

Chromatic collinear facilitation, further evidence for chromatic form perception

TAL ELLENBOGEN^{1,2}, URI POLAT^{3,*} and HEDVA SPITZER¹

¹ *Department of Biomedical Engineering, Faculty of Engineering, Tel Aviv University, Tel Aviv, Israel*

² *The Abramson Center of Medical Physics, Sackler Faculty of Exact Sciences, Tel-Aviv University, Tel Aviv, Israel*

³ *Goldschleger Eye Research Institute, Tel-Aviv University, Sheba Medical Center, Tel Hashomer, 52621 Tel Aviv, Israel*

Received 13 September 2005; accepted 5 May 2006

Abstract—Collinear facilitation of contrast detection of achromatic stimuli has been studied over the past decade by different groups. We measured collinear facilitation of chromatic contrast detection under equal-luminance (photometric quantity) and under isoluminance (minimum motion technique) conditions, as two different controls. The facilitation was tested for chromatic contrast detection of a foveal Gabor signal flanked by two high chromatic-contrast Gabor signals. The results indicated a significant facilitation in the presence of spatial adjacent collinear chromatic contrast signals, when the flankers were located at a short distance, across all observers for three chromatic channels. The facilitation was compared to a non-collinear flanker configuration. The results indicated no facilitation effect at the opposing phase configuration, at a short flanker distance, whereas a small facilitation was observed with a configuration at a longer flanker distance. The findings suggest that the performance and specificity of chromatic collinear facilitation is not impaired with regard to achromatic mechanisms.

Keywords: Lateral facilitation; color vision; isoluminance; visual cortex; contrast; collinear.

INTRODUCTION

The appearance of a visual stimulus, chromatic or achromatic, is modulated by context. There are opposite contextual modulation phenomena: the induction effects and the collinear facilitation of contrast detection. Induction is a psychophysical phenomenon associated with a change in color or luminance perception caused by the presence of a different surrounding average color (or luminance). Contrast induction is the result of surrounding contrast (color or luminance) modulating

*To whom correspondence should be addressed. E-mail: urip@post.tau.ac.il

the perceived contrast of the central area (D'Zmura and Singer, 1996; Singer and D'Zmura, 1994). These induction phenomena are suggested as mechanisms for enhancing the differences in contrast between surfaces or objects. When the contrast of the central stimulus is lower than the surrounding contrast, the induction will cause it to be perceived with even less contrast, an effect that is also known as lateral masking, lateral suppression, or lateral inhibition. When the contrast of a central stimulus is higher than the surrounding contrast, the induction will cause it to be perceived with even higher contrast.

In addition to induction phenomena there are opposite context-based phenomena such as the collinear facilitation of contrast detection, in which the similarity of the stimulus and its context is enhanced.

It has been shown that the visibility of a local target (Gabor patch, GP) improves when the target is presented between two collinear flankers (Polat and Sagi, 1993). The achromatic target threshold facilitation was found when the target was presented with the flankers (Adini and Sagi, 2001; Adini *et al.*, 1997; Bonnef and Sagi, 1998; Cass and Spehar, 2005; Polat and Sagi, 1993, 1994a, b; Solomon and Morgan, 2000; Williams and Hess, 1998; Woods *et al.*, 2002). Facilitation of the contrast threshold occurs preferentially with collinear flankers (Polat and Sagi, 1993, 1994a, b), suggesting that facilitation might occur preferentially along the collinear configurations (Chen and Tyler, 1999; Polat, 1999; Polat and Norcia, 1998; Polat and Tyler, 1999).

The collinear facilitation has also been shown in the early visual cortex, at the level of single neurons (Crook *et al.*, 2002; Kapadia *et al.*, 1995, 2000; Mizobe *et al.*, 2001; Polat *et al.*, 1998), suggesting the existence of early cortical loci for the effect.

The effect of collinear facilitation on contrast detection is a task that can be reasonably correlated to the early processes of form perception. Although there are presently no data on the effect of chromatic collinear facilitation, there is evidence of chromatic contour detection in search tasks (Mullen *et al.*, 2000), and chromatic spatial facilitation of a line target in the Kaniza paradigm (Dresp and Grossberg, 1999).

The simultaneous induction effect needed to enhance differences was also shown to exist when the stimuli are composed only of isoluminance chromatic information (Semo *et al.*, 1998; Wesner and Shevell, 1992). We wanted to investigate whether the opposite context mechanism, based on lateral interactions between color- and orientation-selective cells, which enhances the similarity of chromatic visual objects, also exists in the visual chromatic information processing system.

To test the existence of chromatic lateral interactions, mediating collinear facilitation of contrast detection, we used a paradigm similar to that used by Polat and Sagi (1993), but under equal-luminance (photometric quantity) and isoluminance (minimum motion technique, Anstis and Cavanagh, 1983; Cavanagh and Anstis, 1991) conditions, separately; moreover, we applied the degree of chromaticity contrast instead of luminance contrast composing the Gabor signals. Our results indicated

collinear facilitation of chromatic contrast detection, similar to the luminance domain.

METHODS

Apparatus

The stimuli were displayed on a Sony Multiscan G200 17" computer screen, with a spatial resolution of 1024×768 pixels, occupying a 12.2×8.7 visual degree area. In the equal-luminance sessions the display, as well as all the stimuli, was presented under equal luminance conditions of 26 cd/m^2 (Minolta CS-100; calibration was performed in CREO laboratories). The gamma values of each of the RGB channels were corrected to linear (Minolta CS-100 chroma meter). The stimuli were generated with a GeForce3 Ti 500 Graphics Processor. The experimental parameters were generated in Matlab, using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997).

Stimuli

The first part of the experiment was performed with stimuli that were under equal-luminance conditions (Table 1); it was also controlled with stimuli that were under isoluminance conditions (for each observer, separately, Table 2). We will describe the equal-luminance conditions first, and later we will describe the experiments under isoluminance conditions.

The stimuli consisted of one or three chromatic Gabor signals arranged vertically. The spatial chromatic modulation of the Gabor stimuli was determined according to pairs of colors that defined the modulation's extremum points. The chromaticity distance was calculated according to the Euclidian distance, in the CIE XYZ 1931 xy chromaticity diagram, for the specific chromaticity point (on the xy chromaticity diagram) from the White point (on the xy chromaticity diagram). The spatial

Table 1.

CIE 1931 xy chromaticity values for all contrasts end points at all tested channels: Red — Cyan are the end points of channel 1, Green — Magenta → channel 2, Orange — Greenish cyan → channel 3

| Chromatic channel | Color name | x chromaticity value | y chromaticity value |
|-------------------|---------------|------------------------|------------------------|
| 1 | Red | 0.434 | 0.336 |
| | Cyan | 0.236 | 0.334 |
| 2 | Green | 0.319 | 0.432 |
| | Magenta | 0.351 | 0.237 |
| 3 | Orange | 0.436 | 0.380 |
| | Greenish cyan | 0.236 | 0.383 |

Table 2.

