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Spatial color contrast matching: broad-bandpass functions and the flattening effect

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Abstract

The contrast matching function (CMF) is the reciprocal of test contrast that perceptually matches the contrast of standard pattern, measured as a function of test spatial frequency (SF). Achromatic CMFs usually flatten as the contrast of the standard is raised, and are broader than the achromatic, bandpass, contrast sensitivity function (CSF). This report investigates whether chromatic CMFs have similar characteristics. For this purpose, the red–green color channel was defined using minimum flicker and hue cancellation techniques. Spatially localized (D6), vertical, equiluminant patterns (SFs: 0.063–8 cpd; contrast: 3–80%) were used to measure the CSF and CMF of isoluminant patterns presented with a temporal Gaussian envelope. CMFs were measured using a randomized double-staircase procedure and the two-interval forced choice technique. Two color-normal observers, whose task was to select the interval that had higher color contrast, participated in experiments. Results show that: (a) the color CMFs are lowpass functions of SF at low standard contrasts (3–12.5%), broad-bandpass at intermediate contrasts (6.25–60%), and near-flat at high contrasts (80%); and (b) isoluminant CMFs have higher upper cut-off frequencies than isoluminant CSFs. It is concluded that: (i) color-contrast-constancy (CMF independent of SF) is partly achieved at high contrasts because color CMFs flatten as contrast increases; (ii) the information processing at suprathreshold levels is different from that at the threshold levels; and (iii) the model that explained achromatic CMFs using achromatic threshold mechanisms could not explain chromatic CMFs using chromatic threshold mechanisms.

Keywords: Suprathreshold; Lowpass; Broad-bandpass; Color contrast matching function; Color contrast constancy; Normalization; Divisive inhibition; Spatial frequency tuned mechanisms

1. Introduction

Previous research has used the measurement of contrast matching functions (CMFs) to investigate the mechanisms responsible for suprathreshold achromatic vision (Georgeson & Sullivan, 1975; Swanson, Wilson, & Geise, 1984; Swanson & Wilson, 1985; Swanson, Georgeson, & Wilson, 1988; Cannon & Fullenkamp, 1988, 1991a,b). These studies have shown that suprathreshold CMFs are more spatially broadband than CSF (contrast sensitivity function). This result has been explained by a *contrast-matching model* (Swanson et al., 1984; Swanson & Wilson, 1985; Swanson et al., 1988), which implicitly proposes that multiple mechanisms stimulated above their respective detection thresholds are mutually inhibitive. This inhibition produces a normalization of mechanism response, in which the peak response of the most responsive mechanism is divided by that of the other mechanisms (Swanson et al., 1988) to yield scaling factors called *mechanism gains*. [Response normalization by divisive inhibition is described in other investigations as well (Heeger, 1992; Foley, 1994; Graham & Sutter, 1998).]

In the color domain, the CSF exhibits lowpass behavior (Mullen, 1985; Pandey & Vimal, 1993, 1994; Vimal, 1998a,b) unlike the bandpass achromatic CSF (Wilson, McFarlane, & Phillips, 1983). Here, we investigate whether chromatic CMFs and achromatic CMFs behave similarly, and whether less sensitive, high spatial frequency (SF) color mechanisms raise their sensitivities at suprathreshold contrasts. We also test whether color

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CMFs can be predicted by chromatic threshold mechanisms with normalized mechanism responses, as is the case for achromatic stimuli.

Our results show that the lowpass color CMF at low contrasts changes to a broad-bandpass function of SF at intermediate contrasts and then flattens at high contrasts. In addition, we show that the color CMFs are broader than the color CSF on the high SF side. Furthermore, the color CMF data can not be explained satisfactorily by the normalization of the responses of multiple, independent, parallel mechanisms.

2. Methods

2.1. General

The apparatus and test stimuli are described in further detail in Vimal (1997). The stimuli were generated by a PC/AT 486 and ATVista graphic system (60 Hz, non-interlaced) and were presented on a Sony GDM-1936 color monitor. The viewing angle was $27.6 \times 20.5°$ at 80 cm from the monitor for test SFs less than or equal to 1 cpd. For test SFs greater than 1 cpd, the distance from the monitor was 652.5 cm ($3.5 \times 2.6°$ viewing angle). The monitor was calibrated with a Pritchard photometer, whose measurements were used to generate a red–green–blue linearizing lookup table.

Longitudinal chromatic aberration was minimized by a Powell achromatizing lens (Powell, 1981) with a 2-mm artificial pupil. Transverse chromatic aberration was minimized (a) by aligning the eye with vertical red–blue nonius lines (so that they looked aligned) through the lens system and then (b) by nullifying the color fringes around a purple (red-and-blue) rectangular field for more accurate alignment; the rectangular field and the nonius lines were displayed on the color monitor.

Stimulus contrast was defined as the ratio of the maximum phosphor modulation in time and space to the mean phosphor luminance. The stimulus contrasts of the red, green, and blue components covaried. (In this paper, the term 'contrast' is usually used for the stimulus contrast, unless otherwise noted.) A dithering technique, based on the principle of spatial summation, was used to achieve a lower contrast. In this technique, if one out of n (two or four) pixels is randomly illuminated, the contrast will be $(1/n)$ of the original contrast.

The chromatic channels were isolated from the achromatic channel by use of the minimum-flicker technique. A red pattern was flickered with a green pattern at 30 Hz, and the mean luminance of the green pattern was adjusted to achieve minimum flicker. The $R–G$ channel was then isolated from the yellow–blue channel by use of the hue cancellation technique (Jameson & Hurvich, 1955). In this technique: (i) the mean luminances of the red and the green patterns (estimated from the minimum flicker technique) are combined to create a 'solid-yellow' field, and the blue is then added to obtain a neither-yellow-nor-blue criterion. The method of adjustment and the method of limits were used. In addition (ii) the yellowness of red pattern was canceled by adjusting the mean luminance of blue (spatially inphase with the red) pattern by the neither-yellow-nor-blue criterion. (iii) Similarly, the yellowness of green pattern was canceled by adjusting the mean luminance of the blue pattern. (iv) To verify the measurements, when all the patterns (reddish: red + blue, and greenish: green + blue) were combined spatially inphase, the subjects reported the neither-yellow-nor-blue perception. In addition, the sum of the blue from (ii) and the blue from (iii) were not significantly different from the blue estimated from (i); $P > 0.05$ by the two-tailed t-test was found. Although there is a growing body of evidence suggesting that unique hues do not isolate the chromatic mechanisms (Mollon, 1997), the hue-cancellation technique defines the $R–G$ opponent channel which is very close to the reddish–greenish cardinal axis defined by the habituation technique (see Krauskopf, Williams, & Heeley, 1982). Therefore, the $R–G$ Channel isolated here and in our papers (Vimal, 1997, 1998a,b), and its characteristics, should be close to that of the reddish-greenish cardinal axis. Moreover, the $R–G$ channel was found to be linearly related to: (a) color matching functions (Larimer, Kranz, & Cicerone, 1974); and (b) cone signals (Werner & Wooten, 1979; Shevell & Knoblauch, 1998: R/G equilibria were linear). The isolation of the $R–G$ channel (along with the minimization of chromatic aberrations) was further tested experimentally by comparing the contrast sensitivity for color-detection with that for pattern-detection (color, luminance, or both) at the isoluminant point. The two were not significantly different from each other ($P > 0.05$ by the two-tailed t-test). The above techniques yielded the space averaged luminances as $11.7R + 14G + 1.2B = 26.9$ cd/m^2 for observer RV, $11.7R + 12G + 1.3B = 25$ cd/m^2 for RP, and $11.7R + 14.2G + 2.5B = 28.4$ cd/m^2 for SP. These mean luminances remained unchanged in the experiments.

2.2. Test and standard stimuli

The test stimuli were spatially localized (sixth derivative of a Gaussian (D6)) patterns along the (horizontal) x-axis. They were Gaussian along the (vertical) y-axis with four times the space constant of the D6. The stimuli were presented with a Gaussian temporal envelope with a 0.5-s time constant and a 2-s duration.

