Effect of overlaid luminance contrast on perceived color contrast: Shadows enhance, borders suppress

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Natural scenes contain both color and luminance variations at different sizes and orientations that are sometimes spatially overlaid and sometimes not. Here, we explore visual interactions between overlaid color and luminance contrast that are both suprathreshold and highly visible. We used a color-luminance plaid in which the perception of the color contrast and luminance contrast components were measured separately using a method of constant stimuli, to reveal how overlaid cross-oriented luminance contrast affects perceived color contrast, and how color contrast affects perceived luminance contrast. Binocular, monocular, and dichoptic viewing conditions were used for different spatial frequencies (0.375–1.5 cpd, 2 Hz) and base contrasts. We find that overlaid, cross-oriented luminance contrast enhances perceived color contrast by an average of 32% (monocularly and binocularly) across a wide range of luminance contrasts, but interocularly suppresses color contrast. For the reverse condition, we found no effect of color contrast on perceived luminance contrast. If, however, the cross-oriented arrangement is changed to co-oriented, specifically with the color and luminance borders aligned and in-phase, the color enhancement disappears and becomes mild suppression. Likewise, if the phase of the co-aligned components is varied, color enhancement returns once the color and luminance borders are misaligned and out of phase. Thus the relative position of the color and luminance borders is a crucial factor in determining the type of interaction, with color suppression occurring when the luminance and color borders coincide, as when demarcating an object boundary, and color enhancement when they do not coincide, as occurs in shadows and shading.

Introduction

Natural scenes contain both color and luminance contrast at different spatial scales and orientations that are sometimes spatially overlaid and sometimes not. Hence, the study of the interactions between the visual response to color and luminance contrast is fundamental to the understanding of visual processing under natural conditions. These interactions have been investigated extensively. The consensus of these studies is that, at very low contrasts near detection threshold, responses to color and luminance behave independently and are attributable to separable neural processes. Support for this comes from studies showing that responses to color and luminance contrast do not summate at detection threshold (Chaparro, Stromeyer, Kroneauer, & Eskew, 1994; Cole, Hine, & McIlhagga, 1993; Eskew, McLellan, & Giulianini, 1999; Mullen, Cropper, & Losada, 1997; Mullen & Sankeralli, 1999; Sankeralli & Mullen, 1996; Stromeyer, Cole, & Kronauer, 1985). Masking experiments determine the effect of a suprathreshold mask on the detection of a test stimulus and have revealed some complex interactions. The most consistent effect is the facilitation of color detection by luminance contrast masks. This typically occurs over a wide range of contrasts, particularly for stimuli of low spatial and temporal frequency, and has been demonstrated using a wide array of suprathreshold luminance masks, including co-aligned gratings (Chen, Foley, & Brainard, 2000a; Gowdy, Stromeyer, & Kronauer, 1999; Mullen & Losada, 1994; Switkes, Bradley, & DeValois, 1988), cross-oriented gratings (Mullen, Kim, & Gheiratmand, 2014), noise masks (Gegenfurtner & Kiper, 1992; Giulianini & Eskew, 1998; Sankeralli & Mullen, 1997), as well as pedestals and rings (Cole et al., 1990; Eskew, Stromeyer, Picotte, & Kronauer, 1991). This effect has been interpreted as an interaction between separate color and luminance mechanisms (Chen et al., 2000a, 2000b; Mullen & Losada, 1994; Switkes et al., 1988) rather than a direct combination of color and luminance contrast (Chen et al., 2000a, 2000b; Mullen

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& Losada, 1994; Switkes et al., 1988). The reverse effect, facilitation of luminance detection by a color mask, is typically weaker or absent (Chen et al., 2000a, 2000b; Gegenfurtner & Kiper, 1992; Giulianini & Eskew, 1998; Gowdy et al., 1999; Losada & Mullen, 1995; Mullen & Losada, 1994; Switkes et al., 1988).

A very different picture emerges when both contrasts are suprathreshold and highly visible, with wide-ranging examples of interactions between color and luminance contrast arising from many different stimulus arrangements. A large body of work comes from studies that show the effects of surrounds on test stimuli, either luminance surrounds on color appearance (Bimler, Paramei, & Izmailov, 2009; Shevell & Kingdom, 2008; Xing et al., 2015), or color induction in a central achromatic test with different colored surrounds (Brown & MacLeod, 1997; Gordon & Shapley, 2006). Xing et al. (2015) systematically measured the effect of luminance surrounds on the perceived saturation of a colored test patch and found that the luminance contrast of the border reduced perceived color saturation. While this study was on the effect of luminance surrounds, because the color and luminance borders are coincidental, it is difficult to distinguish between the effect of overlaid versus surround contrasts. At least for luminance contrast masking, overlaid and surround contrasts typically have different effects (Petrov, Carandini, & McKee, 2005).

Here we investigate suprathreshold interactions between overlaid color and luminance contrasts. We first use cross-oriented color and luminance Gabor stimuli overlaid to form a plaid to reveal how suprathreshold luminance contrast affects perceived color contrast and vice versa. The cross-orientation format is thought to target "cross channel" interactions at a cortical level because different orientation-tuned mechanisms respond to each stimulus (Bonds, 1989; Carandini & Heeger, 2012; Foley, 1994; Geisler & Albrecht, 1992; Heeger, 1992; Holmes & Meese, 2004; Meese & Hess, 2004; Meier & Carandini, 2002; Petrov et al., 2005). We directly compare the two effects within the same stimulus—luminance contrast on perceived color contrast and color contrast on perceived luminance contrast—by measuring contrast matches to either the color or the luminance components of the plaid. We go on to compare cross-oriented interactions with those for co-oriented stimuli, and the role of co-aligned versus misaligned borders on color-luminance contrast interactions.

Our findings reveal an interesting asymmetry. While perceived luminance contrast is unaffected by color contrast for all conditions, perceived color contrast is enhanced by cross-oriented luminance contrast. This color enhancement disappears and becomes mild suppression when the stimulus is changed from cross-oriented to co-oriented with the color and luminance borders aligned and in phase. Hence color enhancement only occurs when the color and luminance borders do not coincide, revealing the importance of relative border position. Superimposed luminance and color contrast without co-alignment commonly occurs in natural scenes when shadows or shading fall on a colored surface, whereas co-aligned color and luminance borders are indicative of object and material boundaries, suggesting these two situations activate different color-luminance interactions.

Methods

Apparatus

Stimuli were generated using a ViSaGe videographic card (Cambridge Research Systems, Kent, UK) with 14-bit contrast resolution and presented on a Sony Trinitron (GDM 500DIS) monitor (Sony Corporation, Tokyo, Japan) at 120-Hz frame rate and 1024×768 spatial resolution. The monitor was gamma corrected and calibrated as described previously (Kim, Gheiratmand, & Mullen, 2013). The background was achromatic with a mean luminance of 51 cd/m^2 at the screen center. Stimuli were viewed at a distance of 58 cm in a dimly lit room, with a mirror stereoscope for the dichoptic and monocular conditions and without for the binocular condition. Chromatic and achromatic stimuli were controlled independently by lookup tables, and stimuli were overlaid by interlacing with frame-by-frame cycling.