CIE 1931 xy chromaticity values for contrasts end points at for the isoluminance experiment, the values are presented for the two observers

| Observer | Color name | Y value (Cd/m ²) | x chromaticity value | y chromaticity value |
|----------|------------|-----------------------------------|---------------------------|---------------------------|
| AR | Red | 22.8 | 0.442 | 0.328 |
| | Cyan | 28 | 0.246 | 0.345 |
| JG | Red | 22.5 | 0.442 | 0.328 |
| | Cyan | 27.6 | 0.246 | 0.347 |

chromatic distribution of each Gabor signal, \vec{C} , was adjusted as follows:

$$\vec{C}(i, j|i_0, j_0) = \vec{A}_c \cos\left(\frac{2\pi}{\lambda}((i - i_0) \cos \theta + (j - j_0) \sin \theta)\right) \times \exp\left(-\frac{(i - i_0)^2 + (j - j_0)^2}{\sigma^2}\right), \quad (1)$$

where i and j represent the pixel i, j on the computer monitor, while pixel i_0, j_0 is the Gabor's central pixel. The symbol λ represents the wavelength of the Gabor signal (expressed in pixel units) and σ is the decay factor of the signal's Gaussian envelope (pixel units). θ specifies the Gabor's orientation such that under condition $\theta = 0$, the Gabor is determined as vertically aligned. The symbol \vec{A}_c represents the amplitude of the chromaticity distance of the Gabor signal. The symbols \vec{C} and \vec{A}_c are vectors since they represent xy values on the CIE xy chromaticity diagram. Figure 1 presents an illustration of the spatial chromaticity distribution function, according to equation (1).

Parameter λ was chosen to be 0.25 deg. (i.e. spatial frequency of 4 cpd) at a viewing distance of 1.5 m for all experiments and all Gabor signals. The parameter σ was determined to be equal to λ and thus enables one to observe at least one cycle of the flankers' Gabor signals, while, at the same time, avoids an overlap of target and flankers at the minimal Gabor flankers-target distance.

The presentation of three Gabor signals, shifted by Δj , as specified by equation (2), describes the stimuli used in the following experiments (Polat and Sagi, 1993):

$$\vec{C}(i, j|i_0, j_0) = \vec{C}_f(i, j|i_0, j_0 - \Delta j) + \vec{C}_t(i, j|i_0, j_0) + \vec{C}_f(i, j|i_0, j_0 + \Delta j) + \vec{C}_0, \quad (2)$$

where \vec{C}_f and \vec{C}_t are the chromaticity spatial modulations of flankers and target Gabor signals, correspondingly and \vec{C}_0 is the background chromaticity. All vectors represent points on the CIE xy chromaticity diagram.

Three pairs of colors were chosen to form three different chromatic contrast channels. Each of the chromatic channels was built under equal-luminance conditions (26 cd/m²), and in these experiments all the chromatic Gabor signals and the background had equal luminance measured using the Minolta CS-100. All the colors that formed a Gabor signal were modulated along the chromaticity line that was de-

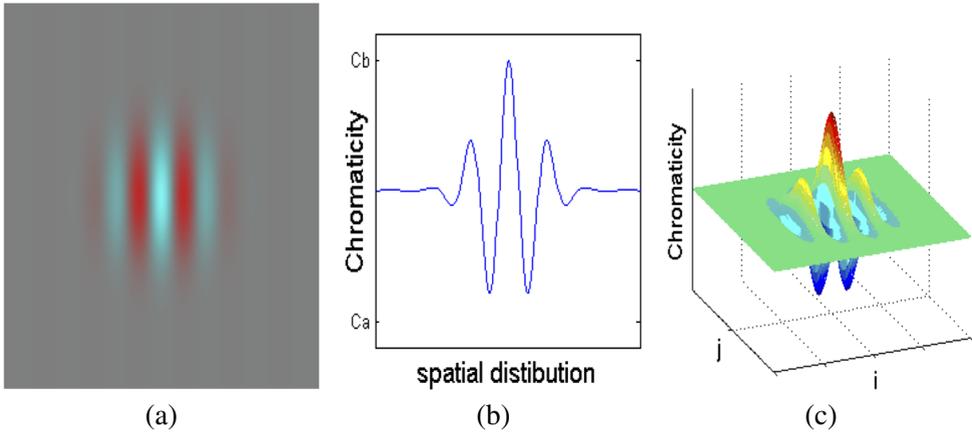


Figure 1. (a) A demonstration of a Gabor signal. (b) A schematic spatial chromaticity profile of the Gabor signal. The Gabor signal's chromaticity distribution is assessed according to the line defined between two points of the CIE xy chromaticity diagram, and according to the Gabor's spatial function (Equation (1)). (c) A schematic illustration in 2 spatial dimensions that demonstrate the Gabor's spatial chromaticity distribution according to the spatial Gabor function modulation. This figure is published in colour on <http://www.ingenta.com>

finer by a pair of chromatic points on the xy chromaticity diagram. This modulation is described by the Gabor function of equation (1) (Figs 1b, c and Fig. 2). We chose two pairs of colors that defined the Gabor signal to consist of complementary colors (i.e. colors that can be additively mixed to produce an achromatic color; in other words, located on a straight line across the White point in, for example, the CIE xyz chromaticity diagram), and a third pair to consist of non-complementary colors, Fig. 2 and Table 1. In this way, the three different pairs of colors defined three different chromatic contrast channels. The stimuli were chosen to consist of color pairs that are complementary, in order to test whether the effect of chromatic collinear facilitation is similar or opposite to the effect of chromatic color induction, where the induced color is complementary to its chromatic inducer (Krauskopf *et al.*, 1986; Semo *et al.*, 1998; Spitzer and Barkan, 2005; Webster and Mollon, 1995). To include this question in the current study, we were obliged to choose a color space that would enable us to choose these complementary colors easily, and therefore we chose CIE XYZ, which is defined by luminance rather than luminance perception.

The background chromaticity of each channel was the middle point of the chromaticity line defining the channel. All maximum chromaticity distances were determined to be ~ 0.1 in the CIE xy chromaticity diagram. The CIE xy values of their maximum chromaticity are shown in Table 1 and Fig. 2.