The spatiotemporal characteristics of the standard stimuli were the same as those of the test. The SFs of both test and standard patterns varied between 0.0625 and 8 cpd. The contrast of the standard patterns ranged from 3.1 to 80%. The spatiotemporal characteristics of test and standard patterns are mathematically described in Eqs. (A1)–(A9) of Appendix A of Vimal (1997).

2.3. Observers

In our experiments, observers RV (46-year-old male), RP (38-year-old female), and SP (27-year-old-female) had normal color vision as tested by Ishihara color plates, Nagel anomaloscope, and FM-100 hue test (Vimal, Pokorny, Smith, & Shevell, 1989). Observer RV participated in CSF and CMF, RP in CSF, and SP in CMF experiments.

2.4. Procedure and observer's task

The color CSFs were measured by the method of constant stimuli with the two-interval (each 2 s duration with 0.5 s gap) forced choice technique (Vimal, 1998a). The color CMFs were measured by the two-interval forced choice procedure with randomized double staircases. The standard pattern was presented randomly in one of the intervals and the test pattern in the other interval. The observer initially adapted to the mean luminance (white field) for 2–3 min and then initiated a trial by a button press. The observer's task was to report the interval that appeared to have higher color contrast. The contrast of the test pattern was increased if the observer chose the interval containing the standard pattern; the contrast of the test pattern was decreased if the interval with the test pattern was correctly chosen on two consecutive trials ('one up, two down' procedure). The contrast step size in the staircase procedure was 1.2%. A session consisted of two to ten double random staircases each with ten reversals. The first three reversals were ignored. The number of sessions for each standard contrast varied from two to eight to achieve a standard error within 20% of the mean.

3. Results

3.1. Color matching functions (CMFs): raw data

Color contrast matching data were averaged over sessions for each standard spatial frequency at each standard contrast. The raw averages are plotted in Fig. 1 (ten panes: A–J) for observer RV and in Fig. 2 (six panes: A–F) for observer SP. Fig. 1I and J are enlargements of Fig. 1F and G, respectively, to better show their bandpass characteristic. Large open circles show matches made when the test and standard stimuli were identical in SF; these matches were useful in the normalization of CMFs across sessions by the algorithm described in Appendix A. The other symbols show the matches made when the test-SF differed from the standard-SF.

In general, the data of Figs. 1 and 2 can be categorized into three groups based on the shape and the behavior of the CMFs: lowpass, bandpass, and near-flat CMFs. This classification is also consistent with that based on the low, intermediate, and high contrast, respectively. Various curve-fitting procedures were explored to describe these data: Gaussians, difference of Gaussians (DOGs), and squared DOGs were all unsatisfactory; this is not surprising because multiple mechanisms contribute to a CMF (Swanson et al., 1984,1985,1988). Bandwidths at half-height were estimated from Figs. 1–3 (by eye): (a) for lowpass CSFs, the range for right bandwidth from 0.0625 cpd was 3.4–3.7 octaves; (b) for lowpass CMFs, it was 6.2–7.7 octaves; and (c) for bandpass CMFs, the range for full bandwidths was 5.2–26.4 octaves.[1] To verify the shape of the CSFs and CMFs, we performed a two-tailed t-test (Welkowitz, Ewen, & Cohen, 1976) between relevant data points of each curve: the significance level varied from $P < 0.05$ to $P < 0.001$. According to the multiple t-test (Vimal, 1998b), the adjusted significance level is $P_{adj} < 0.01$ (for $N_{dp} = 5$ and $P < 0.05$). N_{dp} is the number of data-point pairs used to verify the shape of functions. We also used the directional t-test to show the bandpass behavior, i.e. contrast matching sensitivities at the lowest and highest SFs were less than the contrast matching sensitivity at the middle SF to show bandpass behavior. [The term 'sensitivity', in general, is defined as the reciprocal of contrast. For CSFs, this contrast is threshold contrast; for CMFs, it is test contrast, which is above threshold level; this terminology follows Swanson et al. (1984) and Swanson and Wilson (1985).] We have assumed that the determination of the shape of each transfer function requires at least five data points per subject. Initial determination of the shape of CSFs and CMFs was done visually ('by eye') in Figs. 1–3 and is found to be consistent with the statistical analysis. The following classification is based on the above statistical analysis.

3.1.1. Lowpass CMFs

The color CMFs are lowpass functions of SF for the standard contrasts of 3.1% for RV (Fig. 1A) and 6.25% for SP (Fig. 2A).

3.1.2. Broad-bandpass CMFs

The color CMFs exhibit broad-bandpass behavior for the standard contrasts of 6.25–60% for RV (Fig. 1B–G, I, and J) and 25–60% for SP (Fig. 2C–E). For

[1] The table for bandwidths of CMFs (see Section 3.1) and cut-off SFs (see the last paragraph of Section 3.2.2), and the summary figure (see the last paragraph of Section 3.2.2) are available upon email request to vimalram@hotmail.com.

example, (i) at 6.25% standard contrast (Fig. 1B), the contrast matching sensitivity at 1 cpd is significantly higher than that at 0.0625 and 8 cpd for RV ({$t = 6.6$, df = 2, $P < 0.02$} and {$t = 7.4$, df = 2, $P < 0.01$}, respectively, using two-tailed t-test: Welkowitz et al., 1976). There are seven pairs of data whose elements are significantly different for this CMF at 6.25% standard contrast and consistent with the bandpass characteristic. At this contrast, RV reported that the 1-cpd pattern appeared to have a higher contrast than the 0.0625-cpd pattern of the same stimulus contrast. Furthermore, the broad-bandpass characteristic of CMFs at standard contrasts of 50 and 60% can be visualized better in Fig. 1I and J, which are enlargements of Fig. 1F and G. Here, the contrast matching sensitivity at 1 cpd is significantly higher than that at 0.0625 and 8 cpd ($P < 0.01$ to $P < 0.001$). (ii) For SP, the transformation of the lowpass CMF to the broad-bandpass CMF was not complete until the standard contrast was raised to 25%. This might be because of individual differences or task difficulty, as she was naive to the purposes of experimental design and data collection. For this 25% standard contrast (Fig. 2C), the contrast matching sensitivity at 2 cpd is significantly higher than that at 0.5 and 8 cpd ({$t = 3.3$, df = 10, $P < 0.001$} and {$t = 4.1$, df = 6, $P < 0.001$}, respectively). (iii) The significance level (P) for the broad-bandpass characteristic of the remaining CMFs varied between 0.001 and 0.05. The number of data-point pairs that have $P < 0.01$ varied from one to six for the lower SF side of the broad bandpass curves.

