Collinear facilitation in color vision

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The detection of a luminance-defined Gabor is improved by two high contrast, aligned, flanking Gabors, an effect termed collinear facilitation. We investigate whether this facilitation also occurs for isoluminant chromatic stimuli, and whether it can occur for chromatic targets with luminance flanks and vice versa. We measured collinear facilitation for Gabor stimuli (0.75 cpd, 1 octave bandwidth) of three different contrast types: achromatic, red-green that isolates the L/M-cone opponent mechanism, and blue-yellow that isolates the S-cone opponent mechanism. Three conditions were investigated: (1) target and flanks all of the same contrast type and spatial phase; (2) target and flanks of the same contrast type but opposite phases (0° and 180°); and (3) target and flanks of different contrast types (chromatic with achromatic contrast) and two opposite phase combinations. We find that a similar degree of collinear facilitation occurs for the isoluminant chromatic stimuli as for the achromatic stimuli, and all exhibit phase dependency. Facilitation did not occur, however, between chromatic and achromatic target and flanking stimuli. This suggests that at the level of collinear facilitation, the chromatic and the achromatic postreceptoral mechanisms have their own spatial interactions that are segregated from one another.

Introduction

It is well known that the detection of a luminance-defined stimulus can be modulated by its neighboring elements. If the neighboring elements form a common global alignment, the detection threshold of the target decreases, a phenomenon called collinear or flank facilitation (Polat, 1999; Polat & Sagi, 1993; Woods, Nugent, & Peli, 2002). A typical stimulus configuration is shown in Figure 1, in which the detection threshold of a central target is compared in the absence and presence of two high contrast collinear flanks. The neural basis of this phenomenon is not well understood although the response of cells in V1 has been implicated because it has been shown that their response can be modulated by the presence of spatially aligned stimuli falling outside the classical receptive field (Kasamatsu, Polat, Pettet, & Norcia, 2001; Mizobe, Polat, Pettet, & Kasamatsu, 2001; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Yao & Li, 2002). In addition, a number of psychophysical mechanisms have been proposed, which include high-level uncertainty effects (Petrov, Verghese, & McKee, 2006), within channel masking/facilitation (Solomon, Watson, & Morgan, 1999; Williams & Hess, 1998; Woods et al., 2002) and between-channel interactions (Polat, 1999),

possibly involving long range cortical afferents (Hirsch & Gilbert, 1991; Ts'o, Gilbert, & Wiesel, 1986; Weliky, Kandler, Fitzpatrick, & Katz, 1995).

One of the important issues in color vision is to understand the role of chromatic mechanisms in spatial vision. The general approach to this issue is to investigate the characteristics of spatial vision with stimuli that are based purely on color contrast. Although an early view was that color plays the minimal role in spatial tasks, such as illusory contours, stereoscopic vision, and shape from shading (Gregory, 1977; Gregory & Heard, 1983; Livingstone & Hubel, 1988, 1987; Lu & Fender, 1972), a number of lines of evidence now indicate that color vision has the early spatial processing capabilities to support form perception and spatial tasks. For example, it has been shown that, like luminance vision, color vision has multiple band-pass spatial frequency filters with a similar bandwidth to the luminance system (Bradley, Switkes, & De Valois, 1988; Losada & Mullen, 1994, 1995; Mullen & Losada, 1999), albeit within an overall low-pass contrast sensitivity envelop (Mullen, 1985). In addition, chromatic spatial frequency discrimination and orientation discrimination thresholds are only marginally below those for luminance stimuli, for both spatially narrow band (Reisbeck & Gegenfurtner, 1998; Webster, De Valois, & Switkes, 1990; Wuerger, Morgan, Westland, & Owens,
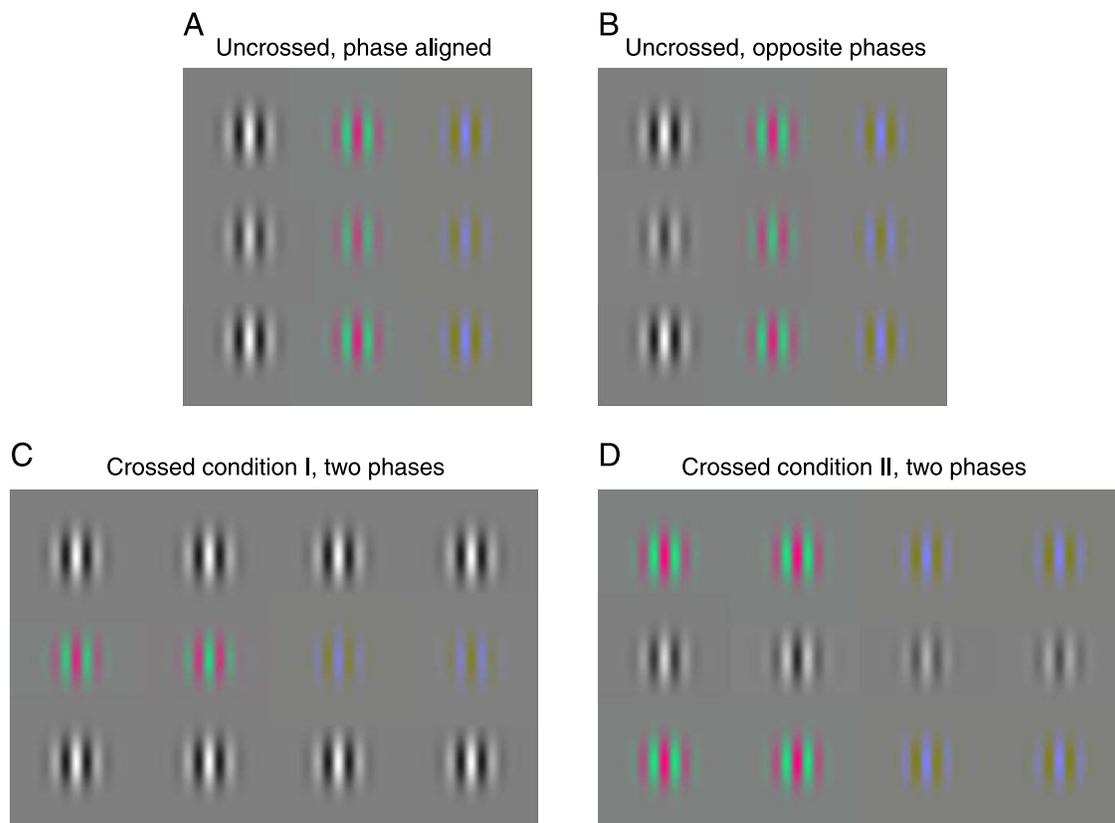
Figure 1. Examples of the stimulus configurations used in each experiment. (A) "Uncrossed" condition in which target and flank stimuli are all chromatic (red-green or blue-yellow) or all achromatic presented in-phase alignment, as used in Experiment 1. (B) As in panel A except that the target and the flank stimuli have a 180° phase difference, as used in Experiment 2. (C) "Crossed" condition with chromatic target and achromatic flanking stimuli of both phase combinations (0° and 180°), as used in Experiment 3. Both red-green and blue-yellow chromatic targets were tested. (D) "Crossed" condition with achromatic target and chromatic flanking stimuli of both phase combinations (0° and 180°), as used in Experiment 3. Both red-green and blue-yellow chromatic targets were tested.

