and 3 display results for chromatic axes that are intermediate to the LM isoluminant and achromatic luminance directions. Data for contrast thresholds in the (ΔL, ΔM) plane provide the classic demonstration of LM and luminance second-stage opponent mechanisms, i.e. the more sensitive mechanism determines threshold (Cole et al., 1993; Poirson & Wandell, 1990). Fig. 3 also compares contrast thresholds and suprathreshold contrast salience for chromaticities in this plane. These data indicate a contrast threshold model with separable LM and luminance mechanisms and an approximate "greatest responding, winner-take-all" detection rule in not applicable to suprathreshold contrast salience. Either a more complicated rule for combining the responses of LM and luminance channels or additional mechanisms responding to a variety of chromaticities could underlie these observed differences.

Using a power-law response expression:

$$r(cc_\theta) \propto cc_{\theta,\text{LM}}^\gamma + (k_{\text{lum}} cc_{\theta,\text{lum}})^\gamma$$

we have also investigated empirical, two-parameter, fits for the salience data in the LM vs lum plane (Fig. 2a). The results of the fits are given in Table 2. The two-parameter fit gives an average error of 7% for the two observers. The relative contribution of luminance cone contrast is about 40% that of LM-cone contrast (however, note that the luminance cone contrast is 1.73 times the traditional Michelson luminance contrast). The non-empirical Geisler equivalent contrast does not provide an adequate description of the data (Fig. 2b).

Acknowledgments

References

Anstis, S., & Cavanagh, P. (1983). A minimum motion technique for judging equiluminance. In J. D. Mollon & L. T. Sharpe (Eds.), *Color vision: Physiology and psychophysics* (pp. 155–166). London, UK: Academic Press.

Banks, M., Vlaskamp, B., Hillis, J., & Gardner, J. (2007). Stereopsis at isoluminance. *Journal of Vision*, 7 (9), 806–806a. Available at: <http://journalofvision.org/7/9/806/>. doi:10.1167/7.9.806.

Beer, R. D., & MacLeod, D. I. (2000). Pre-exposure to contrast selectively compresses the achromatic half-axes of color space. *Vision Res., 40*(22), 3083–3088.

Bradley, A., Switkes, E., & De Valois, K. (1988). Orientation and spatial frequency selectivity of adaptation to color and luminance gratings. *Vision Res., 28*(7), 841–856.

Brainard, D. H., Roorda, A., Yamauchi, Y., Calderone, J. B., Metha, A., Neitz, M., et al. (2000). Functional consequences of the relative numbers of *L* and *M* cones. *J Opt. Soc. Am. A Opt. Image Sci. Vis., 17*(3), 607–614.

Carney, T., Shadlen, M., & Switkes, E. (1987). Parallel processing of motion and colour information. *Nature, 328*(6131), 647–649.

Chaparro, A., Stromeyer, C. F., 3rd, Huang, E. P., Kronauer, R. E., & Eskew, R. T. Jr., (1993). Colour is what the eye sees best. *Nature, 361*(6410), 348–350.

Chen, C., Foley, J. M., & Brainard, D. H. (2000a). Detection of chromoluminance patterns on chromoluminance pedestals. I: Threshold measurements. *Vision Res., 40*(7), 773–788.

Chen, C., Foley, J. M., & Brainard, D. H. (2000b). Detection of chromoluminance patterns on chromoluminance pedestals. II: Model. *Vision Res., 40*(7), 789–803.

Cole, G. R., Hine, T., & McIlhagga, W. (1993). Detection of mechanisms in L-, M-, and S-cone contrast space. *J. Opt. Soc. Am. A., 10*(1), 38–51.

Comerford, J. P., & Kaiser, P. K. (1975). Letter: Luminous-efficiency functions determined by heterochromatic brightness matching. *J. Opt. Soc. Am., 65*(4), 466–468.

Dacey, D. M., & Packer, O. S. (2003). Colour coding in the primate retina: Diverse cell types and cone-specific circuitry. *Curr. Opin. Neurobiol., 13*(4), 421–427.

De Valois, K. K., & Switkes, E. (1983). Simultaneous masking interactions between chromatic and luminance gratings. *J. Opt. Soc. Am., 73*(1), 11–18.

De Valois, R. L., & De Valois, K. K. (1993). A multi-stage color model. *Vision Res., 33*(8), 1053–1065.

Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *J. Physiol. (London), 357*(1), 241–265.

Engel, S., Zhang, X., & Wandell, B. (1997). Colour tuning in human visual cortex measured with functional magnetic resonance imaging. *Nature, 388*(6637), 68–71.

Frome, F. S., Buck, S. L., & Boynton, R. M. (1981). Visibility of borders: Separate and combined effects of color differences, luminance contrast, and luminance level. *J. Opt. Soc. Am., 71*(2), 145–150.