A schematic illustration of the stimulus, which consists of the target and the flankers, is presented with its spatial chromatic profile in Fig. 3. The central Gabor signal is the target, and the two adjacent Gabor signals are the flankers. The Δj in equation (2) was chosen to equal 3λ and 4λ . At these Gabor signal separations,

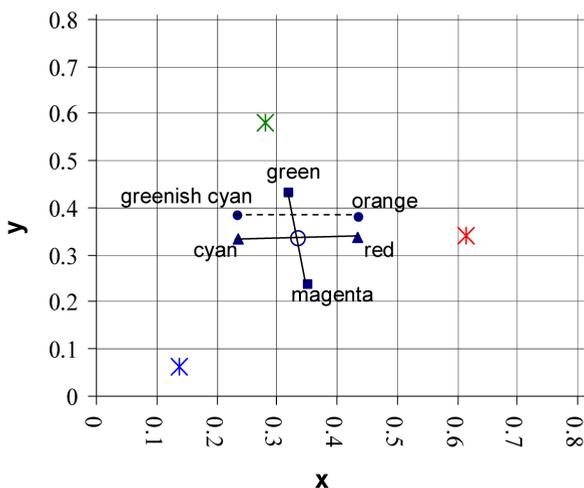


Figure 2. The chromaticity values of the three different color channels presented on the CIE 1931 xy chromaticity diagram. Each chromatic contrast channel is defined by two hues, complementary (solid lines) or non — complementary (dashed line). The full points represent the maximum values of the chromaticity distance of each of the color channels. Each pair of hues defines a chromatic Gabor signal, presented by the straight lines (solid or dashed). The complementary colors (squares and triangles) cross the CIE 1931 white point (empty circle). The non-complementary colors (dark circles) do not cross the white point. The three stars present the monitor’s color gamut. This figure is published in colour on <http://www.ingenta.com>

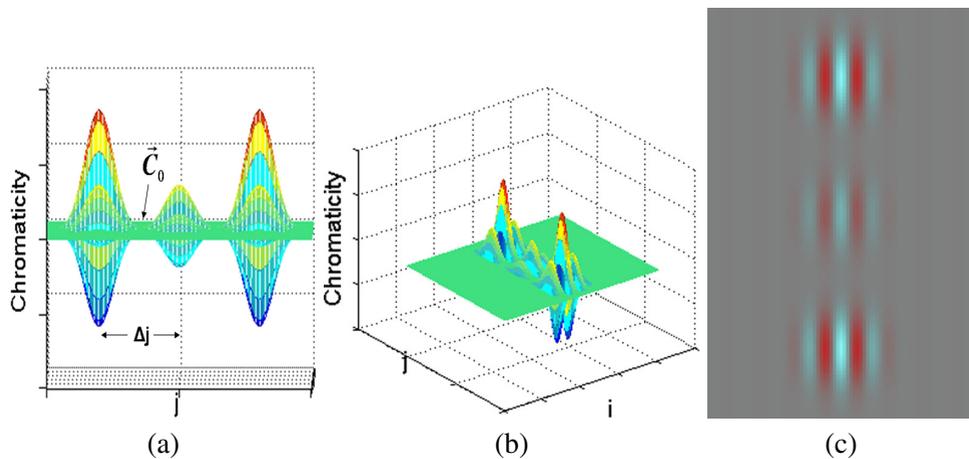


Figure 3. Illustration of a stimulus consisting of 3 Gabor signals, 2 flankers, and 1 target (central Gabor signal). (a) Spatial chromaticity profile plot of the stimulus. \bar{C}_0 is the background chromaticity and Δj is the distance between the center of the target to the centers of the flankers; here Δj is equal to 4λ . (b) Mesh plot of the spatial chromaticity distribution of the three Gabor signals. (c) The stimulus described in (a) and (b). This figure is published in colour on <http://www.ingenta.com>

we obtained conditions with no constructive interference (overlapping) in the center Gabor signal (target).

The spatial frequency of the Gabor was set to 4 cpd, in accordance with the spatial frequency used in the achromatic paradigm of Polat and Sagi (1993, 1994). It has been suggested that 4 cpd is somewhat high for a chromatic stimulus and consequently may be susceptible to chromatic aberrations (Anstis and Cavanagh, 1983; Cavanagh and Anstis, 1991). However, we have selected the following stimulus parameters and made control experiments that avoid artifacts in our study. (1) 4 cpd is still not above the limit that can cause luminance artifacts due to the display's limitations and due to chromatic aberrations. Since the observers sat at a viewing distance of 1.5 m from the display, each cycle of the 4-cpd stimuli occupied 21 pixels, which are sufficient to avoid luminance artifacts. (2) This spatial frequency is also sufficiently low to avoid luminance artifacts caused by chromatic aberrations (Cottaris, 2003; Delahunt *et al.*, 2005). (3) The main aim of our study was to explore collinear facilitation. If indeed there is a luminance artifact on an order of 10% (Anstis and Cavanagh, 1983; Cavanagh and Anstis, 1991), then the luminance contrast of the flankers may be too low to induce facilitation at 3λ . (4) We performed a control experiment with one subject (AR) in which we tested the collinear facilitation at 3λ with flankers having a luminance contrast of 10%. The results indicate no facilitation at all. (5) To be on the safe side, however, we also performed control experiments using 3-cpd stimuli under isoluminance conditions, along with a minimum motion technique (Anstis and Cavanagh, 1983; Cavanagh and Anstis, 1991) for two observers subjected to red-cyan chromatic stimuli (see below).

The different stimulus configurations for target and flankers were as follows: target in void with $\theta = 0^\circ$, target and masks shifted with $\Delta y = 3\lambda$ and 4λ equally oriented ($\theta = 0^\circ$, collinear), target and masks shifted with $\Delta y = 3\lambda$ and perpendicularly oriented with $\theta_f = 90^\circ$ and $\theta_t = 0^\circ$ (not collinear).

We also tested the contrast detection for two configurations of flankers and target with opposing spatial Gabor phases as detailed below. The different stimulus configurations in this case were target in void with $\theta = 0^\circ$, target and masks shifted with $\Delta y = 3\lambda$ and with $\theta = 0^\circ$, target and masks shifted with $\Delta y = 4\lambda$ and with $\theta = 0^\circ$.

Figure 4 presents all the stimulus configurations; the details about the procedure will be described in the experimental procedures section.

We added the experiments under isoluminance conditions in order to eliminate the possibility that the luminance domain may contribute to the chromatic effect, due to different luminance perceptions of the different chromatic stimuli regions. For this purpose, we built a separate set of isoluminance stimuli for each observer (Table 2). The stimuli under isoluminance conditions were chosen to be with a spatial frequency of 3 cpd, in order to lower the probability of chromatic aberrations. The minimum motion technique (Anstis and Cavanagh, 1983; Cavanagh and Anstis, 1991) was used to test two observers for isoluminance conditions with red-cyan chromatic stimuli (Table 2). This test of isoluminance was performed on the part of the screen that occupies the area of the target and its flankers. One of the two observers was tested under both equal-luminance and isoluminance conditions.