2000) and spatially broad band stimuli (Beaudot & Mullen, 2005), providing the stimulus contrasts are scaled to be equally detectable by the chromatic and achromatic mechanisms. Moreover, color vision can support both contour integration and some forms of global shape perception (McIlhagga & Mullen, 1996; Mullen & Beaudot, 2002; Mullen, Beaudot, & McIlhagga, 2000).

One of the most parsimonious explanations for the similarities of spatial processing by color and luminance vision is that both use common neural mechanisms that can respond to either chromatic or achromatic contrast. On the other hand, psychophysical evidence suggests that at detection, threshold color and luminance systems are mediated by independent pathways, as determined by studies of cross adaptation (Krauskopf, Williams, & Heeley, 1982), cross masking (Mullen & Losada, 1994; Switkes, Bradley, & De Valois, 1988), noise masking (Giulianini & Eskew, 1998; Sankeralli & Mullen, 1997), and subthreshold spatial summation (Mullen, Cropper, & Losada, 1997; Mullen & Sankeralli, 1999; Sankeralli &

Mullen, 1996). For some tasks particularly at suprathreshold contrast levels, however, there is evidence for interactions between chromatic and luminance responses (Cole, Stromeyer, & Kronauer, 1990; Gowdy, Stromeyer, & Kronauer, 1999; Sankeralli, Mullen, & Hine, 2002; Ueno & Swanson, 1989; Webster & Mollon, 1994). Thus, the psychophysical segregation of color and luminance processing in the spatial domain and its underlying mechanism remain very controversial.

This paper addresses the following issues. Firstly, we aim to quantify and compare the amount of collinear facilitation in the three postreceptoral mechanisms to see if this elementary spatial interaction and its phase dependency are properties of both luminance and chromatic processing. Secondly, we want to determine the extent of any interaction between chromatic and achromatic mechanisms for collinear facilitation in order to distinguish between two possible models. One model is that the chromatic and the achromatic elements are encoded by a common low-level pathway (e.g., V1), predicting that

they have a similar amount of collinear facilitation. An alternative model is that color and luminance pathways are functionally separate, which predicts a lack of interaction between target and flanking stimuli when they activate different postreceptoral mechanisms. We test these predictions by measuring collinear facilitation under three different conditions: (1) target and flanks all of the same color and spatial phase; (2) target and flanks of the same color but different phases (0° and 180°); and (3) target and flanks of different colors and two phase combinations. The first condition compares the degree of collinear facilitation within achromatic, L/M-cone opponent (R/G), and S-cone opponent (B/Y) mechanisms. The second condition determines the phase dependence of collinear facilitation for both achromatic and chromatic stimuli in order to compare the properties of collinear facilitation in the chromatic and the achromatic systems and to test for the presence of chromatic aberrations. The third condition establishes whether collinear facilitation can occur between chromatic and luminance stimuli, hence assessing the level of segregation of chromatic and luminance mechanisms.

Methods

Apparatus

The stimuli were presented on an Electrohome (Retro III) back-projection CRT monitor (138 cm by 104 cm) with a resolution of 1024×768 and a frame rate of 120 Hz. The projector was controlled by the VSG2/5 graphics board (Cambridge Research Systems) with 15 bits of contrast resolution. The projector was gamma corrected after measuring its luminance output with an optical photometer. The spectral emissions of the three guns of the projector were calibrated by a Photo Research PR-700-PC SpectraScan. The Smith and Pokorny fundamentals were used to calculate the matrix for conversion of R, G, and B phosphor contrasts to L-, M-, and S-cone contrasts. The mean luminance of screen center was 68 cd/m^2. The phosphor chromaticities were $x = 0.610$, $y = 0.340$ for the red gun, $x = 0.280$, $y = 0.594$ for the green gun, and $x = 0.140$, $y = 0.070$ for the blue gun.

Subjects

Four subjects (HT, MS, PCH, and SGT) participated in the experiments and all had normal color vision measured on the Farnsworth Munsell 100-Hue test. All were experienced psychophysics observers with normal or corrected-to-normal vision. HT was a subject for

Experiments 1 and 2, and the other three subjects ran all experiments.

Stimuli and color space

The stimuli were achromatic or chromatic Gabor patches defined by the equation

$$L(x,y) = L_0 + L_0 \times c \times \cos(2\pi x/T - \rho) \times \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right). \qquad (1)$$

Where L_0 was the mean luminance, c was the contrast of the Gabor, defined as the vector length in cone contrast units, T was the period of the carrier, σ was the standard deviation of the Gaussian envelope, and ρ was the phase of the stimuli with respect to the center of the Gaussian window. The viewing distance was 208 cm, and the spatial frequency was 0.75 cpd with 0° phase angle, the space constant (σ) was 0.94°, and consequently the bandwidth of the Gabor was about 1 octave. The size of the Gabor patch was five times σ. The peak spatial frequency of the target and flanks was low (0.75 cpd) to reduce luminance artifacts due to chromatic aberration (Bradley, Zang, & Thibos, 1992).

Three types of cardinal stimuli were used (see Figure 1), each isolating one of the three postreceptoral mechanisms (R/G, B/Y, or Ach), respectively. Stimuli were defined within a three-dimensional cone contrast space in which each axis represents the response of the L-, M-, or S-cone type normalized to the response to the white background. Stimulus chromaticity and contrast are given within this color space by a vector direction and magnitude, respectively. The achromatic (Ach) cardinal stimulus has an L-, M-, and S-cone response ratio of 1:1:1, respectively; the blue-yellow (B/Y) cardinal stimulus is the S-cone axis of the cone contrast space and the cone response ratio is 0:0:1; and the red-green (R/G) cardinal stimulus has the isoluminant direction in the L/M-cone contrast plane and was determined individually for each subject using a minimum motion method. To determine isoluminance, the subject viewed a constantly drifting vertical grating (1 Hz, 0.75 cpd) in a Gaussian envelope ($\sigma = 1.85°$), and a method of adjustment was used to vary the M:L-cone ratio to determine a minimum in stimulus drift speed. This procedure was repeated 10 times and the average was obtained. The L:M isoluminant cone ratios were 1:−3.2, 1:−3.8, 1:−6.7, and 1:−4.1 for HT, MS, PCH, and SGT, respectively, which are all within the normal range.