Gegenfurtner, K. R., & Kiper, D. C. (1992). Contrast detection in luminance and chromatic noise. *J. Opt. Soc. Am. A, 9*(11), 1880–1888.

Geisler, W. S. (1989). Sequential ideal-observer analysis of visual discriminations. *Psychol. Rev., 96*(2), 267–314.

Georgeson, M. A., & Sullivan, G. D. (1975). Contrast constancy: Deblurring in human vision by spatial frequency channels. *J. Physiol., 252*(3), 627–656.

Guth, S. L., Massof, R. W., & Benzschawel, T. (1980). Vector model for normal and dichromatic color vision. *J. Opt. Soc. Am., 70*(2), 197–212.

Johnson, E. N., Hawken, M. J., & Shapley, R. (2001). The spatial transformation of color in the primary visual cortex of the macaque monkey. *Nat. Neurosci., 4*(4), 409–416.

Jordan, J. R., III, Geisler, W. S., & Bovik, A. C. (1990). Color as a source of information in the stereo correspondence process. *Vision Res., 30*(12), 1955–1970.

Kaiser, P. K., & Comerford, J. P. (1975). Flicker photometry of equally bright lights. *Vision Res., 15*(12), 1399–1402.

Klug, K., Herr, S., Ngo, I. T., Sterling, P., & Schein, S. (2003). Macaque retina contains an S-cone off midget pathway. *J. Neurosci., 23*(30), 9881–9887.

MacLeod, D. I., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *J. Opt. Soc. Am., 69*(8), 1183–1186.

Mullen, K. T. (1985). The contrast sensitivity of human colour vision to red–green and blue–yellow chromatic gratings. *J. Physiol., 359*, 381–400.

Mullen, K. T., & Losada, M. A. (1994). Evidence for separate pathways for color and luminance detection mechanisms. *J. Opt. Soc. Am. A, 11*(12), 3136–3151.

Poirson, A. B., & Wandell, B. A. (1990). The ellipsoidal representation of spectral sensitivity. *Vision Res., 30*(4), 647–652.

Poirson, A. B., & Wandell, B. A. (1996). Pattern–color separable pathways predict sensitivity to simple colored patterns. *Vision Res., 36*(4), 515–526.

Regan, D. (2000). *Human perception of objects: Early visual processing of spatial form defined by luminance, color, texture, motion, and binocular disparity*. Sunderland, Mass: Sinauer Associates. pp. xxix–577.

Roorda, A., & Williams, D. R. (1999). The arrangement of the three cone classes in the living human eye. *Nature, 397*(6719), 520–522.

Sankeralli, M. J., & Mullen, K. T. (2001). Bipolar or rectified chromatic detection mechanisms? *Vis. Neurosci., 18*(1), 127–135.

Scharff, L. V., & Geisler, W. S. (1992). Stereopsis at isoluminance in the absence of chromatic aberrations. *J. Opt. Soc. Am. A, 9*(6), 868–876.

Smith, V. C., & Pokorny, J. (1996). Color contrast under controlled chromatic adaptation reveals opponent rectification. *Vision Res., 36*(19), 3087–3105.

Solomon, S. G., & Lennie, P. (2005). Chromatic gain controls in visual cortical neurons. *J. Neurosci., 25*(19), 4779–4792.

Solomon, S. G., & Lennie, P. (2007). The machinery of colour vision. *Nat. Rev. Neurosci., 8*(4), 276–286.

Switkes, E., & Crognale, M. A. (1999). Comparison of color and luminance contrast: Apples versus oranges? *Vision Res., 39*(10), 1823–1831.

Valberg, A. (2005). *Light Vision Color*. Chichester: John Wiley and Sons, Ltd.

Vimal, R. L. (2000). Spatial color contrast matching: broad-bandpass functions and the flattening effect. *Vision Res., 40*(23), 3231–3243.

Webster, M. A., & Mollon, J. D. (1994). The influence of contrast adaptation on color appearance. *Vision Res., 34*(15), 1993–2020.

Wilson, J. A. (1999). *Spatiochromatic interactions in the processing of form. Psychology*. Berkeley: University of California.

Wilson, J. A., & Switkes, E. (2005). Integration of differing chromaticities in early and midlevel spatial vision. *J. Opt. Soc. Am. A Opt. Image Sci. Vis., 22*(10), 2169–2181.

Wyszecki, G., & Stiles, W. S. (1982). *Color science: Conceptual methods, quantitative data and formulae*. New york: Wiley.

Yaguchi, H. (1987). Heterochromatic brightness matching with checkerboard patterns. *J. Opt. Soc. Am. A, 4*(3), 540–544.