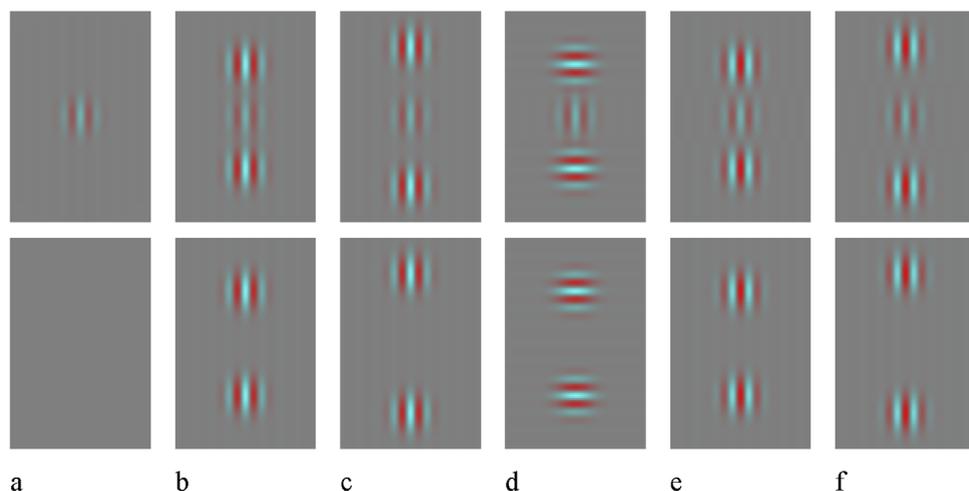


Figure 4. The different stimulus configurations used in this study. The two alternative forced choice stimuli are presented separately in the upper row and the lower row. During the presentation of the different stimuli 4 visible crosses appeared at the sides of the screen. The upper row shows the different stimulus configurations that included the target. The lower row shows the corresponding stimulus configurations without the targets. The different stimulus configurations are: (a) Target in void. (b) Collinear flankers with equal spatial phases, shifted by 3λ (i.e. the distance between the center of the target to the centers of the flankers is 3 times the wavelength of the Gabor signals). (c) Collinear flankers with equal spatial phases, shifted by 4λ . (d) Flankers perpendicular to the target shifted by 3λ . This stimulus configuration was regarded as a control experiment. (e) Collinear flankers with opposing spatial phases (the spatial phases of the flankers is opposite that of the spatial phase of the target) shifted by 3λ . (f) Collinear flankers with opposing spatial phases shifted by 4λ . This figure is published in colour on <http://www.ingenta.com>

Experimental procedures

The experiment was preceded by a short practice session to familiarize the observers with the task procedure. Before each experiment the observers became adapted (for at least 5 min) to the screen luminance in an otherwise dark room. We used a temporal two-alternative forced-choice procedure (TAFC). The stimuli with and without target were presented in a random order and contained clearly visible crosses at the sides of the stimuli area on the screen, so that the observer was well aware when a stimulus was presented and when only the background was presented.

At the beginning of each trial the observer was required to fixate on a small cross in the center of the screen. The trial sequence was initiated by pressing a mouse key. Figure 5 shows the time sequence of events during a single trial of all the experiments. Each sequence began with a background chromaticity image. The background chromaticity point is the middle point of the line of the chromatic channel in the CIE xy chromaticity diagram, Fig. 2, Table 1. In the case of complementary channels the background is achromatic. The background image was first presented for a randomized time interval between 270 and 360 ms; then the first stimulus (one of the TAFC stimuli) was presented for 100 ms. An inter-stimuli

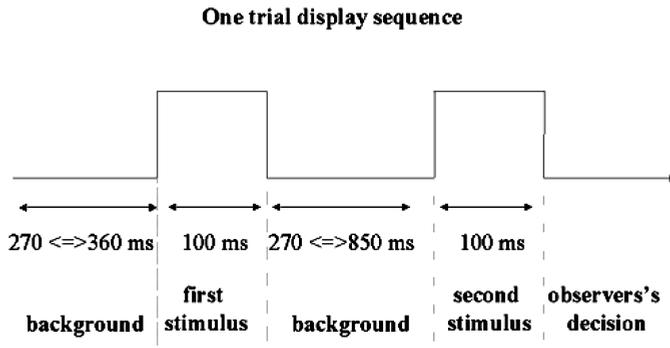


Figure 5. A schematic time sequence of events in a single trial. The time sequence is initiated by the observer pressing a mouse key. At the end of the sequence the observer, by pressing the appropriate mouse key, decided whether the target appeared in the first or the second stimulus.

interval of background chromaticity was shown for a randomized time between 270 and 850 ms (Polat and Sagi, 1993), and then the second stimulus was presented for another 100 ms. After the presentation of two stimuli, the observer had to decide whether the target appeared in the first or in the second stimulus, by pressing the mouse key. Auditory feedback was given for an incorrect trial response.

The contrast detection threshold was estimated using the following staircase procedure: Increasing the target chromatic contrast by 0.1 log units for each incorrect response, and decreasing the target chromatic contrast by 0.1 log units after three consecutive correct responses. The units represent the percentage of applied contrast in relation to the maximum contrast of a contrast channel (Table 1). A change in the direction of the target contrast modulation, i.e. increasing the target contrast following a previous decrease in the target contrast, or *vice versa*, is termed a reversal. A block of trials consisted of 8 reversals. The mean logarithmic contrast during the last 6 reversals was used as the threshold estimate. This staircase method has 79% correct convergence (Levitt, 1971). A threshold datum point consisted of an average of 4 to 5 threshold estimates for each observer at each stimulus configuration.

The observers were required to perform one experimental session per day, approximately 1 h each. Each session consisted of three approximately 20-min sub-sessions, each of which was with a different color channel, followed by a break. Each sub-session included threshold estimations of all 4 configurations of flankers and targets, as shown in Fig. 4a–d. The order of configuration presentations at each sub-session was randomized, and the presentation of each configuration included a full staircase procedure.

In order to determine the spatial phase specificity of the effect, we added an additional experiment, to test the configurations of 3λ and 4λ distances with opposing spatial phases between target and flankers, as shown in Fig. 4e and f. We tested the spatial phase specificity across two observers, using the red–cyan color contrast channel (Table 1). This experiment was performed according to the

same procedure and parameters (except for the spatial phases) as the experiment with equal phases.

Observers

The equal-luminance experiments were performed across four naive observers; the isoluminance experiments were performed across two other naive observers. All observers were young (less than 30 years old) and were tested to ensure that they have normal or corrected-to-normal visual acuity and normal color vision.

RESULTS

The effect of chromatic collinear flankers on the chromatic contrast detection thresholds of foveal Gabor signals (i.e. targets) was determined. The effect was determined mainly for equal-luminance stimuli, but was also confirmed for isoluminance stimuli. The results for the equal-luminance stimuli will be presented first, followed by the results for the isoluminance stimuli.

Using the equal-luminance stimuli, we tested three different chromatic contrast channels, at two different configurations with equal phases of target and flankers (i.e. target Gabor and flankers Gabors of the same cosine spatial phase), as shown in Fig. 4a–d, and two different configurations of opposing phases of target and flankers (i.e. target Gabor and flankers Gabors of the opposite cosine spatial phase), as shown in Fig. 4e and f. The threshold facilitations (threshold of target and flankers divided by the threshold of target in void in log units) were calculated and are presented (with the opposite sign for viewing purposes) at Figs 6–9.