The accuracy of the B/Y cardinal direction was checked for each subject by determining a minimum in cone contrast sensitivity as follows. The vector direction of a

grating stimulus of fixed cone contrast (the same stimulus as used for the minimum motion paradigm) was varied within the isoluminant plane, whose axes are the R/G isoluminant axis and the S-cone axis, and the subject determined, using an adjustment method, the vector direction of the chromatic stimulus that is least visible. The vector direction at minimum visibility indicates the chromatic stimulus that isolates the B/Y mechanism from the R/G mechanism. Each subject obtained a vector direction at or very close to 90°, indicating that the S-cone axis corresponds to the B/Y cardinal direction and the two cardinal axes are orthogonal in cone contrast space.

Procedures

A temporal, two-alternative forced-choice (2AFC) staircase procedure, with feedback, was used to measure the detection thresholds of the Gabor patches. Cone contrast sensitivity for R/G Gabor stimuli is highly sensitive in the fovea but falls off steeply across the visual field (Mullen, 1991). Cone contrast sensitivities to Ach and B/Y stimuli fall below those for R/G in the central vision but have a shallower decline with eccentricity (Mullen & Kingdom, 2002; Mullen, Sakurai, & Chu, 2005). To compare the collinear facilitation effect in achromatic and chromatic conditions, we measured the flank detection thresholds for each type of Gabor stimulus prior to the main experiment and flank stimulus contrast was matched in multiples of detection threshold.

We measured detection thresholds for the two flanking stimuli (without the central Gabor) using a 2AFC staircase method. The subject was asked to fixate the center of the screen and to choose which interval contained the flanks. Each presentation of the stimulus was 1 s with a stimulus temporal Gaussian envelope of 125 ms. A two-down and one-up staircase was used, in which target contrast was increased 0.25 times the contrast following the incorrect response and decreased 0.125 times the contrast following two correct responses. The threshold was calculated as the average of last five reversal points and corresponded to the 81.6% correct level. This was repeated four to eight times to obtain a mean and standard deviation. To measure collinear facilitation, we measured detection thresholds for the target (the central Gabor) in the presence and absence of the two flanking stimuli using a double staircase method to determine both thresholds at the same time. The contrast of the flanking Gabors was set to five times the detection threshold for subject PCH and four times the detection threshold for the three other subjects (HT, MS, and SGT).[1] The center-flank Gabor separation was varied (2, 3, 6λ), equivalent to 2.7°, 4°, and 8° of visual angle, respectively.

In Experiment 1, we measure the collinear facilitation effect for Gabor stimuli with the same color and phase, at three different target–flank distances (2, 3, 6λ).

Experiment 2 was similar to Experiment 1, except that a phase difference between target and flanks of 180° was used. In Experiment 3, crossed conditions were measured, in which the target and flank Gabors of different achromatic and chromatic combinations were tested. The sequence of each condition was randomized within each experiment.

The collinear facilitation index is defined according to the equation:

$$\text{Log threshold ratio} = \log_{10}(\text{TH}_{\text{with flanks}}/\text{TH}_{\text{with flanks}}). \tag{2}$$

For each staircase measurement, the collinear facilitation index was calculated, and the plotted data points are the average of four to eight such measurements. A Student t test was used to test if the facilitation index was significantly different from zero ($p = .05$), indicating significant facilitation in the presence of the flanks.

Results

Control experiment: flank detection thresholds

As described in the Methods section, to match the visibility of the flanks across different conditions, the flank detection thresholds for each separation and color were measured prior to main experiment. Table 1 shows the flank detection thresholds at three different center-flank separations. A one-way repeated measured ANOVA shows the detection threshold for achromatic flanks did not change with the target–flank separations, $F(2, 4) = 1.741$, $p = .286$. However, the detection threshold for the R/G and B/Y color opponent mechanisms varied with the center-flank separations, $F(2, 4) = 499.393$, $p < .05$; $F(2, 4) = 148.716$, $p < .05$ for R/G and B/Y stimuli, respectively.

Experiment 1: Collinear facilitation with stimuli of the same color and phase

The stimulus configuration for Experiment 1 is shown in Figure 1A. Figure 2 shows the log threshold ratio for each color combination and target–flank separation for four subjects and their average. Levels of collinear facilitation that reach significance are marked for each condition. All subjects show a significant effect of collinear facilitation, although there is some variability between them. Specifically, in the achromatic condition, collinear facilitation occurs in SGT at 2 and 3λ, in PCH and MS at 2, 3, and 6λ, and in HT at 3λ. In the R/G

		Separation (λ)		
		2	3	6
Ach	HT	0.055	0.063	0.082
	MS	0.062	0.066	0.074
	PCH	0.055	0.063	0.071
	SGT	0.064	0.045	0.057
	AVG	0.059	0.059	0.071
R/G	HT	0.033	0.038	0.055
	MS	0.021	0.028	0.051
	PCH	0.017	0.022	0.045
	SGT	0.012	0.017	0.038
	AVG	0.021	0.026	0.047
B/Y	HT	0.093	0.106	0.174
	MS	0.059	0.087	0.132
	PCH	0.074	0.087	0.129
	SGT	0.058	0.083	0.127
	AVG	0.071	0.091	0.141

Table 1. Flank detection thresholds.

condition, MS shows facilitation at 2 and 6λ, PCH shows collinear facilitation at 2λ only, SGT shows flank facilitation at 2 and 3λ, and HT shows facilitation in 2, 3, and 6λ. In the B/Y condition, PCH shows the collinear facilitation at 2, 3, and 6λ, MS shows facilitation at 2 and 3λ, HT shows facilitation at 3λ, and SGT shows no facilitation. For the average data, significant facilitation occurs at 3 and 6λ in the Ach condition, at 2 and 3λ in the R/G condition, and at 2, 3, and 6λ in the B/Y condition. We conclude that overall a comparable degree of collinear facilitation occurs with both achromatic and chromatic stimuli.