Observers

Nine subjects participated in the study, including one author (YJK) and eight naive subjects (CK, SH, JWZ, IO, AR, HCS, YSW, and BJ). All subjects had normal or corrected-to-normal visual acuity and normal color vision. The experiments were performed in accordance with the Declaration of Helsinki and approved by the institutional ethics committee of McGill University Health Center. Each subject signed an informed consent form.

Color space

Stimuli were represented in a three-dimensional cone-contrast space (Cole et al., 1993; Sankeralli & Mullen, 1996) in which each axis is defined by the contrast of the stimulus to each cone type. The calibration of this space has been described previously (Kim et al., 2013). Stimulus contrast is defined as the vector length in cone contrast units (C_C):

$$C_c = \sqrt{(L_C)^2 + (M_C)^2 + (S_C)^2} \quad (1)$$

where L_c, M_c, and S_c represent the L, M, and S Weber cone-contrast fractions in relation to the L, M, and S cone values of the achromatic background. The isoluminant point for the red-green (RG) mechanism was estimated by a minimum motion task for each observer and for each spatial frequency.

Stimuli and experiments

All stimuli were Gabors (phase = 0) with a Gaussian envelope scaled to a fixed space constant ($\sigma = 2°$), sinusoidally modulated at 2 Hz and presented in a Gaussian temporal envelope ($\sigma = 125$ ms) within a time window of 500 ms. Experiments 1 and 2 used cross-oriented plaid stimuli that combine color and luminance components (see Figure 1). In Experiment 1, we measured the perceived contrast of the color component in the presence of the luminance component. The test stimulus was the horizontal isoluminant RG component Gabor overlaid by the orthogonal luminance Gabor (termed the "mask"; Figure 1a, right column). The subject made a contrast match of the color test to a variable reference stimulus, which was a horizontal RG isoluminant Gabor presented alone (Figure 1a, left column). In Experiment 2, we measured perceived contrast of the luminance component in the presence of the color component. The test stimulus was the horizontal luminance component of the plaid viewed in the presence of an overlaid vertical color component (the mask; Figure 1b, right column). For the luminance contrast matching experiment, the variable reference stimulus was a horizontal luminance Gabor presented alone (Figure 1b, left column). Reference and test stimuli both have the same spatiotemporal frequency and phase.

Three different spatial frequencies were used in the color matching experiment (0.375, 0.75, and 1.5 cpd) and two in the luminance matching experiment (0.375 and 1.5 cpd). Contrast is expressed in multiples of detection threshold for the Gabor stimuli presented alone (unmasked). The test and reference stimuli were presented under binocular, monocular (right eye), and dichoptic conditions. In the dichoptic condition, the test and reference stimulus of the same contrast type were presented to the right eye and the mask of a different contrast type to the left eye (e.g., color test and color reference to the right eye and luminance mask to the left eye).

In Experiment 3, we varied the orientation of the luminance mask component relative to a horizontal color test component and measured the effect on perceived color contrast. This was tested at five different relative orientations of the luminance mask from 0° (horizontal) to 90° (vertical) and using two opposite phases. This experiment was run for binocular viewing at a low spatial frequency (0.375 cpd, at 2 Hz) stimulus only.

In Experiment 4, we use overlaid, co-oriented color and luminance gratings and determined the effect of the relative spatial phase between component gratings on perceived color and luminance contrast. Eight relative spatial phases (0, ±45°, ±90°, ±135°, and 180°) were tested. A relative phase of 0° indicates that the red bars overlay the light bars, and green bars overlay the dark bars, with 180° as the reverse. The experiment was run for binocular viewing at the low spatial frequency (0.375 cpd, at 2 Hz) only. For color contrast matching, the subject adjusted a RG Gabor to match the perceived color contrast of the co-aligned color and luminance stimulus. For luminance contrast matching, the subject adjusted a luminance Gabor to match the perceived luminance contrast.

Procedure

For the contrast matching we used a two-interval forced-choice method of constant stimuli to find a point of subjective equality (PSE) between the reference Gabor presented alone and the test Gabor presented as a component of the plaid. In one interval, the reference stimulus was presented at one of six possible contrast levels and in the other interval the test stimulus appeared as part of the plaid. Each temporal interval was 500 ms with a 400 ms interstimulus interval. The subject's task was to indicate with a button-press which interval contained the higher contrast stimulus. If the task was a color matching task, both test and reference stimuli were chromatic and the subject was instructed to match the color contrast in the color-luminance plaid. Likewise, if the task was a luminance matching task, both test and reference stimuli were achromatic and the subject was instructed to match the luminance contrast in the color-luminance plaid. There was no feedback. In the matching task, each contrast level of the test was presented 80–100 times. Data were fitted with a logistic psychometric function described below (Kingdom & Prins, 2010), which plots the probability of choosing the reference stimulus as having the higher contrast than the test as a function of the actual reference contrast, with the 50% point taken as the PSE.

$$F_L(x; \alpha; \beta) = \frac{1}{1 + \exp\Big(-\beta(x - \alpha)\Big)} \quad (2)$$

Here x is the logarithm of reference contrast, α is the PSE, and β is the slope of the function. The fitting