Figure 6 presents the threshold facilitations for the target stimulus at three different configurations of equal phases of target and flankers, as shown on Fig. 4b–d, across three different chromatic contrast channels (Table 1). The figure presents a comparison of target threshold facilitations, while the target and flankers were allocated in the collinear vertical orientation at distances of 3λ and 4λ (white bars and gray bars, correspondingly). The control experiment was a third stimulus configuration, where the flankers were at a horizontal orientation perpendicular to the vertically oriented target, as seen in Fig. 4d.

Results are presented separately for each of the 4 observers (Fig. 6a–d) across all three chromatic channels (1–3 on the x axis). The results for all 4 observers show significant facilitation ($p < 0.05$, t -test) in all collinear stimulus configurations and all chromatic channels, therefore supporting the existence of collinear lateral facilitation in chromatic channels (under equal-luminance conditions). The results also show small, but significant, facilitation for most of the control configurations of a flanker perpendicular to the target. These prominent effects are shown in Fig. 6, which shows significantly larger threshold facilitations of the target when the flankers were placed at 3λ distance than the results of the control experiment, where the flanker configuration was not collinear (dark bars). This effect was found for all the three chromatic contrast channels tested for all observers.

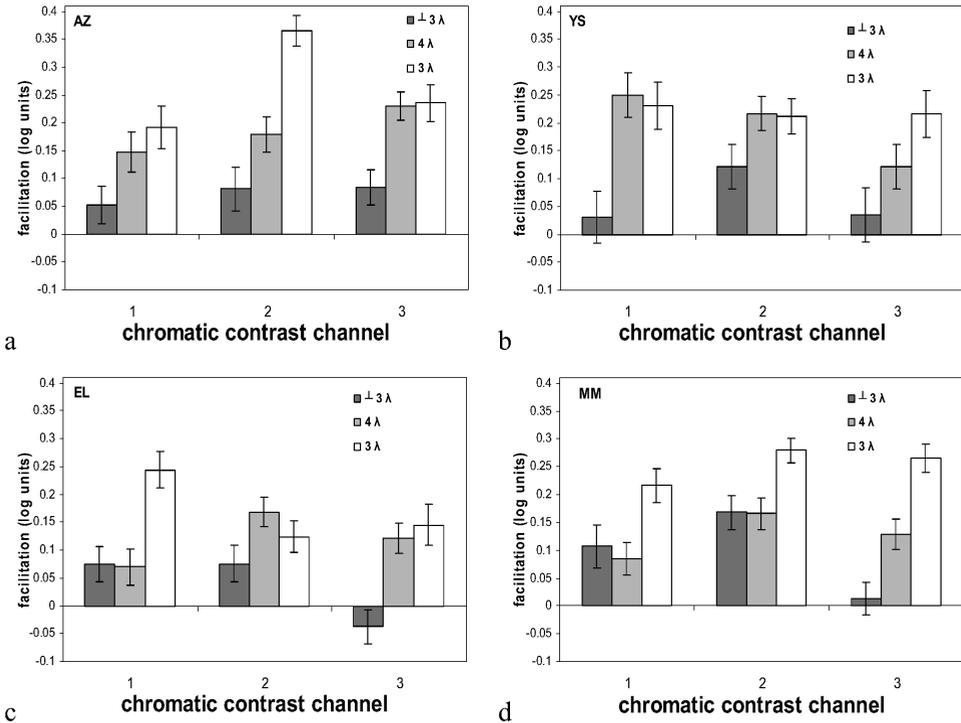


Figure 6. The effect of the flankers on target detection for 4 different observers, a–d. The results show facilitation of the detection threshold of the target due to flankers in most of the stimulus configurations. The bar legend are dark bars — control experiment, flankers perpendicular to the target, gray bar — collinear flankers at 4λ distances, white bar — collinear flankers at 3λ distances. The three chromatic contrast channels are marked with 1–3 on the x axis, Table 1. The y axis represents the threshold facilitation of the targets due to their presentation with the flankers. The facilitations are calculated as the logarithmic value of threshold of the target when presented with flankers divided by the threshold of the target when presented in void.

The results for all observers indicate a larger facilitation effect at the 3λ configuration than the non-collinear configuration (worst case $p = 0.08$, other cases $p < 0.05$, t -test), across all chromatic channels, except for one observer (EL), whose results show a larger though not significant effect ($p = 0.25$, t -test) for one of the chromatic channels. Nine out of the twelve stimulus configurations yielded a significantly larger facilitation effect at 4λ in the collinear configurations in comparison to the control configuration. Notably, in 8 out of 12 control configurations (flanker perpendicularly oriented to the vertical target with a distance of 3λ from the target) a small but significant facilitation was observed.

Figure 7a–d, shows the detection threshold of the target stimulus while it was presented in void, across 3 chromatic channels (1–3 on the x axis), for all 4 observers (a–d). Three of the 4 observers showed lower detection thresholds at channel 2 (green magenta complementary channel), but only one was significantly lower ($p < 0.05$, t -test). One of the observers (YS) showed an overall higher

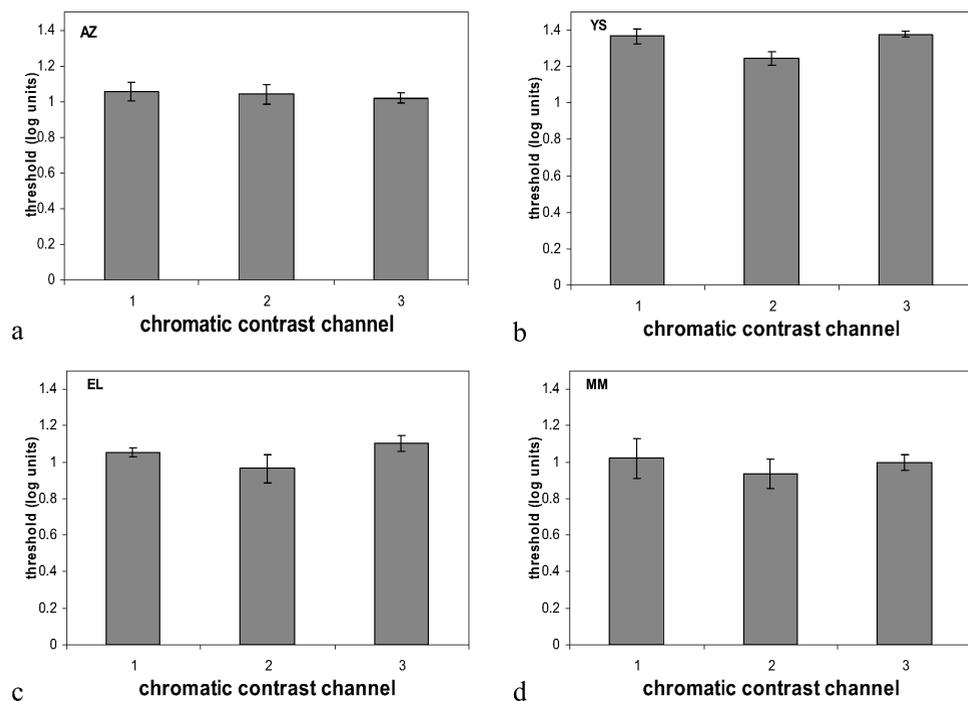


Figure 7. The results of absolute contrast detection thresholds of targets in void are presented across 4 different observers, a–d. The y axis presents the contrast detection thresholds in log units. The results are presented for the three color channels tested, 1–3 on the x axis (CIE chromaticity values are presented in Fig. 2 and Table 1).

detection threshold than the others, who showed similar threshold values. Note that the threshold facilitations were calculated separately for each observer and for each chromatic channel in comparison to the results of the threshold of the target in void.