Experiment 2: Collinear facilitation with stimuli of the same color and different phase

The procedure of Experiment 2 was the same as Experiment 1, except that target and flanks were now 180° out of phase. The stimulus configuration is shown in Figure 1B and the results are shown in Figure 3 for four subjects and their average. These results show no significant facilitation for Ach or B/Y stimuli in any of the four subjects. The R/G condition, however, shows significant masking (threshold elevation) in three out of four subjects at the smallest separation (2λ) but this effect disappears at larger separations. In summary, there is no facilitation in the out of phase conditions, indicating that the collinear facilitation is phase dependent in both chromatic and achromatic conditions.
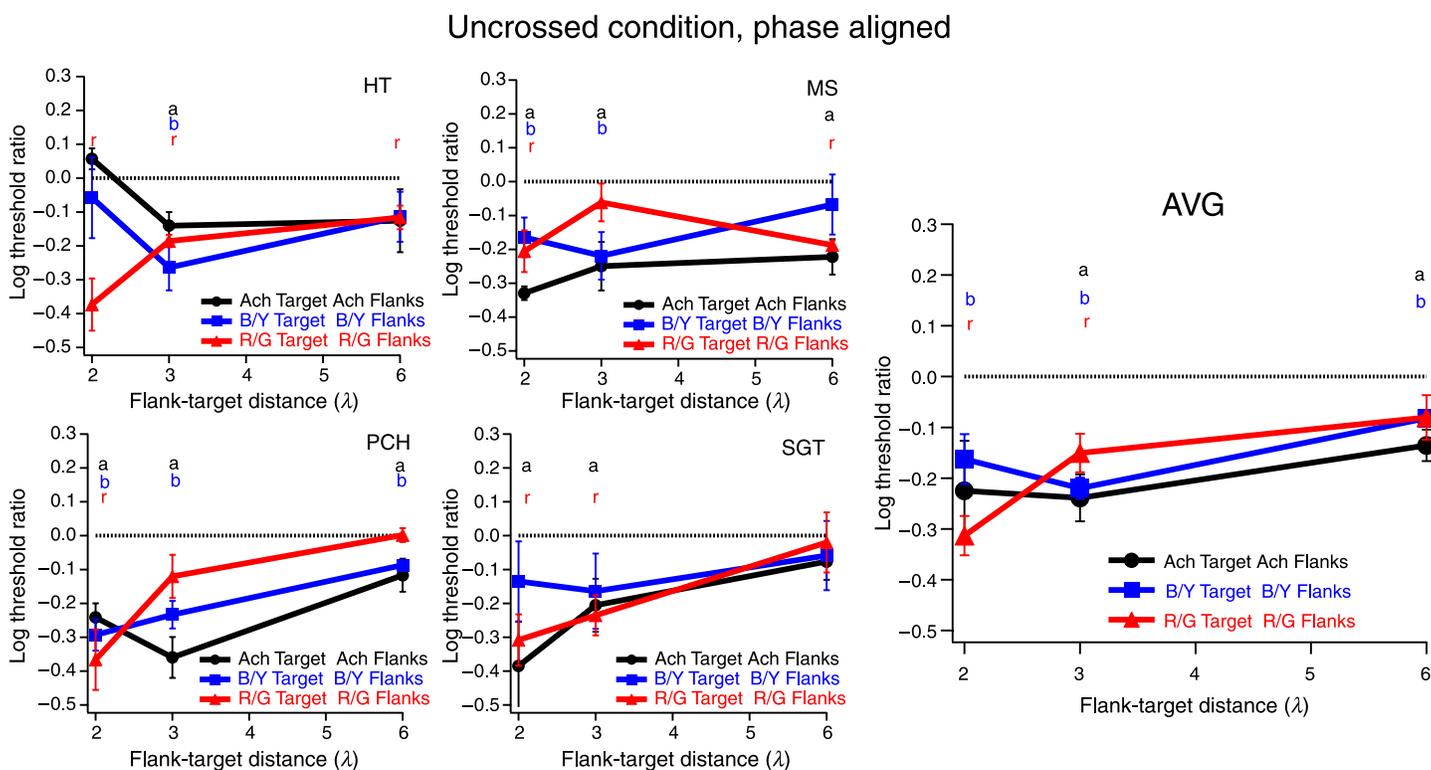

Figure 2. Results for the uncrossed, phase aligned condition. Log threshold ratios are plotted as a function of target and flank separation expressed in stimulus periods (λ) in the uncrossed condition with target and flanks of the same phase. Results are for four subjects with the average data shown on the right. The small letters "r," "b," and "a" indicate that the amount of facilitation effect is significantly different from zero ($p \leq .05$) for R/G, B/Y, and Ach stimuli, respectively. The error bars represent ±1 SE.
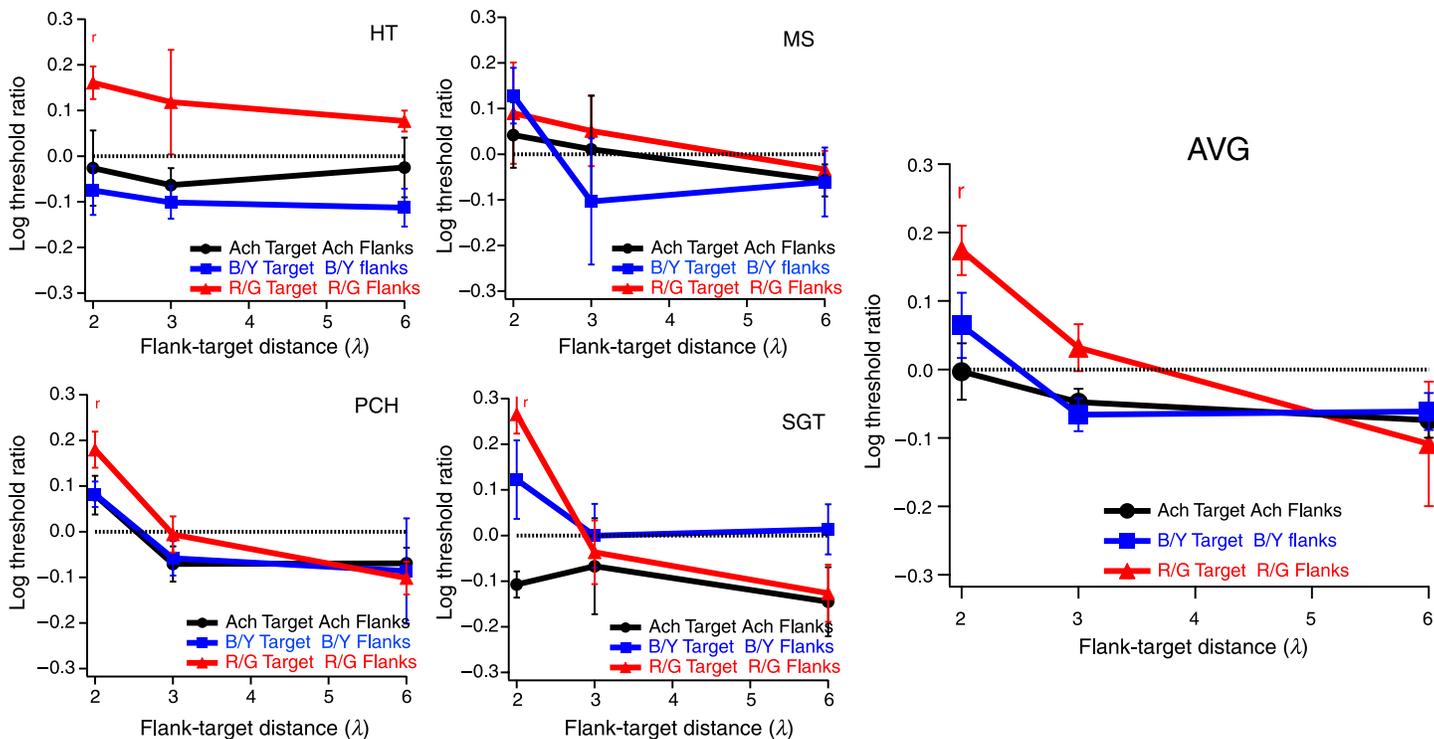
Figure 3. Results for the uncrossed, opposite phase condition. Log threshold ratios plotted as a function of target and flank separation expressed in stimulus periods (λ) in the uncrossed condition with target and flanks 180° out-of-phase. The letter "r" indicates that the amount of inhibitory effect is significantly different from zero for R/G stimuli.