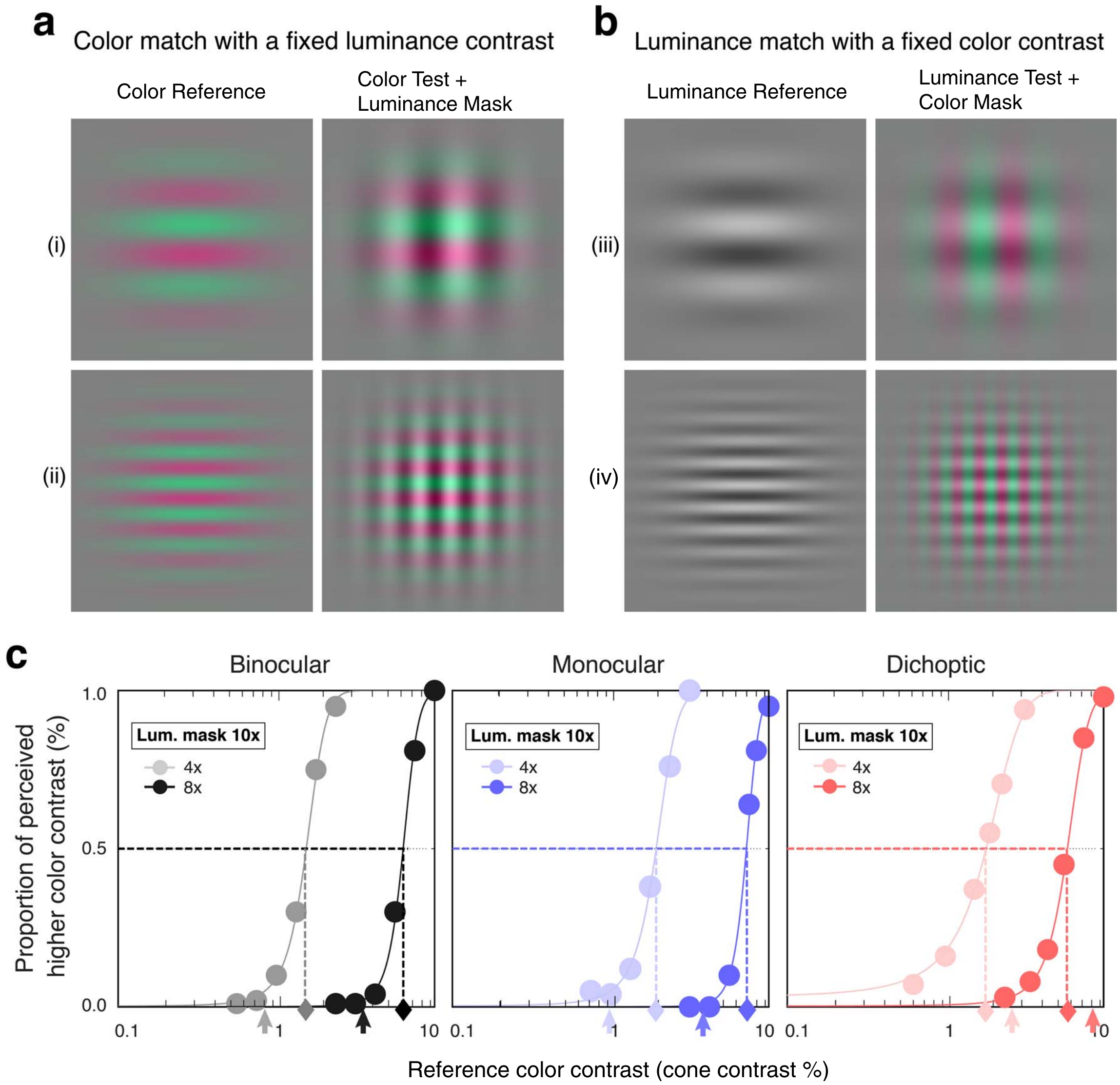

Figure 1. Examples of the test and plaid stimuli used in the contrast matching experiments. (a) In the color matching experiment, a color reference stimulus presented alone (a, left column) is matched to a color test stimulus overlaid by a cross-oriented luminance mask that together form a plaid (a, right column). (b) In the luminance matching experiment, a luminance reference stimulus (b, left column) presented alone is matched to a luminance test stimulus overlaid by a cross-oriented color contrast mask, together forming a plaid (b, right column). A low spatial frequency (0.375 cpd) is shown in Examples i and iii, a midspatial frequency (0.75 cpd) in ii, and a higher spatial frequency (1.5 cpd) in iv. (c) Three examples of plots of data for a color-contrast matching experiment done under binocular (left), monocular (middle), and dichoptic (right) viewing conditions. The contrast of the color reference stimulus varies from trial to trial as indicated on the abscissa. In these examples, the luminance mask contrast is fixed at 10× detection threshold and the different curves indicate different contrasts of the color test (4× and 8× detection threshold). Data are fitted with a logistic function (solid line) showing the probability that the color reference stimulus is chosen to have a greater color contrast than the color test in the plaid (see Methods). The reference contrast corresponding to 50% probability is the PSE, indicated by filled diamonds on the *x*-axis. The test color contrast is denoted by arrows on the *x*-axis.

procedure used a maximum likelihood criterion and the errors on the PSE and slope free parameters were estimated by parametric bootstrap analysis. Example psychometric functions are shown in Figure 1c. Color contrast matching was done in Experiments 1, 3, and 4 and luminance contrast matching was done in Experiments 2 and 4.

We evaluated the effect of the mask on perceived contrast by taking the ratio of the reference contrast at the PSE to the corresponding test contrast used in the matching experiment. Ratios above 1.0 indicate enhancement of perceived contrast by the overlaid mask, since physically a higher test contrast is needed to match the reference. Conversely, ratios below 1.0

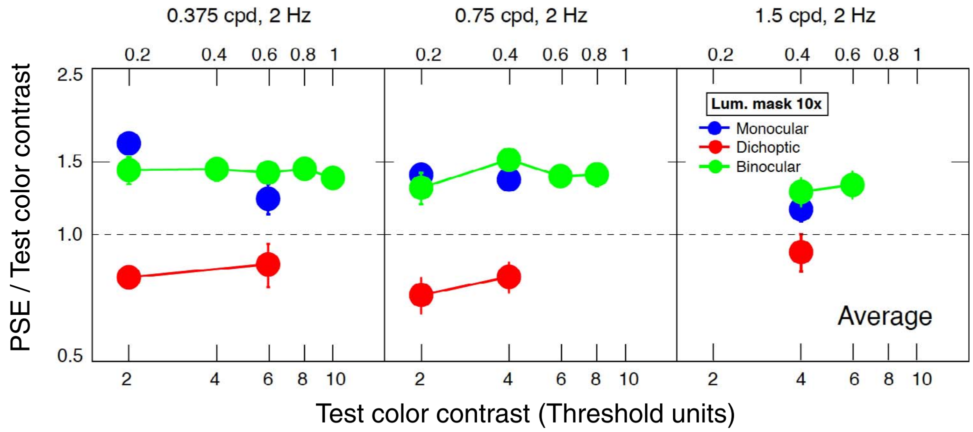

Figure 2. Perceived color contrast in the presence of fixed luminance contrast. The matched color contrast, expressed as the ratio of the PSE to the corresponding test color contrast, is plotted as a function of the test color contrasts (i.e., 2×, 4×, 6×, 8×, or 10× detection threshold). The contrast of the luminance mask is 10× detection threshold. The upper *x*-axis shows the contrast ratio of the color test/luminance mask. Results are for three viewing conditions: binocular (green symbols), monocular (blue symbols), and dichoptic (red symbols). Binocular results are the average of five subjects (CK, YJK, IO, SH, and JWZ); monocular and dichoptic results are the average of four (YJK, IO, SH, and JWZ). Individual subject data are shown in Figure 3. Each column shows results for the three spatial frequencies (0.375, 0.75, and 1.5 cpd). Ratios greater than 1.0 indicate enhancement of perceived color contrast by the cross-oriented luminance contrast mask and ratios below 1.0 indicate suppression of perceived color contrast. Error bars are ±1 *SE* of the group mean.

indicate suppression of perceived contrast by the mask.