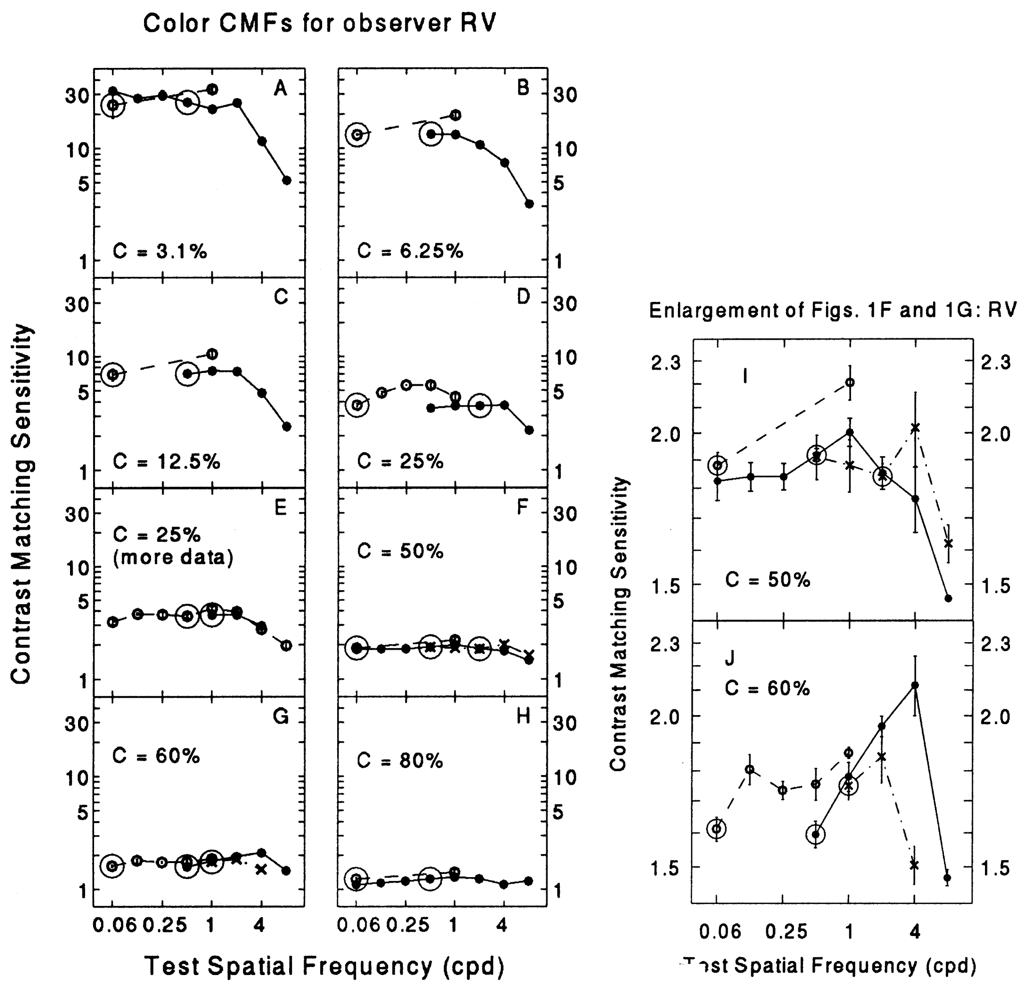

Fig. 1. The color contrast matching sensitivity functions (CMFs) are plotted as contrast matching sensitivity (the reciprocal of measured test contrast that perceptually matched the standard contrast) versus spatial frequency (SF) for observer RV. The data at 'test SF = standard SF' is shown by a large open circle and the data at other test SFs are shown by other symbols (small open circles, filled circles, and symbol ×); data are joined by lines. The error bars represent one standard error (SE) over sessions per standard SF. (A) *Lowpass* CMF: standard contrast (C) = 3.1%. (B) *Broad-bandpass* CMFs: C = 6.25%. (C) *Broad-bandpass* CMFs: C = 12.5%. (D) and (E): *Broad-bandpass* CMFs: C = 25%. (F) *Very broad-bandpass* CMFs: C = 50%. (G) *Very broad-bandpass* CMFs: C = 60%. (H) *Near-flat* CMFs: C = 80%. (I) and (J) are the enlargements of (F) and (G), respectively.

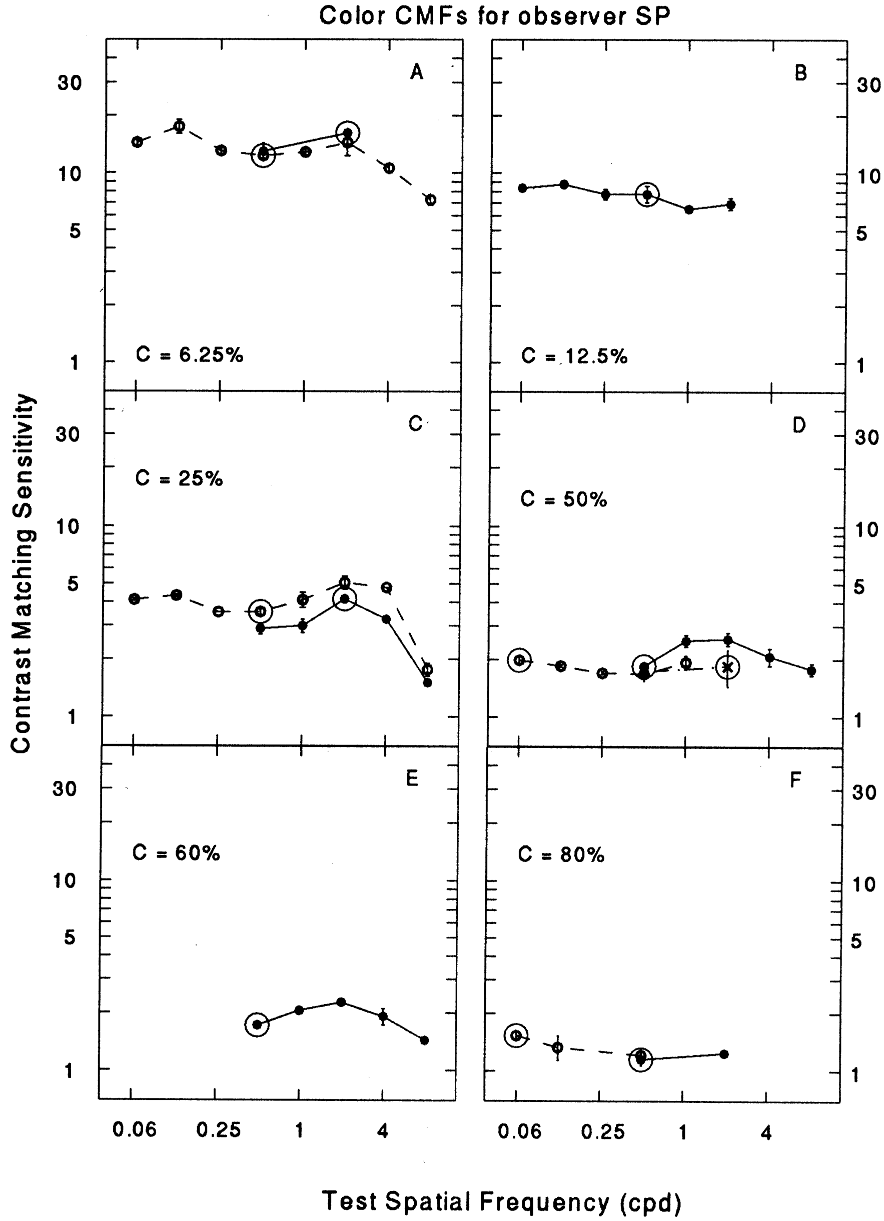

Fig. 2. The CMFs for observer SP. (A) *Lowpass* CMFs: C = 6.25%. (B) *Lowpass* CMFs: C = 12.5%. (C) *Broad-bandpass* CMFs: C = 25%. (D) *Broad-bandpass* CMFs: C = 50%. (E) *Broad-bandpass* CMFs: C = 60%. (F) *Near-flat* CMFs: C = 80%. For details, see Fig. 1.

3.1.3. Near-flat CMFs

These CMFs are flat or nearly so, implying that sensitivity is nearly independent of SF. The color CMFs at 80% standard contrast are plotted in Fig. 1H for RV and in Fig. 2F for SP. For RV, the contrast matching sensitivity at 1 cpd is significantly higher than that at 0.0625 cpd ($\{t = 2.8$, df $= 6$, $P < 0.02\}$ for open circles and $\{t = 6.9$, df $= 12$, $P < 0.001\}$ for solid circles) and 4 cpd $\{t = 3.1$, df $= 10$, $P < 0.02\}$, but it is not true at 8 cpd $\{t = 2.9$, df $= 2$, $P > 0.1\}$. In addition, the full bandwidth at half-height is very large. These observations suggest a near-flat CMF for RV at 80% contrast, i.e. this CMF is a very broad-bandpass function of SF. For SP, the data are not significantly different from each other; for example, $\{t = 0.6$, df $= 2$, $P > 0.2\}$ between 0.5 and 2 cpd; $\{t = 2.5$, df $= 2$, $P > 0.1\}$ between 0.0625 and 0.5 cpd; $\{t = 2.1$, df $= 2$, $P > 0.1\}$ between 0.0625 and 2 cpd. Thus, these CMFs are nearly flat, which implies that sensitivity is nearly independent of SF. Thus, at 80% contrast CMFs exhibit partial spatial color-contrast constancy.