Experiment 3: Collinear facilitation in crossed (different) color/achromatic conditions

In Experiments 1 and 2, we found that collinear facilitation was similar with each of the three cardinal stimuli. Two possible models could explain these results. One is that the chromatic and the achromatic elements are encoded by a common low-level pathway and thus they have a similar amount of collinear facilitation. A second possibility is that color and luminance pathways are functionally separate, and the similarity arises from each pathway having its own, comparable lateral interaction process. Here we address this issue.

The experimental methods and procedures were the same as for Experiment 1. Two main conditions were undertaken: (1) achromatic flanks with chromatic target and (2) chromatic flanks with achromatic target. If the underlying postreceptoral mechanisms involved in collinear facilitation are independent, no facilitation effect would occur in these crossed conditions; otherwise, facilitation would be expected in the crossed conditions. Furthermore, in order to investigate whether any facilitation effect was caused by the intrusion of luminance artifacts, each color combination had two opposite phases

(e.g., white bar aligned with green bar vs. white bar aligned with red bar) tested in separate blocks. If any of the facilitation was due to luminance artifacts in the chromatic stimuli, the amount of facilitation should be phase dependent, particularly for high contrast, peripherally located chromatic flanks.

Figure 4 shows how achromatic flanks influence the detection threshold of an R/G target with achromatic flanks for two opposite phase combinations (see first two columns of Figure 1C for stimulus configuration). Data show results for three subjects and their average. The achromatic flanks have no significant effect on the detection of the R/G target for each separation and phase configuration. When the data points were collapsed across flank–target distance and subjects, achromatic flanks appear to improve the detection of the central target by a small amount, $t(17) = -6.19$, $p < .01$. However, the effect does not vary with the separation of the flanks, indicating that this is not an effect characteristic of collinear facilitation. In addition, this small effect shows no difference between the two different phase conditions. For the purposes of comparison, the data for the achromatic and the R/G uncrossed conditions have been plotted with the averaged data (lower right panel). This shows that the
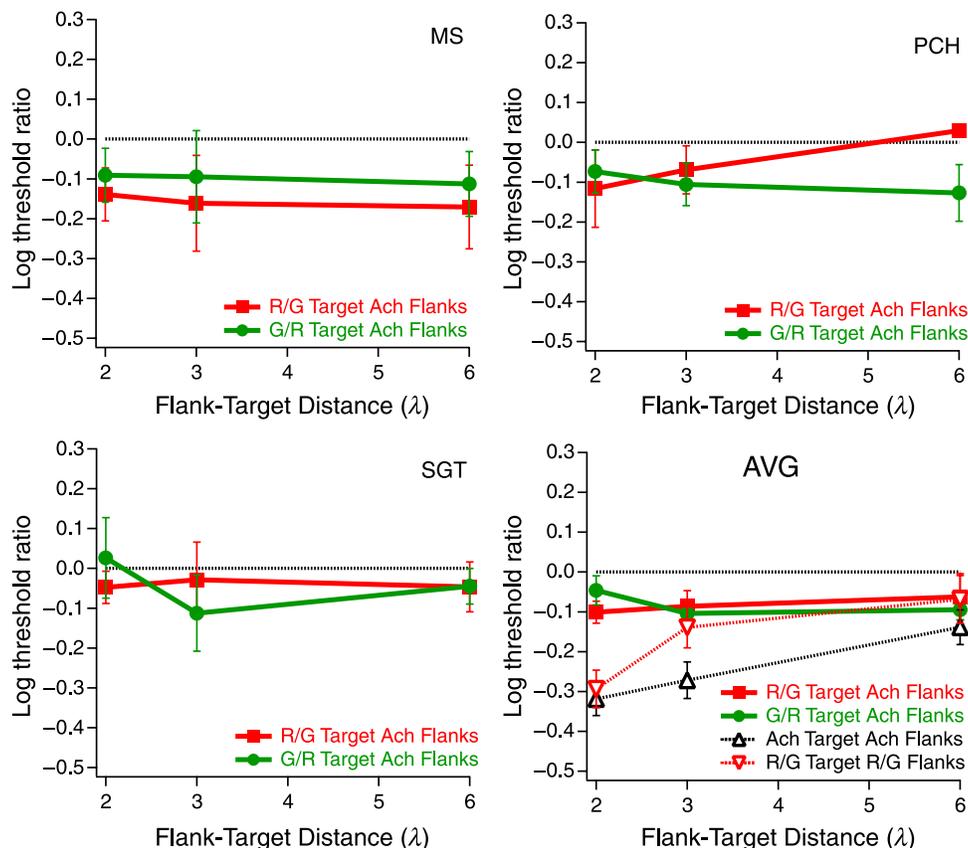
Figure 4. Results for R/G target with Ach flanks. The red line (squares) shows the condition in which a red bar is aligned with the white bar. The green line (circle) shows the conditions in which a green bar is aligned with the white bar. AVG represents the average data from three subjects. The error bars represent ±1 *SE*. For comparison, the average data for three subjects in the uncrossed conditions are also plotted: the black dashed line (upright triangles) represents the achromatic phase aligned condition and red dashed line (inversed triangles) represents the R/G phase aligned condition.

collinear facilitation effect found for the chromatic uncrossed condition (R/G flanks and target), which was significant at 2λ, disappears when achromatic flanks are used.