Results

Experiment 1: Perceived color contrast in the presence of fixed luminance contrast

Figure 2 shows how overlaid cross-oriented luminance contrast affects perceived color contrast. The luminance contrast was fixed at (10× threshold) and the color contrast match made to five different test color contrasts (2×, 4×, 6×, 8×, and 10× detection threshold). Binocular (green symbols), monocular (blue symbols), and dichoptic (red symbols) viewing conditions are shown for three spatial frequencies (0.375, 0.75, and 1.5 cpd). Results are averaged across subjects with the data for individual subjects shown in Figure 3. (Individual psychometric functions are shown in Supplementary Figures S1 and S2a, b). For the binocular and monocular viewing conditions, the perceived color contrast is enhanced in the presence of the luminance contrast, with the proportional increase (the ratio of the PSE color match to the corresponding test color contrast) constant across test color contrast. Ratios are significantly greater than 1.00 across test color contrast, spatial frequency, and for both binocular, $t(67) = 9.312$, $p = 0.000$, and monocular conditions, $t(23) = 7.586$, $p = 0.000$, with an averaged ratio of 1.32 (±0.11 *SD*). Hence the cross-oriented luminance contrast enhances the perceived color contrast by 32%. The effects are similar for all spatial frequencies, although data at the higher test contrasts could not be collected for the spatial frequency of 1.5 cpd as the maximum contrast of the display was reached. In comparison, for the dichoptic viewing conditions, suppression occurred with the averaged ratio (0.87) significantly less than 1.00 across all test color contrasts and spatial frequencies, $t(23) = -4.523$, $p = 0.000$. With respect to spatial frequency, no significant effect was observed across the viewing conditions in Figure 3. We conclude that the overlaid, cross-oriented luminance contrast enhances perceived color contrast under binocular and monocular conditions, but causes suppression when presented dichoptically.

In the next experiment, we evaluate the effect of the luminance mask contrast on the enhancement of color contrast. We measure the color contrast match for one color test contrast (6× threshold) over a range of luminance mask contrasts (2.5×, 5×, 10×, and 20× threshold). This experiment addresses the possibility that the subjects may be matching the overall contrast of the color-luminance plaid to the color test, rather than the contrast of the color component alone. Figure 4a plots the color contrast match made to the test color contrast as a function of luminance mask contrast for four subjects. The ratios across different luminance contrasts are significantly greater than 1.00 for the binocular, $t(15) = 12.297$, $p = 0.000$, and monocular, $t(15) = 11.824$, $p = 0.000$, conditions and are constant as a function of the luminance mask contrast. The

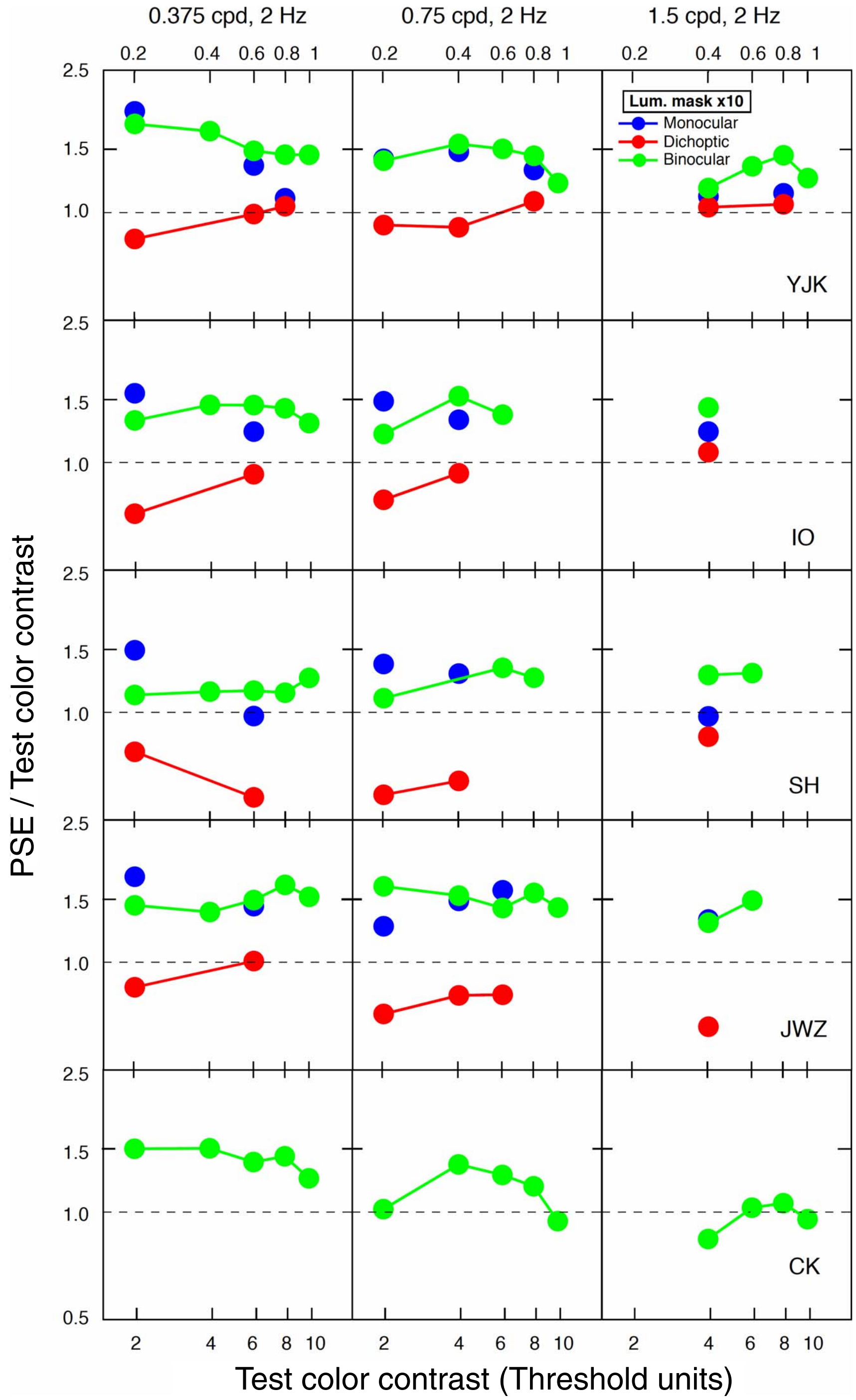

Figure 3. Individual data for the five subjects used to calculate the average in Figure 2. All symbols are as for Figure 2. Error bars are calculated as the ratio of each subject's mean standard error derived by bootstrap analysis and its corresponding reference color contrast.

averaged ratio is 1.28, similar to that obtained previously for the luminance mask contrast of 10× threshold (Figure 2). The fact that the degree of color contrast enhancement is unaffected by the magnitude of the luminance contrast is interesting and suggests that the subject is not perceptually combining the luminance and color contrasts of the plaid to make an overall contrast match. Figure 4b shows the individual psychometric functions that emphasize this point. For the monocular and binocular conditions, the psychometric functions overlap across the different luminance mask contrasts, indicating that the color enhancement (28%) produced by the cross-oriented luminance mask is not dependent on the mask contrast. For the