3.2. Multiple viewing distances and standard SFs and normalized CMFs

3.2.1. Rationale for using multiple viewing distances and multiple standard SFs and for computing normalized color CMFs

Since we used SFs ranging from 0.0625 to 8 cpd (7 octaves), it was necessary to use at least two viewing distances (80 and 652.5 cm from the monitor) to cover such a large range and to minimize spatial artifacts, which were brought into play at different retinal areas. Furthermore, since the selection of the standard SF was arbitrary, it was necessary to use multiple standard SFs (mostly 0.0625 and 0.5 cpd, but 1, 2, and 4 cpd were also used). To remove any effects of viewing distance and standard SF, we normalized color CMFs by use of the algorithm described in Appendix A.

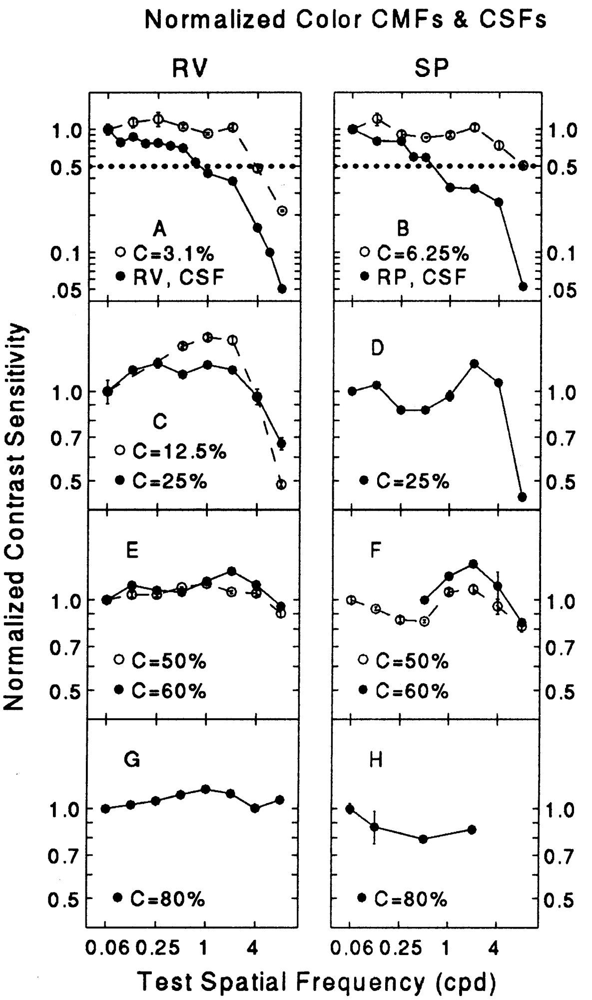

Fig. 3. Normalized color contrast sensitivity function (CSF) and contrast matching function (CMF) are plotted as normalized sensitivity versus spatial frequency (SF). Data are represented by symbols joined by lines. Error bars: 1 SE. The left panes are for observer RV and the right panes for SP. (A) and (B): normalized CSFs are represented by filled circles joined by solid lines. Normalized CMFs are shown by open circles joined by dashed lines at 3.1% standard contrasts (C) in pane A for RV and at C = 6.25% in pane B for SP. The dotted lines are drawn at half-height, i.e. 0.5 from unity. These CSFs and CMFs are *lowpass* functions of SF. (C)–(F): Normalized *broad-bandpass* color CMFs: *pane C* for RV at C = 12.5% (open circles joined by dashed lines) and 25% (filled circles joined by solid lines); *pane D* for SP at C = 25% (filled circles joined by solid lines); *pane E* for RV at C = 50% (open circles joined by dashed lines) and 60% (filled circles joined by solid lines); *pane F* for SP at C = 50% (open circles joined by dashed lines) and 60% (filled circles joined by solid lines). (G) and (H): Normalized *near-flat* CMFs: the CMFs at 80% standard contrast, shown by filled circles joined by solid lines, are close to constant function of SF; pane G is for RV and pane H for SP.

3.2.2. Normalized CMFs

In general, the shape and the behavior of the raw CMF data (i.e. lowpass, broad-bandpass, and near-flat function of SF) appear similar for various standard SFs and viewing distances. This can be visualized in Figs. 1I, 1J, 2C and 2D, where enough data points are available. The algorithm of Appendix A transformed the raw CMF data of Figs. 1 and 2 into the normalized CMFs of Fig. 3. The normalization procedure combines the data of many standard SFs into one CMF at a specific standard contrast to encompass a large (7 octave) range of SFs (0.0625–8 cpd).

In Fig. 3, symbols represent the normalized mean contrast matching sensitivity data; an error bar at each data point indicates the normalized SE of the mean; the panes (A, C, E, G) of the left panel are for RV and the panes (B, D, F, H) of the right panel are for SP. [Note that (for clarity) the range of the normalized contrast sensitivities along y-axis in Fig. 3A–B differs from that of Fig. 3C–H.] The three groups of the normalized CMF data, derived from the raw data of Figs. 1 and 2 (Section 3.1), are given below.

3.2.2.1. Lowpass CMFs and CSFs. The normalized CMF at 3.1% standard contrast, estimated from Fig. 1A for RV, is plotted in Fig. 3A by open circles. Similarly, the normalized CMF at 6.25% standard contrast, estimated from Fig. 2A for SP, is plotted in Fig. 3B. Both CMFs are a *lowpass* function of SF and are broader than the lowpass color contrast sensitivity function (CSF) (filled circles). That is, upper cut-off SF for isoluminant CMF is higher than that for the isoluminant CSF. At cut-off SF, un-normalized sensitivity is 1. For example, the upper cut-off SF is approximately 37 cpd (5.2 octaves) for the CMF at 3.1% standard contrast (Fig. 1A) whereas the upper cut-off SF is 21 cpd (4.4 octaves) for the CSF of RV from Fig. 3A. In Vimal (1998a,b), the cut-off SF for color CSF is 14 cpd when averaged over subjects and estimation-methods. The cut-off SF depends on subject and the method of estimation (Vimal, 1998a,b). In addition, from Fig. 3, the half-peak-SF is 0.7 cpd for the CSFs, 4 cpd for the CMF at 3.1% standard contrast (RV), and 8 cpd for the CMF at 6.25% standard contrast (SP).

3.2.2.2. Broad-bandpass CMFs. The normalized *broad-bandpass* CMFs are plotted in Fig. 3C–F; they were estimated from Fig. 1C–1G (standard contrasts: 12.5–60%) for RV and from Fig. 2C–E (standard contrasts: 25–60%) for SP. This broad-bandpass characteristic of the CMFs is surprising because the color CSF is not generally regarded to be a bandpass function of SF when luminance artifacts are insignificant (see Sections 5.1 and 5.2 for further detail).

3.2.2.3. Near-flat CMFs. The normalized *near-flat* CMFs estimated from Fig. 1H for RV and Fig. 2F for SP are plotted in Fig. 3G and H, respectively.

If the data of Fig. 3 were re-plotted in one graph, it would be easier to see how CMF changes from a lowpass to a broad-bandpass and then to a near-flat function of SF as standard contrast is increased.[1] In general, from Figs. 1–3 it can be estimated that as the CMF's standard contrast increases, (a) the lower and upper cut-off SFs first decrease and then increase and (b) the bandwidths also first decrease and then increase at different rates.[1] This characteristic is a reflection of the change from a lowpass CMF to a broad-bandpass CMF to a near-flat CMF as standard contrast increases. In addition, the CMFs are broader than CSFs.