Figure 5 shows how the detection threshold of B/Y target is influenced by the Ach flanks (see Figure 1C, two right columns for stimulus configuration). The average data show that the achromatic flanks have no effect on the detection of the B/Y target at the three target–flanks separations. There is no difference between the two phase combinations, confirming that luminance artifacts are not present in the chromatic target. We note that subject MS shows weak facilitation in both crossed conditions (R/G and B/Y, Figures 4 and 5, respectively), although not significant. However, in this case the amount of facilitation does not vary with target–flank separation, suggesting that this is not a true collinear facilitation effect. In addition, the facilitation effect in these two crossed conditions of subject MS is much smaller than it is in the achromatic uncrossed condition and may be due to the reduction of uncertainty rather than any neural interaction

between the achromatic and the chromatic systems. We therefore conclude that achromatic flanks do not induce a classic collinear facilitation for the detection of a chromatic target.

Figures 6 and 7 show how R/G and B/Y flanks, respectively, influence the detection threshold of an achromatic target for two opposite phase combinations (for stimulus configuration, see Figure 1D). For the achromatic target with the R/G flanks (Figure 6), no significant facilitation was found, showing that R/G flanks do not facilitate the detection of achromatic stimuli. For the achromatic target with the B/Y flanks (Figure 7), we see a trend toward collinear facilitation with one of the phase conditions (white luminance bar aligned with a blue chromatic bar) but not the other, particularly for subjects SGT and MS. The phase dependence of this effect suggests that the B/Y flanking stimuli may have a small degree of luminance contrast in these subjects; this is especially likely because optical chromatic aberration increases with eccentricity. By averaging the two different phase combinations in the crossed conditions, the amount
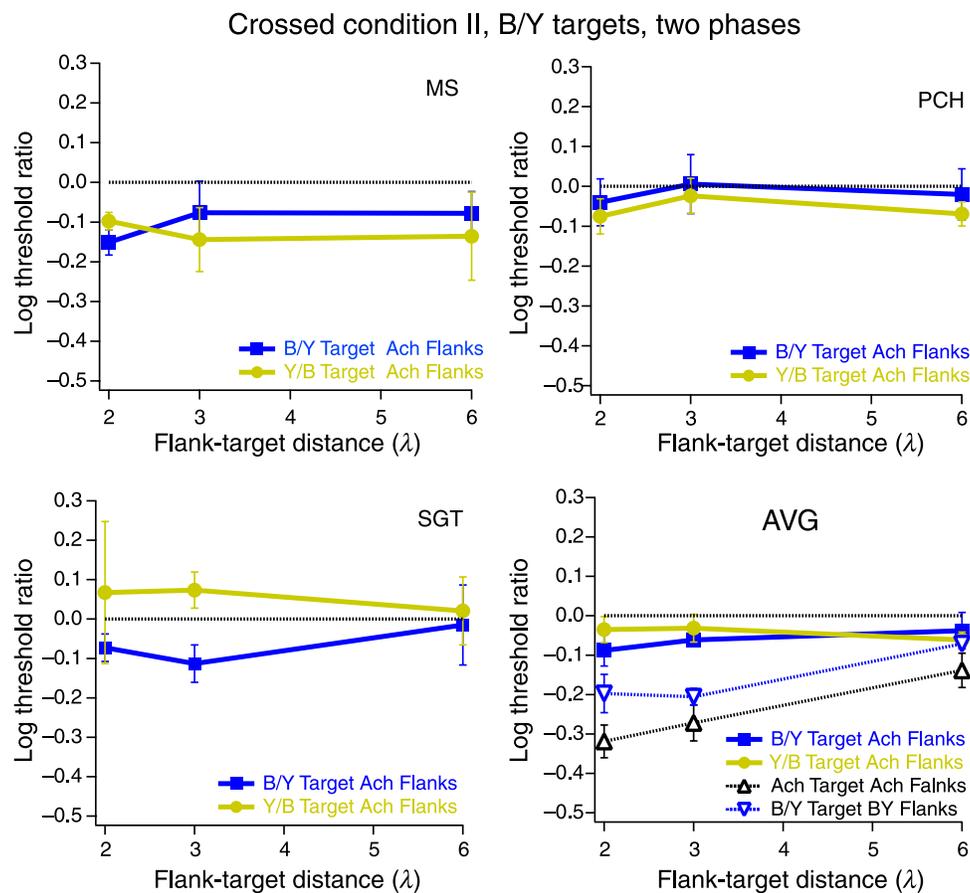
Crossed condition II, B/Y targets, two phases

Figure 5. Results for a B/Y target with Ach flanks. The blue line (squares) shows the condition in which a blue bar is aligned with the white bar. The yellow line (circles) shows the condition in which a yellow bar is aligned with the white bar. The error bars represent ±1 SE. AVG represents the average data from three subjects. For comparison, the average data for three subjects in the uncrossed conditions are also plotted: the black dashed line (upright triangles) represents the achromatic phase aligned condition and red dashed line (inversed triangles) represents the B/Y phase aligned condition.

of facilitation becomes close to zero, suggesting no overall facilitation between achromatic target and chromatic flank stimuli. We note that subject PCH, who shows no evidence for chromatic aberration, displays collinear facilitation for the uncrossed B/Y condition (B/Y target and flanks, Figure 2) comparable to that found for R/G and Ach stimuli, indicating that the B/Y chromatic system supports collinear facilitation in its own right.