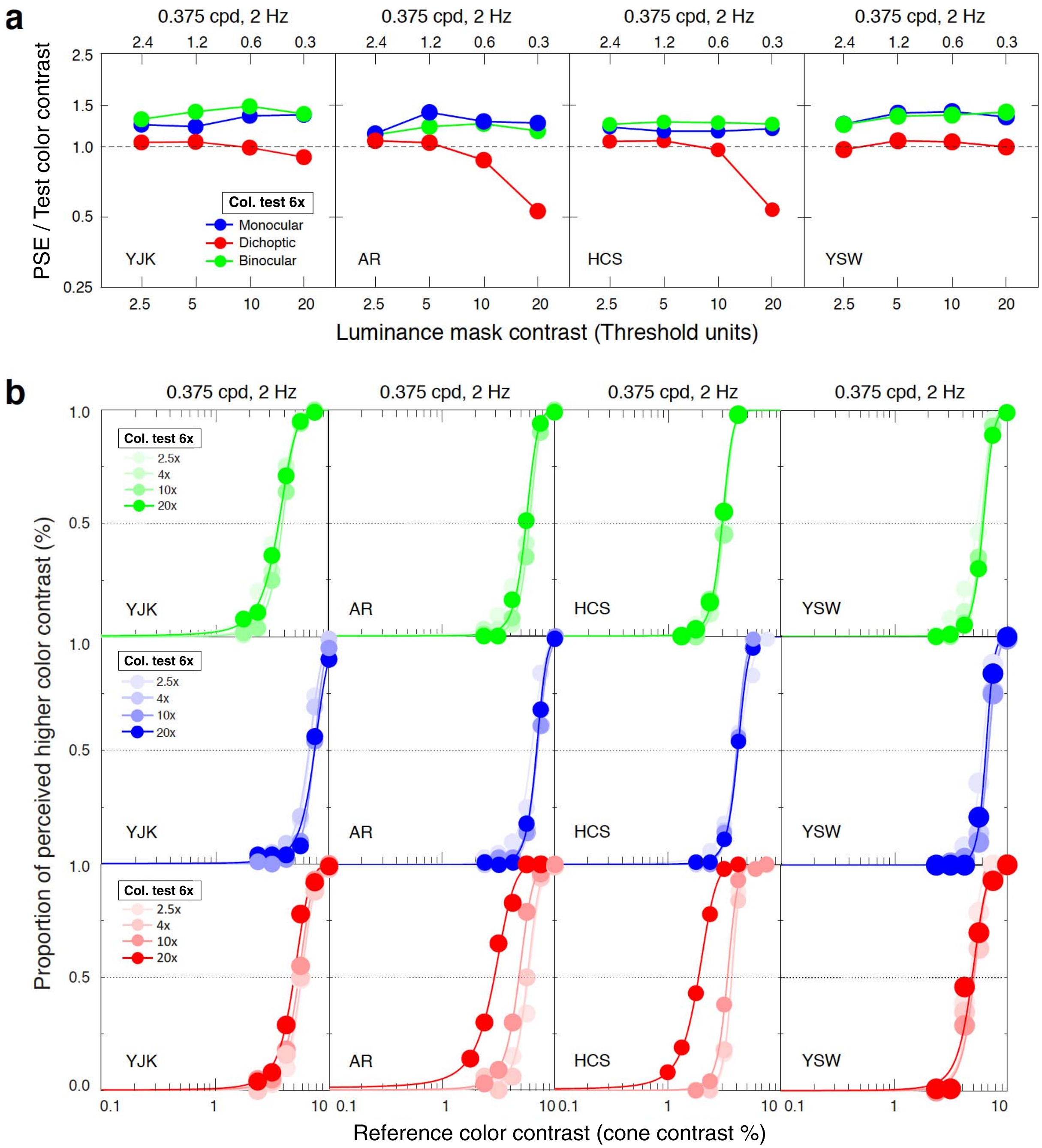

Figure 4. Perceived color contrast in the presence of different luminance contrasts. (a) Matched color contrast is plotted as a function of luminance mask contrast (2.5×, 5×, 10×, and 20× detection thresholds) for one color test contrast (6× detection threshold). Results are for one spatial frequency (0.375 cpd). The upper *x*-axis shows the contrast ratio of the color test/luminance mask. Individual data (YJK, AR, HCS, and YSW) are shown. All symbols and error bars are as for Figure 2. (b) Psychometric functions for the individual data points shown in (a). Error bars are standard errors derived by bootstrap analysis. Error bars are smaller than the symbol.

dichoptic viewing conditions, little effect was observed (Figure 4a, b), although some masking is evident for two subjects at the highest luminance contrasts used.

Figure 5 plots the color contrast enhancement found across all the color to luminance contrast ratios in the plaid (color test contrast/luminance mask contrast). Results are shown for the low spatial frequency (0.375 cpd). This figure confirms that the presence of the cross-oriented luminance contrast enhances perceived color contrast in a fixed proportion to the color test that is constant across a wide range of color and luminance contrasts. The average enhancement for this figure is 1.35 (±0.12 *SD*). Furthermore, results show that the color enhancement

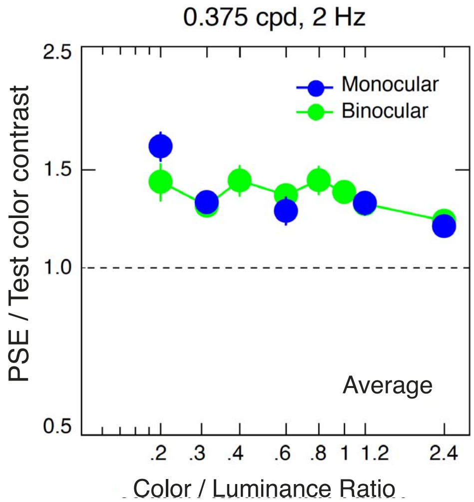

Figure 5. Color enhancement across color/luminance contrast ratios in the plaid. Averaged matched color contrasts replotted as a function of the ratio of test color contrast to luminance mask contrast using the data from Figures 2 through 4 for the low spatial frequency (0.375 cpd). The average ratio across all data points is 1.35 (±0.12 *SD*). Error bars are ±1 *SE* of the group mean.

is very similar for monocular and binocular conditions.

Experiment 2: Perceived luminance contrast in the presence of fixed color contrast

In this section we investigate the effect of color contrast on perceived luminance contrast. Figure 6 shows the luminance contrast match made to different test luminance contrasts (2.5×, 5×, 10×, and 20× detection threshold) in the presence of a color contrast mask (6× threshold). The luminance contrast match is expressed as the ratio of the perceived luminance contrast (PSE) to its corresponding test luminance contrast. Results are for two spatial frequencies (0.375 and 1.5 cpd) for three subjects (YJK, AR, and BJ) with the average of three subjects shown in the top row. (Individual psychometric functions are shown in Supplementary Figure S3a, b). The averaged data show that there is no systematic effect of the color contrast on perceived luminance contrast. Even though there was some tendency to suppression in the binocular data of one subject (YJK), this was not apparent in her monocular results. The luminance contrast matching ratio averaged across the three viewing conditions and two spatial frequencies is 0.99 (±0.07 *SD*), showing neither enhancement nor suppression. We note that similar color/luminance contrast ratios were tested in both the color-matching and luminance-matching experiments.