4. Data analysis

Five contrast matching models were explored to investigate if they can explain the color CMF data by using chromatic threshold mechanisms (Pandey & Vimal, 1993, 1994; Vimal, 1998a): (1) without normalization; (2) with mechanism-sensitivity or mechanism-response normalization (Georgeson & Sullivan, 1975; Swanson et al., 1984; Swanson & Wilson, 1985; Swanson et al., 1988) (average correlation r between the CMF data and the prediction $= -0.04$); (3) with contrast-independent mechanism-gains ($r = 0.69$); (4) with contrast-independent mechanism-gains and nonlinearities as variable parameters ($r = 0.86$); and (5) with contrast-dependent mechanism-gains ($r = 0.9$). We used the generic contrast-matching model described in detail by Swanson et al. (1984) and Swanson and Wilson (1985) and Swanson et al. (1988), except the response F of a mechanism to contrast C is defined by Eqs. (A1)–(A3) of Appendix A of Vimal (1998a). Although all of our tested models were found to be unsatisfactory, Model 5 was the best ($r = 0.9$). Model-2 (Swanson et al., 1984; Swanson & Wilson, 1985; Swanson et al., 1988) can explain a shift from bandpass to a near-flat function as contrast is increased ('the flattening effect') but it cannot explain this shift in conjunction with initially lowpass data at very low contrasts (Figs. 1–3). The subject's criterion may have changed from matching color contrasts to matching colors at low contrasts, but this possibility does not mean that any single model designed to handle, say, contrast matching, is bound to fail at low contrasts. Further investigation is necessary.

5. Discussion

5.1. Findings and their significance

The findings are summarized as follows: (i) the color CMF changes from lowpass to broad-bandpass and then to a near-flat function of SF as the contrast of the standard pattern is raised. In addition, the color CMFs (suprathreshold data) are broader than the CSF (threshold data) on the high SF side. This flattening of the color CMF as standard contrast increases (the *flattening effect*) is consistent with the flattening effect of achromatic CMF (Georgeson & Sullivan, 1975; Swanson et al., 1984; Swanson & Wilson, 1985; Swanson et al., 1988). (ii) The data analysis in Section 4, however, suggests that the color CMF data can not be explained satisfactorily by any of the five models proposed. (iii) That is, the normalization of mechanism-responses that explained so well the achromatic CMF data (Georgeson & Sullivan, 1975; Swanson et al., 1984; Swanson & Wilson, 1985; Swanson et al., 1988) failed to explain the color CMF data. Further investigation with divisive inhibition (Foley, 1994; Foley & Chen, 1997; Chen et al. 2000) may be useful.

The significance of the findings for the understanding of color vision is given below in three specific topics: (a) color contrast sensitivity function; (b) color-contrast constancy and color-induction; and (c) similarities and differences between the processing of color and luminance contrasts.

5.1.1. Color contrast sensitivity function

The contrast sensitivity function (CSF) represents the processing of contrasts at threshold as a function of SF. The color CSF is a lowpass function of SF, consistent with other investigations (Mullen, 1985; Vimal, 1998a). This behavior differs from the broad-bandpass behavior of chromatic CMFs at intermediate contrasts (6.25–60% depending on subjects). At these contrasts, observers reported that they perceived color patterns of intermediate SF (1–2 cpd) as having higher contrast than those of the low (0.0625–0.5 cpd) and high (8 cpd) SF of the same stimulus contrast. These observations suggest that if the color CSFs were measured with the criterion of the detection of 'color contrast' (e.g. the central reddish with respect to the flanking greenish regions) rather than that of the detection of 'color', the color CSF would be a bandpass function of SF. With the 'color' criterion, observers detect the central reddish with respect to the mean field color, the flanking greenish color, or both whichever yields highest sensitivity. With the 'color contrast' criterion, the flanking greenish portion of the pattern at low SFs (less than or equal to 0.125 cpd), being in the non-foveal area, would require more energy for its detection; this would lead to higher threshold contrast and hence bandpass color CSF. If true, then one could ask why the CMF at low contrast was a lowpass function of SF? Since patterns were not clearly visible at low contrasts, observers might have used the 'color' criterion. If they had used the 'color contrast' criterion, the low contrast CMFs would have also been broad-bandpass functions of SF. This was not tested. The instruction to observers was 'which interval had higher color contrast'. We did not specifically define 'color contrast' to the observers. Thus, observers were free to make a decision based on their own definition of color contrast (with respect to the mean field color or with respect to the flanking greenish color or both). Therefore, it would be interesting to investigate if the above hypothesis (bandpass color CSF) is true. Furthermore, Stromeyer, Gowdy, Chaparro, and Kronauer (1999) reported bandpass color CSF on red background field, but CSF remained lowpass function of SF on yellow field. Their subjects had to identify the interval containing test grating in two-interval-forced-choice procedure. The cone-contrast sensitivity for 0.8 cpd (2.8 cycles) red–green grating was lower than that for the 2 cpd (7 cycles) grating on the red field (but not on the yellow field).

Thus, the results and the data analysis lead to further investigation of color contrast processing at: (i) *threshold*: under on what criterion and condition color CSF is a lowpass function of SF and under what criterion and condition it may be a bandpass function of SF; and (ii) *suprathreshold*: how CMFs behave and how threshold SF-tuned color mechanisms with additional assumptions may explain CMFs and hence bridge the gap between threshold and suprathreshold color vision.

5.1.2. Color-constancy and color-induction

Since color-contrast is one of the important factors underlying color-constancy (McCann, McKee, & Taylor, 1976; Shapley & Reid, 1985; Arend & Reeves, 1986; Brainard & Wandell, 1986) and color-induction (Krauskopf, Zaidi, & Mandler, 1986; Shapley, 1986), our findings (Section 3) may be related to these phenomena. The enhanced sensitivity to intermediate SF (1–2 cpd) patterns at intermediate contrasts (the broad-bandpass CMF) is consistent with color-induction. The near-flat color CMF at high contrast (80%) suggests *partial* color-contrast constancy with respect to the variation of SF; this result is consistent with partial color-constancy.

5.1.3. Similarities and differences between the processing of color and luminance contrasts

The *similarities* between the processing of color and luminance contrasts are as follows: (i) the 'flattening effect' is common to both luminance (Georgeson & Sullivan, 1975; Swanson et al., 1984; Swanson & Wilson, 1985; Swanson et al., 1988) and color (Vimal & Pandey, 1993; Figs. 1–3) processing. (ii) At intermediate and high contrasts, CMFs have similar trends (bandpass and near flat) for both achromatic and chromatic channels. (iii) It may be possible to explain CMFs using threshold mechanisms with additional assumptions for both chromatic and achromatic channels. (iv) In addition, previous studies have shown that some of the SF tuning of the filters of the chromatic bandpass mechanisms is similar to that of the corresponding achromatic mechanisms (Losada & Mullen, 1994, 1995; Vimal, 1998a).

On the other hand, our analysis suggests that the *differences* are in the actual mechanics of the processing of color and luminance contrasts. For example: (i) the normalization of mechanism-response (Model-2) that was used to explain the luminance CMF data (Georgeson & Sullivan, 1975; Swanson et al., 1984; Swanson & Wilson, 1985; Swanson et al., 1988) is unable to explain the color CMF data using the chromatic threshold mechanisms extracted from the multiple mechanism model (Pandey & Vimal, 1993, 1994; Vimal, 1998a). However, Model-2 has not been tested using the threshold mechanisms extracted from the multiple mechanism model with divisive inhibition (Foley, 1994) because these mechanisms have not yet been extracted for color. (ii) CSFs and CMFs (at low contrasts) are lowpass functions of SF for the chromatic channel, whereas they are bandpass functions for the achromatic channel. (iii) The $R-G$ color channel has one lowpass and five bandpass SF-tuned mechanisms (Vimal, 1998a) whereas the six mechanisms of the achromatic channel are all bandpass functions of SF (Wilson et al., 1983). The lowpass color mechanism has a lowpass spatial receptive field with *spectral* opponency whereas bandpass mechanisms have bandpass receptive fields with *spatial* opponency (or both *spatial and spectral* double opponency for color) (De Valois, Snodderly, Yund, & Hepler, 1977; Michael, 1985; De Valois & De Valois, 1993). (iv) In addition, results show that: (a) the color acuity or cut-off SF (14–21 cpd) is significantly smaller than the achromatic acuity (32 cpd) (Wilson et al., 1983; Mullen, 1985; Pandey & Vimal, 1993, 1994; Vimal, 1998a,b); and (b) the orientation tuning curves of the chromatic mechanisms are broader (except at 2 cpd) than those of the achromatic mechanisms (orientation half-bandwidths: 68–30° for chromatic and 32–15° for achromatic mechanisms at 0.5–11.3 cpd) (Phillips & Wilson, 1984; Vimal, 1997).