Discussion

We find collinear facilitation in both R/G and B/Y cardinal stimuli, with a similar magnitude and phase dependency to that found for achromatic stimuli, suggesting that lateral spatial interactions occur in chromatic as well as achromatic pathways, at least for our spatial stimuli of 0.75 cpd. We also find that collinear facilitation

is disrupted when flanks and target differ in their chromatic type (chromatic target with achromatic flanks or achromatic target with chromatic flanks), suggesting that the underlying processes are selective for chromaticity and as well as the phase of their inputs. A previous study published in abstract form (Chen & Tyler, 2002) using a 4-cpd target and one flank distance also found the presence of collinear facilitation in the chromatic system. This study, however, also found some facilitation in the crossed condition in which the flanks were chromatic and the target achromatic. It is likely that this reflects the intrusion of luminance artifact from chromatic aberration arising from the use of a relatively high spatial frequency (4 cpd) and high contrast chromatic flanks (10× detection threshold) (Bradley et al., 1992). We used a lower spatial frequency (0.75 cpd) that was less suprathreshold (4–5× threshold) to reduce the effect of chromatic aberration, and we manipulated the spatial phase of the stimuli to verify the absence of luminance artifacts. Ellenbogen, Polat, and Spitzer (2006) have also shown that collinear
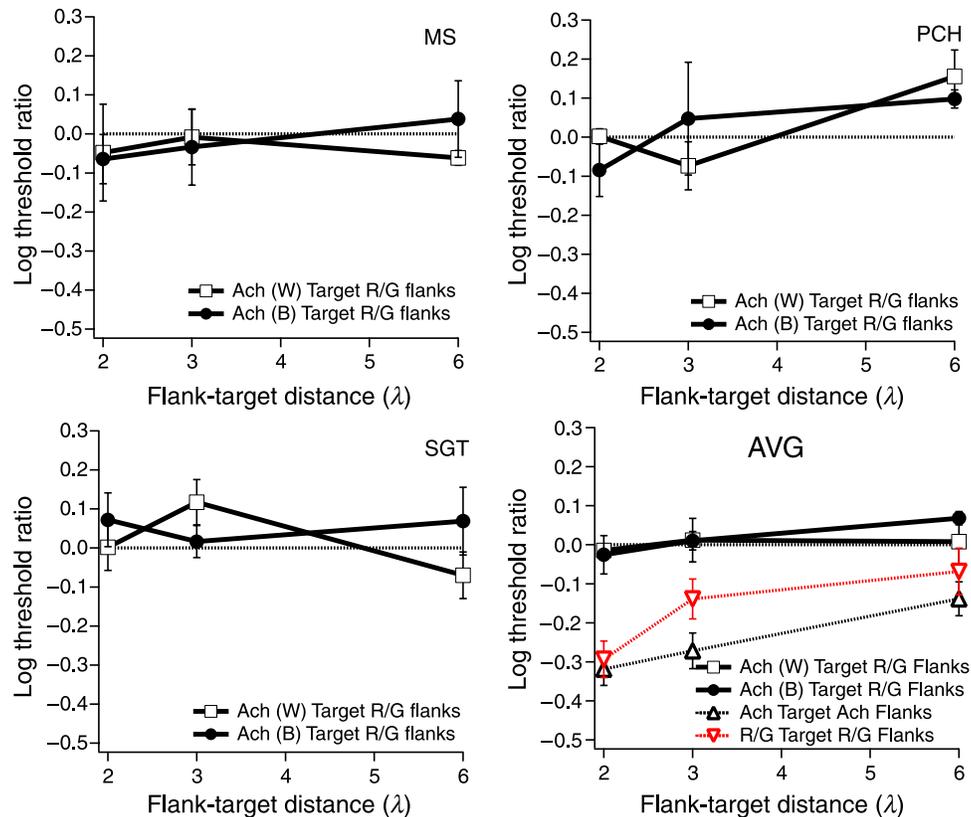
Figure 6. Results for Ach target and R/G flanks. White squares show the condition in which a red bar is aligned with the white bar. Black circles show the condition in which a green bar is aligned with the white bar. The error bars represent ±1 *SE*. AVG represents the average data from three subjects. For comparison, the average data for three subjects in uncrossed conditions are also plotted: the black dashed line (upright triangles) represents the achromatic phase aligned condition and the red dashed line (inversed triangles) represents the R/G phase aligned condition.

facilitation occurs for red green chromatic stimuli and exhibits phase dependence. However, the relatively high spatial frequency used (3 and 4 cpd) leaves open the possibility that there were significant luminance artifact in the isoluminance conditions.

Our findings have two implications. The first relates to the spatial processing of achromatic and chromatic information at the level of the striate cortex. The second relates to the nature of the mechanism underlying collinear facilitation.

The processing of achromatic and chromatic spatial information

These results suggest similar, although segregated, processing of achromatic from R/G and B/Y stimuli at the level of the striate cortex, where collinear facilitation is thought to originate (Kasamatsu et al., 2001; Mizobe et al., 2001; Polat et al., 1998). This adds further psychophysical evidence for the independent processing, at least at threshold, of achromatic and chromatic information already supported by adaptation (Krauskopf et al., 1982),

masking studies (Mullen & Losada, 1994; Sankeralli & Mullen, 1997; Switkes et al., 1988), and subthreshold summation (Mullen & Sankeralli, 1999). This effect is also reminiscent of the results for contour integration using "path stimuli" composed of strings of oriented Gabors because these show that color vision can support contour integration based on local linking of orientation across space (McIlhagga & Mullen, 1996; Mullen et al., 2000). However, this local linking is substantially disrupted when Gabor elements alternate between chromatic and achromatic contrast, indicating that contour integration is selective for the chromaticity of its inputs. Thus, both these tasks, based on orientation-specific lateral interactions, are supported by color contrast and are selective for the color and phase of the co-aligned elements.