In order to assess the general trend of the facilitation of contrast detection across the different chromatic contrast channels, we averaged the results of the 4 observers for each of the different stimulus paradigms (Fig. 8a). Figure 8b presents the average detection thresholds, for 4 observers, of the target presented in void for each of the chromatic contrast channels separately. As shown in Fig. 8a, there was significant facilitation in the average detection thresholds at both 3λ and 4λ across all the three chromatic contrast channels. In addition, the average facilitation of contrast detection was found to be significantly larger at 3λ than at 4λ , across the 3 chromatic contrast channels. It is also interesting to note that an average small, but significant, facilitation was observed for the control configuration (flankers perpendicular to the vertical target) at two of the three chromatic channels ($p < 0.02$, at the third $p = 0.11$, t -test). Channels 1 and 3 (red–cyan and orange–greenish cyan) clearly show similar results for a target in a void detection threshold, whereas channel 2 (green–magenta) shows lower detection thresholds, but not with a significant shift. In all the paradigms tested, we could not find a trend of results

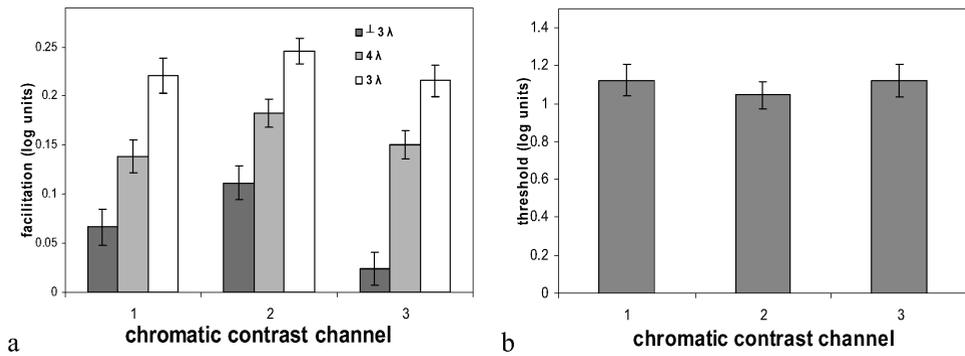


Figure 8. (a) Results of the averaged detection thresholds that show the facilitation for the 4 observers for each stimulus configuration and chromatic contrast channels separately, see Fig. 6. (b) Average contrast detection thresholds of the target presented in void across 4 observers, see Fig. 7.

that distinguish the two complementary channels 1 and 2 (Figs 6–8) from the non-complementary channel, channel 3 (Table 1).

Figure 9 presents a comparison between the detection thresholds' facilitation at the equal phases (Fig. 4b and c), and at the opposing phases' configurations (Fig. 4f and g). The results show no facilitation effect (Fig. 9a and b) at the opposing phase configuration for the 3λ distance (white bar in the right side), i.e. the detection threshold with or without the flankers is similar, with a small facilitation (0.07 log units) for the 4λ configuration. The amount of facilitation in the 4λ configuration is not appreciably different from the control experiment, where the flankers were in a configuration perpendicular to the target (dark bar). The two observers showed the same trend of results (Fig. 9a and b), and their averaged results are shown in Fig. 9c. In comparison to the equal phase case, the results clearly show a different trend. More specifically, the equal phase configurations show a larger facilitation at 3λ than at 4λ, whereas the anti-phase configuration shows no facilitation at 3λ and a small facilitation at 4λ, at the same order of magnitude as the control experiment of flankers oriented perpendicular to the target.

To test whether the chromatic facilitation resulted from different luminance perceptions of different stimuli regions, we performed additional experiments under isoluminance conditions. Figure 10a–c, presents the results for chromatic lateral facilitation of two other observers, under isoluminance conditions. The results of both observers show a significant facilitation for collinear 3λ flankers at the red-cyan channel (Table 2). Both observers show slight suppression for the non-collinear configuration (for the perpendicular flanker configuration). Figure 10c shows the averaged results with significant facilitation for the two observers at the collinear configuration, whereas for the non-collinear condition, the averaged results show a trend of suppression but not significant ($p < 0.18$, t -test). Figure 11 compares the performance of one of the observers under equal-luminance and isoluminance conditions for the same stimuli. For the non-collinear configuration, different trends of results were observed: the equal-luminance stimuli yielded a slight facilitation

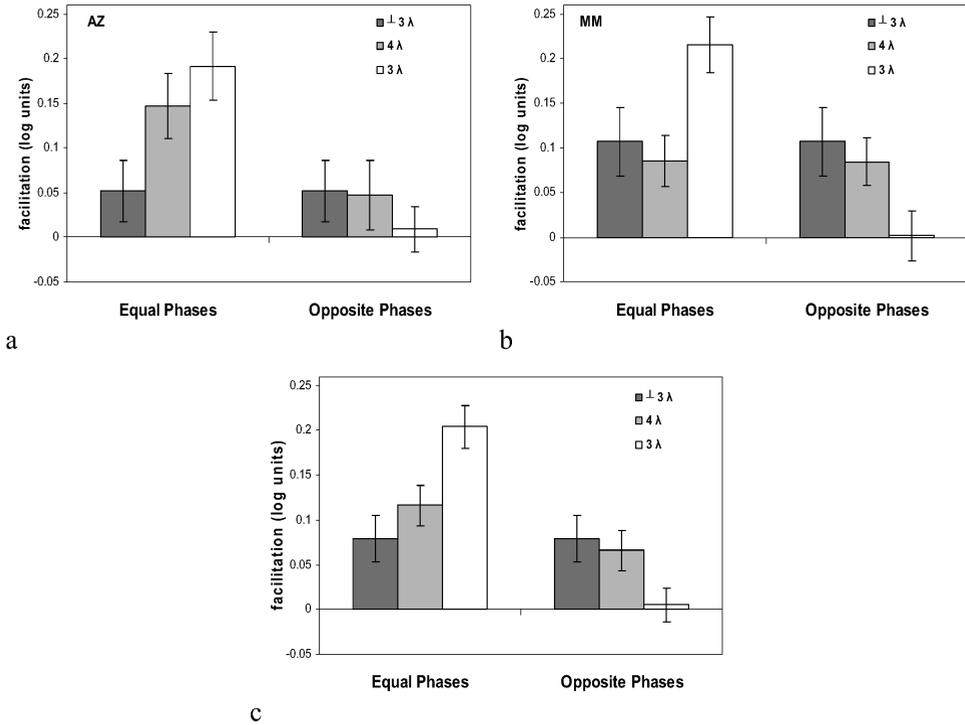


Figure 9. The contrast threshold facilitations for the configurations of flankers and target with opposing phases in comparison to the equal phase results, across two observers, a, b, and the averaged thresholds of the 2 observers, c. The left side of each bar plot presents detection threshold facilitations for the equal phase configurations. The right side indicates detection threshold facilitations for the opposing phase configurations. The control configurations of flankers perpendicular to the vertically oriented target (dark bars at the left and right sides) were taken from the same block of trials for the two stimulus configurations. 4λ distances (middle gray bars), 3λ distances (light bars) are presented.