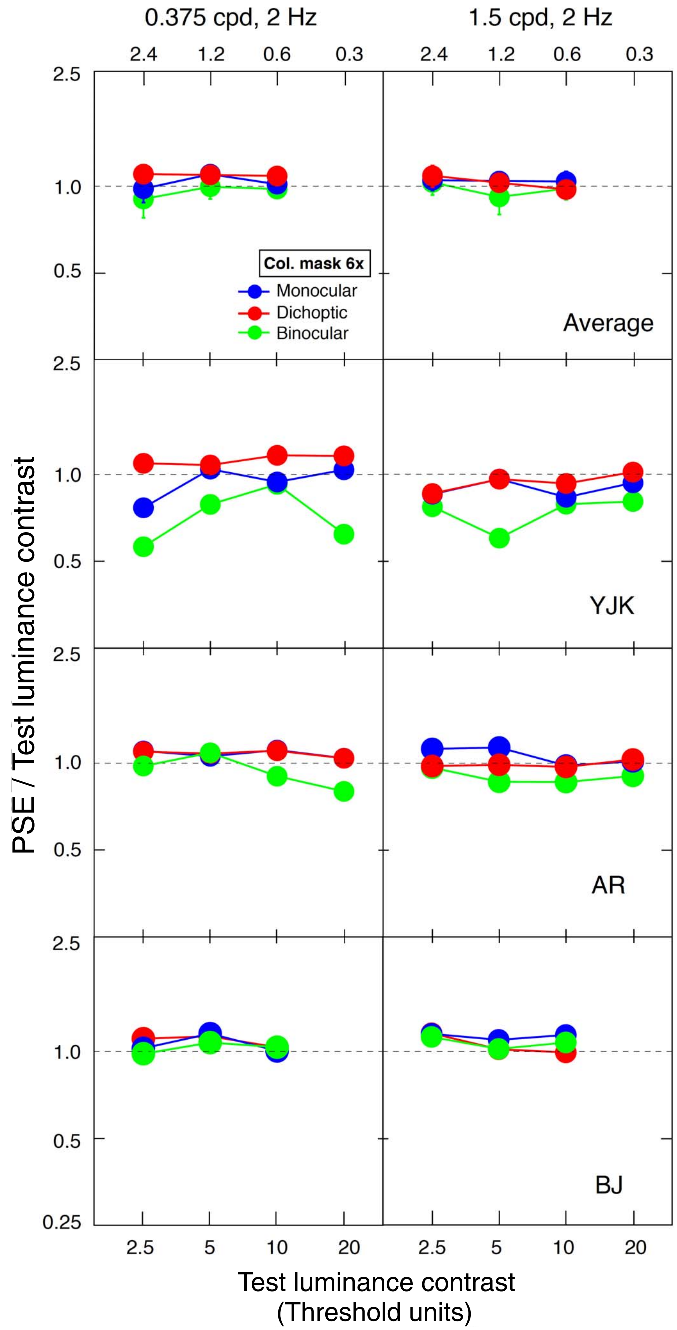

Figure 6. Perceived luminance contrast in the presence of fixed color contrast. Matched luminance contrast, expressed as a ratio of perceived contrast (PSE) and its corresponding test luminance contrast, is plotted as a function of the test luminance contrast (2.5×, 5×, 10×, and 20× detection threshold). The contrast of the color mask is 6× detection threshold. The upper *x*-axis shows the contrast ratio of the color mask/luminance test. Each column shows results for a different spatial frequency (0.375 and 1.5 cpd). The top row shows the average of the three subjects (±1 *SE*) whose data are in the rows below (YJK, AR, and BJ). Individual error bars and symbols are as for Figure 2.

In the next two experiments we investigate the role of the relative color and luminance border positions on color contrast enhancement by evaluating the effect of the orientation difference between the color and luminance component gratings from cross-oriented to co-oriented (Experiment 3) and the effect of spatial phase on the co-oriented condition (Experiment 4).

Experiment 3: The effect of relative orientation on color contrast enhancement

Figure 7 shows the effect on perceived color contrast of varying the relative orientation of the luminance mask from cross-oriented (90°) to co-oriented (0°). One fixed color test contrast (11× detection) with one luminance mask (4× detection) contrast was used for the low spatial frequency stimulus (0.375 cpd) with binocular viewing. Two phases of co-aligned color and luminance contrast combinations were used (0° and 180°, see legend). Results are for three subjects (YJK, AR, and HCS) with their average in the top left panel. There is a significant effect of the luminance mask orientation on color contrast enhancement, with enhancement decreasing from 1.30 (±0.12 *SD*) for the cross-oriented mask to weak suppression (0.91 ± 0.14 *SD*) for the co-oriented and co-aligned mask averaged across both phases.

To determine the orientation tuning bandwidth, the data were fitted with a Gaussian function (solid lines, see legend). This provided a good fit, capturing the dependence of perceived color contrast on luminance mask orientation and accounting for 84% ± 9% ($n = 3$) of the variance of the data. The Gaussian tuning curve has a half-bandwidth of 51° averaged across left and right sides and across three subjects. This experiment shows that the color contrast enhancement by luminance contrast is specific to the cross-oriented arrangement of the stimuli. The result suggests that, as the luminance and color contrast borders become increasingly overlaid and coincidental, the color contrast enhancement is reduced and converts to mild suppression for co-oriented stimuli.

Experiment 4: The effect of relative phase on color contrast enhancement

Figure 8a shows the effect on perceived color contrast of varying the relative spatial phase for co-oriented color and luminance contrasts. One fixed color test contrast (10× detection) with one luminance mask (4× detection) contrast was used for the low spatial frequency stimulus (0.375 cpd) with binocular viewing. Perceived color contrast is plotted as a function of the relative spatial phase of the co-oriented color and luminance gratings using a polar plot. Results are the average of four subjects (YJK, AR, HCS, and YSW). (Individual data are shown in Supplementary Figure S4a, b). There is a significant effect of the relative spatial phase of the co-oriented luminance mask on color contrast enhancement, $F(8, 27) = 5.552$, $p = 0.001$. Enhancement decreases from a factor of 1.24 (±0.11 *SD*) when the color and luminance stimuli are out of phase (90° and 270°) and becomes weak suppression (0.92 ± 0.13 *SD*) for stimuli that are co-aligned in-phase (0° and 180°). This effect is significant, $t(7) = 4.060$, $p = 0.005$, and shows that color enhancement is greatest when the luminance contrast borders are located in the middle of a red or green bar (90° and 270° phases), but is lost and becomes mild suppression when color and the luminance borders co-align (0° and 180° phases).

Figure 8b shows the effect of relative spatial phase on perceived luminance contrast. A luminance contrast match is made to a luminance test contrast (10× threshold) in the presence of a color contrast mask (6× threshold) and results are plotted as a function of the relative spatial phase of the co-oriented color and luminance contrast. Data are the average of two subjects (YJK and AR). Results show that perceived luminance contrast is not dependent on the relative spatial phase, $F(8, 9) = 0.409$, $p = 0.888$, with an average contrast matching ratio of 0.96 (±0.04 *SD*). This demonstrates that the lack of an effect of a cross-oriented color mask on perceived luminance contrast seems to generalize to co-oriented stimuli and across all spatial phases.