5.2. Models and the comparison of results with other investigations

We have considered several adaptations of the contrast-matching model to explain the color CMF data, but none of them are satisfactory. To adequately explain the data, these models need to evolve to a more general purpose model, such as separable mechanisms with divisive inhibition (Bonds, 1989; Heeger, 1992; Foley, 1994; Foley & Chen, 1997; Graham & Sutter, 1998; Vimal, 1998a,b; Wilson & Kim, 1998; Chen, Foley, & Brainard, 2000) along with more complex normalization of individual mechanism responses at suprathreshold level. One could argue that the gradual reduction of spatial response pooling with the increase of contrast (Cannon & Fullenkamp, 1988, 1991a,b) should be included in the model to obtain a smooth transition from threshold to suprathreshold contrast perception. This reduction could be included in the model by replacing k of Eqs. (A1) and (A2) of Vimal (1998a) with k multiplied by a term similar to THRESH of Eq. (3) of Cannon and Fullenkamp (1991a) when sinusoidal stimuli are used. However, we used D6 localized patterns to minimize spatial response pooling effects.

Furthermore, the measured bandpass characteristics of the color CMFs are consistent with: (i) color-form interaction; (ii) color-luminance interaction; and (iii) luminance artifacts in color stimuli. Regarding *color-form interaction*, the perception of chromatic form is assumed to be due to color-contrast, a kind of melted boundary (Boynton, 1973) between two isoluminant colors (the central reddish and the flanking greenish colors). As discussed in Section 5.1.1, it would be easy to explain the bandpass CMF as a flattening of color CSF if this CSF were also bandpass function of SF. But so far only a lowpass color CSF has been reported when luminance artifacts are minimized (Mullen, 1985; Vimal, 1998a,b) except under the red field (Stromeyer et al., 1999) as described before in Section 5.1.1. Alternatively, some subset of the chromatic bandpass mechanisms (such as those tuned to 0.5 and 2 cpd: Vimal, 1998a) may become more sensitive at suprathreshold levels, leading to broad-bandpass color CMFs. Further investigation is needed to test these possibilities.

Color-luminance interaction was reported for suprathreshold mask-contrasts in cross-masking experiments (Mullen & Losada, 1994; Switkes, Bradley, & De Valois, 1988; Vimal, 1998b). From these reports, one could argue that patterns, which are isoluminant at threshold level, might activate luminance mechanisms at suprathreshold levels. This activation could be through divisive inhibition (Chen et al., 2000). If this is the case then color CMFs may be a bandpass function of SF just as the luminance CMFs are a bandpass function of SF. Further investigation is needed.

Lastly, the bandpass color CMF could also have some contribution from the *residual luminance artifacts* in stimuli at suprathreshold levels in spite of our rigorous effort for their minimization at threshold levels (discussed later).

Next, the findings are compared to that of Poirson and Wandell (1993) who reported color matches between a uniform color patch and square-wave, isochromatic, luminance-varying gratings. They found that the square wave bars appeared desaturated and had a chromaticity-shift. They explained their color matching data by (a) one spectrally positive (non-opponent) and spatially bandpass mechanism and (b) two spectrally opponent and spatially lowpass mechanisms. They were able to explain also the achromatic contrast matching data of Georgeson and Sullivan (1975) for the standard contrast of 5% or greater. Poirson and Wandell (1993), however, mentioned that nonlinearities observed by Georgeson and Sullivan (1975) were restricted to threshold and near-threshold contrasts. Our measurements are for color contrast matching with equiluminant, color varying, localized patterns, and are not directly comparable with those of Poirson and Wandell. In the contrast matching models that were explored, we used the accelerating and compressive contrast nonlinearities (Wilson, 1980; Wilson et al., 1983; Vimal, 1998a). These nonlinearities were either not present in the data of Poirson and Wandell or the nonlinearities were loaded on the transformation matrices obtained by their curve-fitting procedure.

In addition, Poirson and Wandell corrected their data (sensitivity vs. wavelength, and scale-factors vs. SF curves) for chromatic aberration by modeling (Wandell & Marimont, 1992; Marimont & Wandell, 1994). We have minimized chromatic aberration by using Powell's achromatizing lens and by nullifying the color fringes around a purple rectangular field (Section 2.1; Vimal, 1997, 1998a,b). However, at high SFs (such as 8 cpd) the optical degradation (including residual chromatic aberration) might have raised the mechanism-gains to high values at high contrasts to match with the standard contrasts of lower SF patterns. Any residual chromatic aberration at high SF (such as 8 cpd) would not change the conclusion of the 'flattening effects' because they were also reported for luminance patterns by other investigators (Georgeson & Sullivan, 1975; Swanson et al., 1984; Swanson & Wilson, 1985; Swanson et al., 1988). The change of color CMFs from lowpass to broad-bandpass function of SF cannot be due to the chromatic aberration alone because the chromatic aberrations at high SFs (such as 4–8 cpd) are higher than that at intermediate SFs (such as 1–2 cpd). In addition, we performed heterochromatic flicker photometry (minimum flicker criterion) experiment to measure the relative mean luminance of red and green patterns (and also hue-cancellation measurements) as a function of

SF (0.125–8 cpd) for determining the isoluminant point. We found that the isoluminant point is independent of SF; this is consistent with Cavanagh, MacLeod, and Anstis (1987) who reported that the red/green equiluminant ratio was influenced by temporal frequency but not by spatial frequency. Thus, residual luminance artifacts alone can not explain the broad-bandpass characteristics of chromatic CMFs at intermediate contrasts.

Furthermore, Metha, Bex, and Makous (1998) reported U-shaped iso-apparent-contrast curves for achromatic stimuli, similar to the threshold contrast function (inverted bandpass achromatic CSF). They performed contrast matching between achromatic standard and test patterns with SFs within SF-difference-thresholds (to minimize SF cues), and observed some flattening at high contrasts. They concluded that SF cues are necessary to produce contrast constancy by SF-dependent gain mechanisms. This conclusion is not inconsistent with the data of Figs. 1–3 because the effect of SF on the apparent contrasts can not be ignored even though the observers compared the contrasts, and not the SFs, of the standard and test patterns.

5.3. Physiological links

Double opponent cells have the necessary receptive fields for the processing of color contrasts (Daw, 1984; Michael, 1985). However, their rarity (Ts'o & Gilbert, 1988) brings into question the formation of their receptive fields from LGN signals, and their failure to show poor spatiotemporal resolution (one of the characteristics of color channels) suggests that further research is needed. The threshold SF-tuned bandpass color mechanisms (Vimal, 1998a) may involve these cells. The lowpass color mechanism (Vimal, 1998a) may be related to those cells that have lowpass receptive fields (De Valois et al., 1977; De Valois & De Valois, 1993).

Furthermore, in color contrast matching between low and high SF patterns, many less sensitive high SF color cells might be recruited to match with the responses of the more sensitive low SF color cells. This 'recruiting' phenomenon might be reflected in the estimation of high values of mechanism-gains at high contrasts and high SFs (in Model-5). At high contrasts, the 'flattening effect' leads to partial color-contrast constancy; this phenomenon may very well involve 'recruiting' responses.

The dependence of the transfer properties of retinal cells on stimulus-contrast led some investigators (Shapley & Victor, 1979, 1981; Shapley & Enroth-Cugell, 1984) to postulate a separate and distinct retinal mechanism, which is called the *contrast-gain-control mechanism*. Moreover, there is strong support for fast acting, contrast-gain-control cortical mechanism that scales the input contrast by the average local contrast (Albrecht & Geisler, 1991; Geisler & Albrecht, 1992). In general, this scaling could be due to the retinal (Shapley & Victor, 1979, 1981; Shapley & Enroth-Cugell, 1984), LGN, and cortical (Albrecht & Geisler, 1991; Geisler & Albrecht, 1992) mechanisms. The contrast-gain-control mechanism may be related to the *contrast transfer function* (Eqs. (A1)–(A3) of Vimal, 1998a). Furthermore, the SF-tuned filters of the mechanisms, used in the data analysis, were assumed to remain invariant with contrast. This invariance is consistent with the finding that the selectivity of cortical neurons generally remained invariant with contrast, even after the saturation of the contrast-response function (Albrecht & Hamilton, 1982; Sclar & Freeman, 1982; Albrecht & Geisler, 1991; Geisler & Albrecht, 1992).