(~ 0.1 log units), whereas the non-collinear isoluminance stimuli yielded a slight suppression. Overall, the results of the collinear configuration under both equal-luminance and isoluminance conditions showed significant facilitation.

DISCUSSION

In this study we examined the possibility of the collinear lateral interactions phenomenon existing in chromatic pathways, using equal-luminance and isoluminance stimuli. Importantly, we found a significant facilitation (i.e. a decrease in the target detection threshold) in the presence of spatially adjacent collinear high chromatic contrast signals. This facilitation was observed for three tested chromatic channels. An overall larger facilitation was found under collinear configurations than under non-collinear configurations. We found a pronounced facilitation for the stimuli composed of two pairs of complementary colors, as well as for the pair of non-complementary colors.

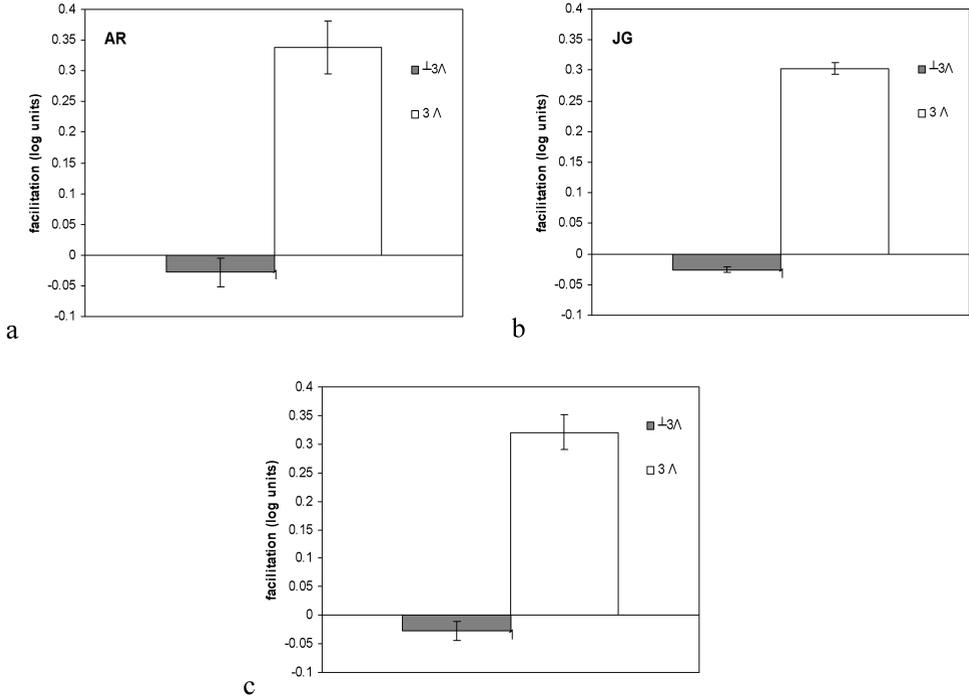


Figure 10. (a), (b) The results of contrast threshold facilitations under isoluminance conditions, for two observers. Under these conditions, the 3-cpd stimuli have been tested; the dark bar represents the facilitation for 3λ non-collinear flanker configuration, and the white bar represents 3λ collinear configuration. (c) Average results for the two observers.

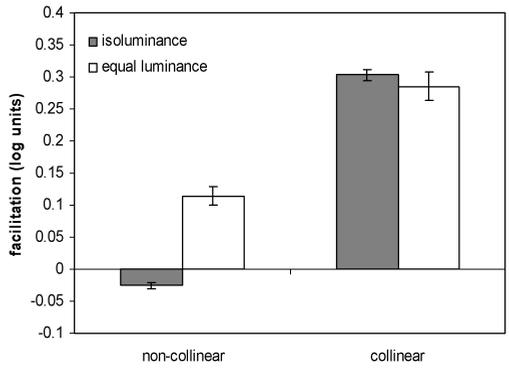


Figure 11. Comparison of performance of one observer to 3-cpd isoluminance stimuli (dark bars) and 3-cpd equal luminance stimuli (white bar); left is the non-collinear configuration and right is the collinear configuration.

Is the collinear facilitation a purely chromatic effect? We used Gabor patches of 4 cpd in accordance with the spatial frequency used in the achromatic paradigm by Polat and Sagi (1993, 1994). It has been suggested that 4 cpd might be a high spatial frequency for chromatic stimuli and may be susceptible to chromatic

aberrations (Anstis and Cavanagh, 1983; Cavanagh and Anstis, 1991). In the Methods section we argued against the contribution of the achromatic aberrations and possible artifacts to our results. However, very importantly, in this study we made some controls to test whether there were artifacts that could be responsible for the effect. The main aim of our study was to explore the effects of collinear facilitation. In the study of Polat and Sagi (1993, 1994) the contrast of the flankers was high (32–40%); however, the lower flanker's contrast may facilitate the target given that they are not too low (Polat, 1999). Thus, if indeed there is a luminance artifact on an order of 10% (Anstis and Cavanagh, 1983; Cavanagh and Anstis, 1991), the luminance contrast of the flankers (in this study) is expected to be too low to induce facilitation at 3λ . Nevertheless, we performed a control experiment with one subject (AR) in which we tested the achromatic collinear facilitation at 3λ with collinear flankers having a luminance contrast of 10%. The results show no facilitation at all. Moreover, to be on the safe side, we also performed control experiments using chromatic 3-cpd stimuli under isoluminance conditions, using a minimum motion technique (Anstis and Cavanagh, 1983; Cavanagh and Anstis, 1991) for two observers on red-cyan chromatic stimuli. The chromatic facilitation was similar under the equal-luminance and isoluminance conditions. Thus, all together, our results seem to be due to chromatic conditions whereas the expected chromatic aberrations did not affect our results.