Control condition

In order to test for a possible effect of temporal frequency on color enhancement, we added a control condition in which we replaced the sinusoidal temporal modulation of the Gabor (2 Hz) with a static stimulus within the same Gaussian temporal envelope. We repeated the color contrast match for one condition (color test contrast of 6× detection threshold with luminance mask contrast of 10× detection threshold). Results for the control condition and the corresponding original condition (shown in Figure 4a) are plotted in Supplementary Figure S5. The results for control condition are no different from the original, indicating that the temporal modulation is not a critical factor in the color contrast enhancement. The modulation at 2 Hz is useful, however, in preventing any color after-images. Interestingly, at detection threshold color facilitation by luminance contrast has been shown to have a relatively rapid time course (figure 4 from Kim & Mullen, 2015).

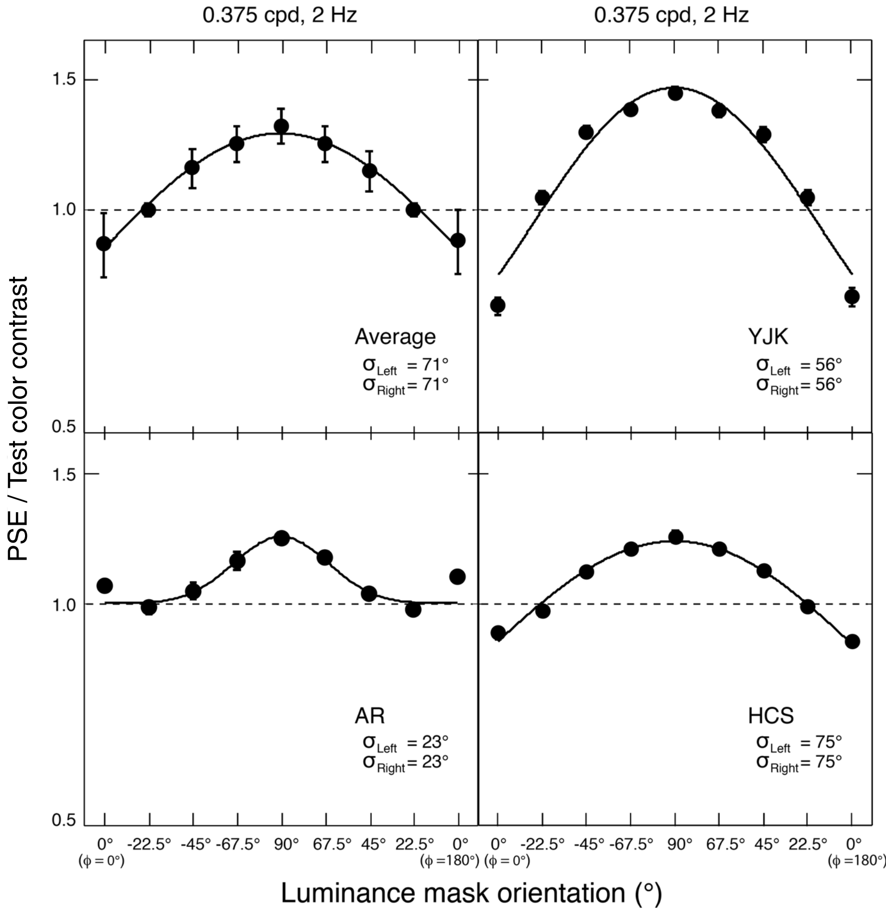

Figure 7. The effect of relative luminance mask orientation on perceived color contrast. Matched color contrast plotted as a function of the relative luminance mask orientation from cross-oriented (90°) to co-oriented and co-aligned (0°). Two opposite phases of color-luminance stimulus combination are used for the co-oriented stimuli: A relative phase of 0° indicates that red overlays the light bars and green overlays the dark bars, and a phase of 180° indicates red overlays the dark bars and green overlays the light bars. A relative phase of 0° used for all other orientations. Stimuli are low spatial frequency (0.375 cpd) and binocular. The color test is 11× threshold and the luminance mask is 4× detection threshold. Average results of the three subjects (YJK, AR, and HCS) is shown in the top left panel and individual data are shown in the three remaining panels. Error bars are calculated as in Figure 2. The data are fitted with the Gaussian function (solid lines) with five parameters (m, σ_{Left}, σ_{Right}, p, and d), given as follows:

$$G_1 = m * \exp\left(-0.5 * \left(\frac{o-p}{\sigma_{\text{Left}}}\right)^2\right)$$

$$G_2 = m * \exp\left(-0.5 * \left(\frac{o-p}{\sigma_{\text{Right}}}\right)^2\right)$$

$$G = G_1 * (o < p) + G_2 * (o \geq p) + d$$

where o is mask orientation. m is amplitude, σ_{Left} and σ_{Right} are half standard deviation with a 1/e height of the left and right of the distribution respectively, p is the peak orientation, and d is the vertical offset. The values of the five parameters are determined using a Matlab *fminsearch* function to optimize the fits.

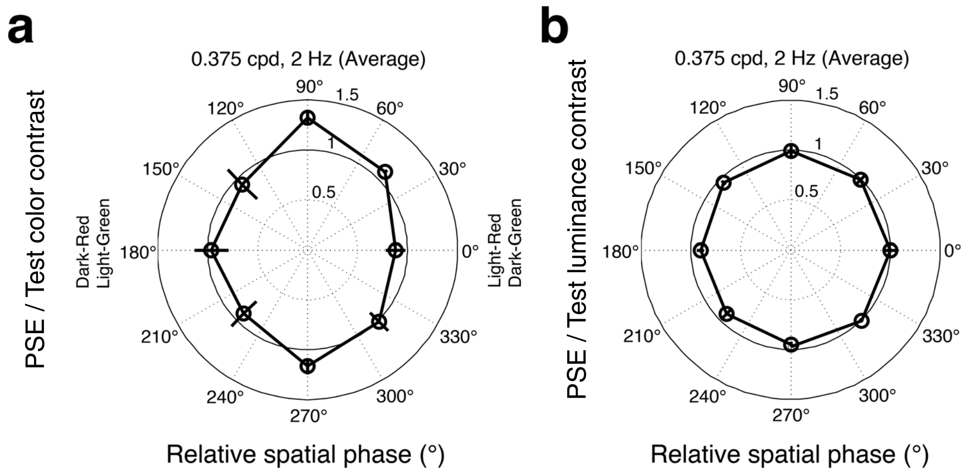

Figure 8. The effect of relative spatial phase of co-aligned color and luminance Gabors on perceived contrast. (a) Matched color contrast plotted as a function of the relative spatial phase between the color and the luminance contrasts (0, ±45°, ±90°, ±135°, 180°). Stimuli are low spatial frequency (0.375 cpd) and binocular. The color test is 10× detection threshold and the luminance mask is 4× threshold. The average of four subjects (YJK, AR, HCS, and YSW) is shown. (b) Same as in (a) except that luminance contrast is matched to a luminance reference. The luminance test contrast is 10× detection threshold and color mask contrast is 6× detection threshold. Results are the average of the two subjects (YJK and AR). Error bars are ±1 *SE* of the group mean and smaller than the symbols.