6. Summary

1. *Results*: The lowpass color CSF (contrast sensitivity function) is narrower than the color CMFs (contrast matching functions) on the high SF side. The color CMF is a lowpass function of SF at low color contrasts (3–12.5%), a broad-bandpass function (slight but significant) at intermediate contrasts (6.25–60%), and a near-flat function at high contrasts (80%) leading to partial color-contrast-constancy. The CMF flattens (bandwidth increases) as contrast is raised. (For detail, see Section 3 and Figs. 1–3.)
2. The effects of standard SF and viewing distance were factored out by the algorithm of Appendix A. The conclusions from the results (item 1 above) before and after the application of this algorithm remain unchanged. (For detail, see Section 3.2 and Appendix A.)
3. We conclude that the processing of both chromatic and achromatic information at suprathreshold levels is different from that at threshold. Furthermore, the models required to explain suprathreshold contrast matching from the responses of detection mechanisms are different for color and for luminance. (For detail, see Sections 3, 4 and 5.2.)

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Appendix A. Algorithm for estimating normalized contrast-matching function (CMF)

As described in Section 3.2, it is useful to estimate the CMFs (contrast matching sensitivity vs. test SF) across the different standard spatial frequencies (SFs) and viewing distances used in the contrast matching experiments. In these experiments some of the test contrasts, needed to match the standard contrast of the patterns of different SFs, were different from each other by a large amount. For example in Fig. 1A, the contrast matching sensitivity (the reciprocal of test contrast) to 1-cpd test pattern was 33 for the standard SF of 0.0625 cpd (open circle) and 22 for that of 0.5 cpd (filled circle) at 3.1% standard contrast. These values could not be considered a random variation because they are significantly different from each other (two-tailed t-test: $P < 0.02$) (Welkowitz et al., 1976). Therefore, the simple averaging procedure could not be used to average out the effects of the standard SFs and viewing distances. A different algorithm is needed to combine these sensitivities to yield normalized CMF. In this algorithm, each data set is normalized to the same values at the common (reference) SF. Using the CMF for RV at 3.1% standard contrast (Fig. 1A) as an example, the algorithm is briefly described below in 5 steps:

(1) *Find the average and the standard error (SE) over staircases (two staircases × number of sessions for a test SF) for each standard SF (group). Plot this averaged data as raw data*. In Fig. 1A, two standard SFs were used. Therefore, there are two groups: one for the standard SF of 0.0625 cpd (group 1) and other for that of 0.5 cpd (group 2). The two staircases (one session) for group 1 were averaged and plotted as open circles in Fig. 1A at test SFs of 0.0625 and 1 cpd for the standard SF of 0.0625 cpd. The six staircases (three sessions) for group 2 were averaged and plotted as filled circles for the standard SF of 0.5 cpd. [It should be noted that some of the test SFs had sessions less than the maximum number of sessions of the group in Figs. 1 and 2.]

(2) Next, *find the contrast matching sensitivities at the test SF that is common to all groups*. At the common test SF of 1 cpd, the contrast matching sensitivity is 33 for group 1 and 22 for group 2.

(3) Then *normalize the contrast matching sensitivities of each staircase with respect to the respective contrast matching sensitivity (at common SF) obtained from step 2*. The contrast matching sensitivities of each staircase of group 1 is divided by 33 and that of group 2 by 22. For example, at the test SF of 0.0625 cpd, the normalized sensitivities are 0.56 (= 18.5/33) and 0.9 for group 1 (one session with two staircases) and 1.34 (= 29.4/22) and 1.56 for group 2 (one session, other two sessions did not have this test SF).

(4) *Find the average and standard error over staircass and groups (standard SFs) (i.e. over two × total number of sessions at each test SF) for the normalized data of step 3*. In the example of step 3, the total number of sessions is two (one for each group), $N = 2 \times 2$; the average sensitivity is 1.09, and its standard error (SE) is 0.22 ($N = 4$) at the test SF of 0.0625 cpd.

(5) Finally, *normalize the contrast matching sensitivities (mean and SE) of step 4 with respect to the contrast matching sensitivity at the desired test SF (here 0.0625 cpd). Plot the normalized contrast matching sensitivity as a function of test-SF*. The test SF, with respect to which the normalization is desired, is selected. Here, 0.0625 cpd is arbitrarily selected. The contrast matching sensitivities are then normalized with respect to the sensitivity at this test SF. For example, the normalized sensitivity is mean $\pm$ SE $= 1 \pm 0.2$ for the example of step 4. The normalized contrast matching sensitivities are plotted as a function of test SF in Fig. 3A (open circles) for 3.1% standard contrast. This CMF is a lowpass function of SF as judged (a) by visual inspection and (b) by t-tests: there are nine data-point pairs (greater than the criterion value of 5, suggested by a reviewer) relevant to test the lowpass behavior of this CMF; both elements of each pair are significantly different from each other,[1] indicating that this CMF is indeed lowpass function of SF.

References

Albrecht, D. G., & Hamilton, D. B. (1982). Striate cortex of monkey and cat: contrast response function. *Journal of Neurophysiology*, *48*, 217–237.

Albrecht, D. H., & Geisler, W. S. (1991). Motion selectivity and the contrast-response function of simple cells in the visual cortex. *Visual Neuroscience*, *7*, 531–546.

Arend, L. E., & Reeves (1986). Simultaneous color constancy. *Journal of the Optical Society of America A*, *3*, 1743–1751.

Bonds, A. B. (1989). Role of inhibition in the specification of orientation selectivity of cells in the cat striate cortex. *Visual Neuroscience*, *2*, 41–55.

Brainard, D. H., & Wandell, B. A. (1986). Analysis of the retinex theory of color vision. *Journal of the Optical Society of America A*, *3*, 1651–1661.

Boynton, R. M. (1973). Implication of the minimally distinct border. *Journal of the Optical Society of America*, *63*, 1037–1043.

Cannon, M. W., & Fullenkamp, S. C. (1988). Perceived contrast and stimulus size: experiment and simulation. *Vision Research*, *28*, 695–709.

[1] The table for bandwidths of CMFs (see Section 3.1) and cutt-off SFs (see the last paragraph on Section 3.2.2), and the summary figure (see the last paragraph of Section 3.2.2) are available upon email request to vimalram@hotmail.com.

Cannon, M. W., & Fullenkamp, S. C. (1991a). A transducer model for contrast perception. *Vision Research*, *31*, 983–998.

Cannon, M. W., & Fullenkamp, S. C. (1991b). Spatial interactions in apparent contrast: individual differences in enhancement and suppression effects. *Vision Research*, *33*, 1685–1695.

Cavanagh, P., MacLeod, D. I. A., & Anstis, S. M. (1987). Equiluminance: spatial and temporal factors and the contribution of blue-sensitive cones. *Journal of the Optical Society of America A*, *4*, 1428–1438.

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

Daw, N. A. (1984). The psychology and physiology of colour vision. *Trends in Neurosciences*, *September*, 330–335 and references therein.

De Valois, R. L., Snodderly, D. M., Yund, E. W., & Hepler, N. K. (1977). Responses of macaque lateral geniculate cells to luminance and color figures. *Sensory Process*, *1*(3), 244–259.

De Valois, R. L., & De Valois, K. K. (1993). A multi-stage color model. *Vision Research*, *33*, 1053–1065 and references therein.

Foley, J. M. (1994). Human luminance pattern-vision mechanisms: masking experiments require a new model. *Journal of the Optical Society of America A*, *11*, 1710–1719.

Foley, J. M., & Chen, C. C. (1997). Analysis of the effect of pattern adaptation on pattern pedestal effects: a two process model. *Vision Research*, *37*, 2779–2788.

Geisler, W. S., & Albrecht, D. G. (1992). Cortical neurons: isolation of contrast gain control. *Vision Research*, *32*, 1409–1410 and references therein.