Our findings are consistent with physiological studies showing segregated processing of color and luminance (Conway & Livingstone, 2006; Livingstone & Hubel, 1984, 1987, 1988; Zeki, 1983). The idea, however, that orientationally selective spatial processing based on color and achromatic contrast is segregated at the level of V1 is not generally supported by neurophysiological results,
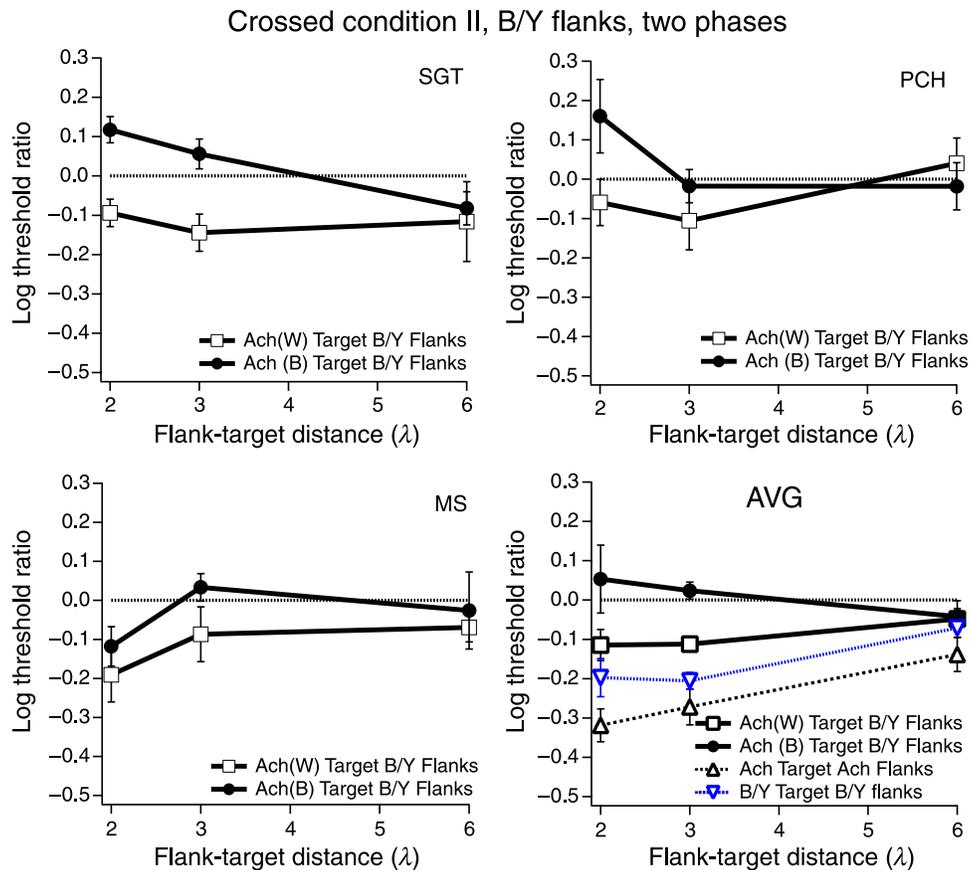
Figure 7. Results for Ach target with B/Y flanks conditions. White squares show the condition in which a blue bar is aligned with the white bar and black circles show the condition in which a blue bar is aligned with the white bar. The error bars represent ±1 SE. AVG represents the average data from three subjects. For comparison, the average data for three subjects in uncrossed conditions are also plotted: the black dashed line (upright triangles) shows the achromatic phase aligned condition and the blue dashed line (inversed triangles) shows the B/Y phase aligned condition.

which tend to find that orientationally tuned single cells typically combine cone opponent and luminance signals at an early cortical stage (Gegenfurtner & Kiper, 2003; Horwitz, Chichilnisky, & Albright, 2005; Johnson, Hawken, & Shapley, 2001, 2004; Lennie & Movshon, 2005), consistent with a more recent view that individual cortical cells can code several features. Our results imply that collinear facilitation may not be a general property of V1 cells because there is no collinear facilitation for our cross conditions (i.e., achromatic vs. chromatic).

What little evidence there is suggests that cardinal mechanisms may be restricted to the geniculocortical synapse in the input layers of the cortex (Tailby, Solomon, Dhruv, Majaj, & Lennie, 2005). If this is so, collinear facilitation may be limited to a subpopulation of cells that receive geniculate input in layer 4c beta of the striate cortex. Recent psychophysics also supports a very early, monocular cortical origin (Huang, Hess, & Dakin, 2006).

Also it is noticeable that the collinear facilitation exhibited by the B/Y mechanism is as strong as that of either of the other two mechanisms despite the fact that B/Y mechanism has a much sparser spatial representation

(Conway & Livingstone, 2006; Curcio et al., 1991; Dacey & Lee, 1994) and there are three times fewer B/Y compared with R/G blobs in V1 (Ts'o & Gilbert, 1988). In contour integration, although the B/Y mechanism also shows a somewhat greater decline with increasing element separation compared to the achromatic mechanism (Beaudot & Mullen, 2003), it generally supports contour integration over a similar spatial range to achromatic vision. Thus, despite the physiological differences in the neural sampling densities, our results suggest at the very least that comparable central processing for B/Y and achromatic postreceptoral mechanisms as far as collinear facilitation is concerned.

The nature of the mechanisms underlying collinear facilitation

Several psychological mechanisms has been proposed to explain collinear facilitation. One hypothesis suggests that facilitation results from the reduction of uncertainty provided by the flanks that provide good spatial and

temporal cues for detecting the central target (Petrov et al., 2006). However, if uncertainty is the sole explanation, we would expect that the crossed in-phase condition (Ach vs. R/G or Ach vs. B/Y) would show similar amount of facilitation to the uncrossed in-phase condition (Ach vs. Ach, R/G vs. R/G, B/Y vs. B/Y) and achromatic flanks should facilitate chromatic targets and vice versa. This is not the case in our main experimental results.

Another hypothesis assumes that facilitation is a special example of the pedestal effect in masking (Solomon et al., 1999; Williams & Hess, 1998). For example, the high contrast flanks, being located in the periphery of the cell's receptive field, would behave like a low contrast pedestal, resulting in facilitation. One prediction of this model is that the relative phase of the target and flanks will be a key factor in determining whether facilitations occur. Only if the target and flanks are in phase would one expect to see facilitation. However, whereas some studies (Polat & Sagi, 1993) report facilitation in the out-of-phase condition, the majority of recent studies have not found facilitation in the out-of-phase condition (Solomon et al., 1999; Williams & Hess, 1998). Our experimental results are consistent with this latter finding of phase dependence and strengthen the link between masking and collinear facilitation. Another prediction based on the masking analogy is that no facilitation will occur between chromatic and achromatic stimuli because there is no pedestal effect under these conditions (Mullen & Losada, 1994; Switkes et al., 1988). This is also the case in the present results.

Our working hypothesis is that the facilitation effect at short separations, where it is phase and chromatic dependent, is a reflection of the pedestal effect in masking or between channel interactions. Because most cortical cells do not exhibit independence for achromatic and chromatic processing (Gegenfurtner & Kiper, 2003; Johnson et al., 2001, 2004; Lennie & Movshon, 2005), our results suggests that collinear facilitation is not a general property of cortical cells, being restricted to only a subset of cells possibly located at the earliest stages of cortical processing.

Acknowledgments

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Footnote

[1]For the B/Y flanking targets at the greatest separation (6λ), a constant multiple of detection threshold could not be obtained as the cone contrast required was outside the gamut of the monitor. In this case, the flank contrast was set to highest cone contrast available (0.5), which was 2.9, 3.8, 3.9, and 3.9 times detection threshold for subjects HT, MS, PCH, and SGT, respectively.

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