Discussion

We have explored visual interactions between overlaid color and luminance contrasts that are both suprathreshold and highly visible. We first used cross-oriented color-luminance plaid stimuli to reveal how the presence of luminance contrast affects the perception of color contrast, and vice versa. We found that the overlaid luminance contrast enhances perceived color contrast in a proportional way, by an average of 32% for both binocular and monocular viewing over a wide range of base color contrasts (2–10× threshold) and including three spatial frequencies. For the reverse condition, we found no effect of the overlaid, cross-oriented color contrast on perceived luminance contrast for any viewing condition, revealing an interesting asymmetry between color and luminance cross-orientation interactions.

A very important feature of the color contrast enhancement is that its magnitude is independent of the luminance contrast used. We tested a wide range of luminance contrasts (2–20× threshold) and the color enhancement was consistently the same regardless of whether the luminance contrast was faint or highly visible. We also tested whether the ratio of color to luminance contrast in the plaid stimulus was important and found that the color contrast enhancement was a consistent proportion of the base color contrast regardless of the color/luminance ratio used (from 0.2 to 2.4). This effect strongly suggests that the subject is making a match between the color reference and the color component of the plaid (test) and is not including the luminance component in their contrast match. For example, they are not matching the overall "contrastiness" of the plaid to the reference. Furthermore, the fact that color contrast perception is enhanced by the presence of luminance contrast but is not dependent on its magnitude rules out that the effect is based on some form of summation of color and luminance contrast into a mechanism with a common neural response to both contrast types, such as the P-cells of the subcortical pathways.

Relatively few studies have investigated contrast summation of the two component gratings of a plaid when both are of the same contrast type (a color-only or luminance-only plaid; Cherniawsky & Mullen, 2016; Georgeson & Shackleton, 1994). These have shown that contrast summation occurs between components, but does not reach full summation. For example, the perceived contrast of a RG color plaid was on average 1.6 greater than its component gratings, and for a luminance plaid 1.8 greater, whereas full summation would predict a 2-fold increase (Cherniawsky & Mullen, 2016). For the color-luminance plaids used here, the interaction between the components is asymmetric, showing that perceived luminance contrast is unaffected by color contrast, but perceived color contrast is enhanced by luminance contrast by an average of 1.32. However, the independence of the color enhancement from the strength of the luminance contrast suggests that it is not based on a combination of color and luminance responses into a common form processing mechanism.

We have also shown that the relative positions of the color and luminance contrast borders play an important role in the color enhancement, since the enhancement of perceived color contrast by luminance contrast disappears when the orientation difference between the color and luminance contrasts is systematically decreased from cross-oriented to co-oriented and co-aligned. Once the color bars are directly co-aligned with the luminance bars, for both spatial phases (0° and 180°), the color enhancement is lost and becomes instead a mild suppression. The importance of the relative positions of the color and luminance borders was shown in the phase experiment: When the color and luminance borders are co-aligned, color enhancement disappears but reappears when the stimuli are out of phase and is maximal when the luminance border falls midway between the color borders. These two experiments show that the color and luminance border locations are crucial, causing suppression when co-oriented or co-aligned but enhancement when spatially independent and separated.

These border effects are interesting in view of how color and luminance contrast co-occur in natural scenes. Material differences are typically associate with a change in spectral reflectance and have an associated luminance contrast, given the rarity of isoluminance in nature. Hence, when material changes occur—for example, on a surface or at the boundaries between objects—color and luminance contrast coincide. On the other hand, shadows and shading are examples of luminance contrast variations without associated color changes. In these terms, we find that perceived color contrast is suppressed when the luminance and color borders are coincidental and likely to be demarcating an object boundary, but enhanced when they are separate and more likely to be representing shading and shadowing effects. For example, Kingdom (2003) demonstrated that a cross-oriented luminance grating overlaid over a RG color grating creates a strong impression of a three-dimensional modulation of the color surface ("shape-from-shading"), which disappears when the contrasts are co-aligned. Our results suggest that different processes are engaged when color and luminance contrast have coincidental borders compared to when they are independently modulated, with differential effects on perceived color contrast.

Many past studies have emphasized the importance of borders in color and luminance surface representations in the early visual cortex (V1; Friedman, Zhou, & von der Heydt, 2003; Hung, Ramsden, & Roe, 2007; Lamme, Rodriguez-Rodriguez, & Spekreijse, 1999; Zweig, Zurawel, Shapley, & Solvin, 2015). Xing et al. (2015) reported the suppression of color contrast by luminance contrast for a colored patch in a luminance surround and that the coincident luminance edges are important in producing local suppression of color contrast, probably mediated in V1 (Xing et al., 2015). Specifically, Zweig et al. (2015) provided evidence that the borders play an important role in surface representation by revealing that population responses in V1 to color and luminance surface are edge enhanced. Furthermore, several studies have reported the responses of primate V1 neurons during figure-ground segregation (Lamme, 1995; Poort et al., 2012). Specifically, when the neuron's receptive field is located inside the boundaries of the figure, its responses are enhanced; however, the responses are absent when the receptive field is located outside the figure boundaries.

As raised in the Introduction, many previous studies have found that color detection thresholds are facilitated in the presence of luminance contrast. Facilitation of color detection thresholds by a luminance mask has been shown using the same type of cross-oriented stimuli as in this study (Mullen et al., 2014). In addition, the effect was largely independent of the magnitude of the luminance contrast. However, there are also considerable differences between this threshold effect and the suprathreshold color enhancement we report here. Specifically, threshold facilitation is typically greatest when color and luminance borders are co-aligned and coincidental (Gowdy et al., 1999; Mullen & Losada, 1994; Switkes et al., 1988) and is enhanced by luminance edges demarcating the color boundaries (Eskew et al., 1991; Gowdy et al., 1999), suggesting it is not part of the same process.

The dichoptic condition also revealed asymmetrical effects between color and luminance contrast. We find the masking of color by luminance is quite strong, but the reverse effect is weak. Perceived color contrast is susceptible to dichoptic masking by cross-oriented luminance contrast, especially at higher luminance contrasts, although there is a lot of intersubject variability, typically found for dichoptic masking (Kim et al., 2013; Mullen et al., 2014). For the reverse condition, we found no dichoptic masking effect of color contrast on perceived luminance contrast, although the strength of the color mask was limited by the color gamut of the monitor. These results may indicate a differential effect of dichoptic masking with color vision more susceptible than luminance to the effects of cross-masking, in line with the binocular and monocular results.

Keywords: color vision, isoluminance, psychophysics, contrast gain, spatial vision

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