Georgeson, M. A., & Sullivan, G. D. (1975). Contrast constancy: deblurring of human vision by spatial frequency channels. *Journal of Physiology* (*London*), *252*, 627–656.

Graham, N., & Sutter, A. (1998). Spatial summation in simple (Fourier) and complex (non-Fourier) texture channels. *Vision Research*, *38*, 231–257.

Heeger, D. J. (1992). Normalization of cell responses in cat visual cortex. *Vision Neuroscience*, *9*, 181–197 and references therein.

Jameson, D., & Hurvich, L. M. (1955). Some quantitative aspects of an opponent-color theory. I. Chromatic responses and spectral saturation. *Journal of the Optical Society of America*, *45*, 546–552.

Krauskopf, J., Williams, D. R., & Heeley, D. W. (1982). Cardinal directions of color space. *Vision Research*, *22*, 1123–1131.

Krauskopf, J., Zaidi, Q., & Mandler, M. B. (1986). Mechanisms of simultaneous color induction. *Journal of the Optical Society of America A*, *3*, 1752–1757.

Larimer, J., Kranz, D. H., & Cicerone, C. M. (1974). Opponent process additivity — I: red/green equilibria. *Vision Research*, *14*, 1127–1140.

Losada, M. A., & Mullen, K. T. (1994). The spatial tuning of chromatic mechanisms identified by simultaneous masking. *Vision Research*, *34*, 331–341.

Losada, M. A., & Mullen, K. T. (1995). Color and luminance spatial tuning estimated by noise masking in the absence of off-frequency looking. *Journal of the Optical Society of America A*, *12*, 250–260.

Marimont, D. H., & Wandell, B. A. (1994). Matching color images: the effects of axial chromatic aberration. *Journal of the Optical Society of America A*, *11*, 3113–3122.

McCann, J. J., McKee, S., & Taylor, T. (1976). Quantitative studies in retinex theory: a comparison between theoretical predictions and observer response 'color mondrian' experiments. *Vision Research*, *16*, 445–458.

Metha, A. B. B, Bex, P. J., & Makous, W. (1998). Contrast constancy requires discriminable spatial frequency content. *Investigative Ophthalmology and Visual Science* (*Supplement*), *39*(4), S424.

Michael, C. R. (1985). Laminar segregation of color cells in the monkey's striate cortex. *Vision Research*, *25*, 415–423.

Mollon, J. D. (1997). On the basis of velocity clues alone: some perceptual themes 1946–1996. *Quarterly Journal of Experimental Psychology*, *50A*(4), 859–878.

Mullen, K. T. (1985). The contrast sensitivity of human color vision to red–green and blue–yellow chromatic gratings. *Journal of Physiology (London) 359*, 381–400 and references therein.

Mullen, K. T., & Losada, M. A. (1994). Evidence for separate pathways for color and luminance detection mechanisms. *Journal of the Optical Society of America A*, *11*, 3136–3151.

Pandey, R., & Vimal, R. L. P. (1993). Threshold elevation curves for the red–green channel estimated by oblique masking. *Investigative Ophthalmology and Visual Science* (*Supplement*), *34*(4), 751.

Pandey, R., & Vimal, R. L. P. (1994). Spatial frequency tuned mechanisms of the red–green channel estimated by oblique masking. *Society for Neuroscience Abstracts*, *20*(Part 2), 1580.

Phillips, G. C., & Wilson, H. R. (1984). Orientation bandwidths of spatial mechanisms measured by masking. *Journal of the Optical Society of America A*, *1*, 226–232.

Poirson, A. B., & Wandell, B. A. (1993). Appearance of colored patterns: pattern-color separability. *Journal of the Optical Society of America A*, *10*, 2458–2470.

Powell, I. (1981). Lenses for correcting chromatic aberration of the eye. *Applied Optics*, *20*, 4152–4155.

Sclar, G., & Freeman, R. D. (1982). Orientation selectivity in the cat's striate cortex is invariant with stimulus contrast. *Experimental Brain Research*, *46*, 457–461.

Shapley, R. (1986). The importance of contrast for the activity of single neurons, the VEP and perception. *Vision Research*, *26*, 45–61.

Shapley, R. M., & Enroth-Cugell, C. (1984). Visual adaptation and retinal gain controls. *Progress in Retinal Research*, *3*, 263–346.

Shapley, R., & Reid, C. (1985). Contrast and assimilation in the perception of brightness. *Proceeding of National Academy of Science USA*, *82*, 5983–5986.

Shapley, R. M., & Victor, J. D. (1979). The contrast gain control of the cat retina. *Vision Research*, *19*, 431–434.

Shapley, R. M., & Victor, J. D. (1981). How the contrast gain control modifies the frequency responses of cat retinal ganglion cells. *Journal of Physiology* (*London*), *318*, 161–179.

Shevell, S. K., & Knoblauch, K. (1998). Red/green and yellow/blue equilibrium hues measured in LMS space: from linearity to non-monotonicity. *Investigative Ophthalmology and Visual Science (Supplement) 39*, S3 (Abstract No. 14).

Stromeyer, C. F., Gowdy, P. D., Chaparro, A., & Kronauer, R. E. (1999). Second-site adaptation in the red-green detection pathway: only elicited by low-spatial-frequency test stimuli. *Vision Research*, *39*, 3011–3023.

Swanson, W. H., Georgeson, M. A., & Wilson, H. R. (1988). Comparison of contrast responses across spatial mechanisms. *Vision Research*, *28*, 457–459.

Swanson, W. H., Wilson, H. R., & Geise, S. C. (1984). Contrast matching data predicted from contrast increment thresholds. *Vision Research*, *24*, 63–75.

Swanson, W. H., & Wilson, H. R. (1985). Eccentricity dependence of contrast matching and oblique masking. *Vision Research*, *25*, 285–295.

Switkes, E., Bradley, A., & De Valois, K. K. (1988). Contrast dependence and mechanisms of masking interactions among chromatic and luminance gratings. *Journal of the Optical Society of America A*, *5*, 1149–1162.

Ts'o, D. Y., & Gilbert, C. D. (1988). The organization of chromatic and spatial interaction in the primate striate cortex. *Journal of Neuroscience*, *8*, 1712–1727.

Vimal, R. L. P. (1997). Orientation tuning of the spatial-frequency-tuned mechanisms of the red-green channel. *Journal of the Optical Society of America A*, *14*, 2622–2632.

Vimal, R. L. P. (1998a). Spatial-frequency tuning of sustained nonoriented units of the red–green channel. *Journal of the Optical Society of America A*, *15*, 1–15.

Vimal, R. L. P. (1998b). Color-luminance interaction: data produced by oblique cross masking. *Journal of the Optical Society of America A*, *15*, 1756–1766.

Vimal, R. L. P., & Pandey, R. (1993). Contrast matching in the red–green channel: flattening effect and color-contrast-constancy. *Society for Neuroscience Abstracts*, *19*, 1802.

Vimal, R. L. P., Pokorny, J. M., Smith, V. C., & Shevell, S. K. (1989). Foveal cone thresholds. *Vision Research*, *29*, 61–78.

Wandell, B. A., & Marimont, D. H. (1992). Axial chromatic aberration and cone-isolation. *Investigative Ophthalmology and Visual Science* (*Supplement*), *33*, 770.

Welkowitz, J., Ewen, R. B., & Cohen, J. (1976). *Introductory statistics for the behavioral sciences* (pp. 304–307). New York: Academic Press.

Werner, J. S., & Wooten, B. R. (1979). Opponent chromatic mechanisms: relation to photopigments and hue naming. *Journal of the Optical Society of America*, *69*, 422–434.

Wilson, H. R. (1980). A transducer function for threshold and suprathreshold human vision. *Biological Cybernetics*, *38*, 171–178.

Wilson, H. R., & Kim, J. (1998). Dynamics of a divisive gain control in human vision. *Vision Research*, *38*, 2735–2741.

Wilson, H. R., McFarlane, D. K., & Phillips, G. C. (1983). Spatial frequency tuning of orientation selective units estimated by oblique masking. *Vision Research*, *23*, 873–882.