In order to test the specificity of the chromatic facilitation effect, we tested the threshold facilitations for targets with an opposing spatial phase to that of the flankers. Our results indicate that the selectivity of the effect is correlated to the phase of the flankers. When the flankers and the target were in the same phase, facilitation at 3λ and 4λ distances between flankers and target was found, whereas in the opposing phase configurations, we found no facilitation at 3λ , and a small facilitation at 4λ (0.07 log units). In fact, this 'facilitation' was smaller than that of the control experiment. Thus, we cannot arrive at a clear-cut conclusion from the current experimental data regarding to the mechanism that caused the different effect under the opposing phase configuration, since there can be several explanations to account for our findings. For example, possibly the relevant cortical chromatic receptive fields are larger, or possibly the cortical receptive fields of the simple cells type do not have sufficient spontaneous activity to enable an opposing effect, a 'negative' response (Spitzer and Hochstein, 1985). On the other hand, it is possible that various connectivity rules among receptive fields can be manifested through different modes.

The performance of the collinear facilitation of contrast detection with both equal-luminance and isoluminance chromatic stimuli was not impaired in comparison to the achromatic mechanism. We also noted a small facilitation when the flankers were orientated perpendicular to the target, only under equal-luminance conditions. However, our results with isoluminance indicated that facilitation had no effect for the non-collinear configuration. Polat and Sagi (1993) reported that the achromatic stimuli had no effect at this configuration, but a later study reported that a small

facilitation was found for this case (Yu *et al.*, 2002). In any case, the fact that larger facilitation was found for the collinear configurations indicates the specificity of the effect, regarding orientation, and also regarding the color domain.

The results regarding achromatic facilitation in the case of flankers with an opposing phase to the target are inconsistent. Polat and Sagi (1993) reported that facilitation occurred for this case. Additional studies found a similar trend with Gabor stimuli and line stimuli (Chen and Tyler, 1999; Dresch and Grossberg, 1999; Solomon *et al.*, 1999). However, Williams and Hess (1998) reported that the collinear interactions in a paradigm similar to that of Polat and Sagi (1993) are phase-dependent, and found no facilitation in the opposing flankers phase. In light of the current inconsistent results of part of the achromatic stimuli, there is no basis for comparison with the chromatic mechanism, which yielded no facilitation of contrast detection under the condition of collinear opposing phases in comparison to the control experiment (which tested the configuration of flankers perpendicular to the target) as seen in Fig. 9.

Collinear facilitatory interactions are believed to subserve major grouping tasks such as contour integration. Our results, presented in Fig. 8, on chromatic facilitation agree with those of Mullen and her colleagues (Mullen *et al.*, 2000) regarding chromatic contour integration. Mullen and her colleagues (Beaudot and Mullen, 2003; Mullen *et al.*, 2000) investigated the performance of the chromatic mechanism of contour integration using a search task. In their experiments, the observers were required to link oriented Gabor elements across space, in order to extract a contour. Their findings showed that the detection of a chromatic isoluminance contour yielded a performance of contour integration similar to the achromatic mechanism mainly when the separation of elements was not large. They also found that performance on isoluminance contours decline more rapidly with increasing separation of elements than on achromatic contours. Accordingly, the chromatic facilitation effect shows a similarity to the existence and the magnitude of the luminance facilitation effect, but the decline of the facilitation effect, as a function of the distance between the target and the flankers, appears to be larger with the chromatic mechanism. Our results (under equal-luminance conditions) indicate that the ratio of magnitudes of facilitation between the 4λ and 3λ separations is 0.69 ± 0.02 . In the achromatic paradigm of the Polat and Sagi experiment (see Fig. 2 in Polat and Sagi, 1993) the ratio of the magnitudes of facilitation between the 4λ and 3λ separations is 0.83. Thus, it appears that the declining trend in the chromatic facilitation is larger (faster decline) than that of the achromatic mechanism.

Many groups studying psychophysical and computational models for collinear lateral interactions and contour integration have suggested that the physiological basis may rely on the long-range connections (Bolz and Gilbert, 1989; Cass and Spehar, 2005; Gilbert and Wiesel, 1985, 1989; Grinvald *et al.*, 1994, Polat *et al.*, 1998; Ts'o *et al.*, 1986). It has been reported that these connections occur between similar orientation columns in V1 (Malach *et al.*, 1993) and that they span large distances and can convey contextual information (Fitzpatrick, 1996; Gilbert

and Wiesel, 1983; Schmidt *et al.*, 1997). Levi and his colleagues (Levi *et al.*, 2002) argued that since long-range connections in primate V1 area are known to be around 1–2 mm, they extend over a distance of only about 3–6 min of arc in the fovea (Levi, 1999), and this distance is too short to account for the effects observed psychophysically. Regardless of the length of the horizontal connections, it was suggested that long-range horizontal interactions can be established through cascades of (local) lateral connections. This enables signals to be conveyed over much longer distances than can be revealed by monosynaptic connections of the horizontal connections (Polat, 1999; Polat and Sagi, 1994b; Polat and Sagi, 1995). This view recently received support from the study of Li and Gilbert (2002).

It has also been suggested that single cells in area V2 bridge contour gaps of 1–3.5 degrees, although with a weaker response, than the response of the same neuron to a continuous bar (Peterhans and von der Heydt, 1989). Such receptive fields might play a role in the collinear facilitation effect, also due to the correspondence between the range of gap distances in the physiological and the psychophysical experiments (Polat and Sagi, 1993; methods). Long-range color-specific interactions have also been found between cytochrome-oxidase (CO) blobs, inter blobs and ocular connections in V1 and V2 (Malach *et al.*, 1994; Roe and Ts'o, 1999; Ts'o and Gilbert, 1988; Yoshioka *et al.*, 1996).

Many recent studies claimed no clear segregation between color-selective cells and orientation-selective cells (Friedman *et al.*, 2003; Gegenfurtner *et al.*, 1996; Leventhal *et al.*, 1995; Shapley and Hawken, 2002). Additional studies found the same trend of results while using optical imaging combined with electrophysiological recordings (Landisman and Ts'o, 2002a, 2002b). These studies showed that patches activated by isoluminance chromatic stimuli were highly correlated with the CO blobs, but were larger than the CO blobs and sometimes even bridged different blobs. Landisman and Ts'o (2000a, 2000b) found cells with mixed properties of color selectivity and orientation selectivity in the inter blobs' connections and the patches' border areas. Friedman and his colleagues (Friedman *et al.*, 2003) found that V1 and V2 contained a significant amount of cells, about 40%, which exhibited color selectivity as well as orientation selectivity. These recent physiological findings emphasize the absence of clear segregation between chromatic and form (i.e. luminance and orientation) mechanisms. This approach disputes earlier studies that suggested anatomical physiological and functional segregation between the color and form processing (Livingstone and Hubel, 1984, 1987, 1988; Zeki, 1983).

The effect of collinear facilitation (chromatic and achromatic) appear to be with an opposing mechanism rather than a related effect that consists of the induction effect and an adaptation mechanism (Dahari and Spitzer, 1996; Spitzer and Barkan, 2005). These two opposing processes enhance a patch (or an object) through the difference in the composition of its intensity, color or texture from its context, on the one hand, and facilitate its contours on the other hand. Although many computational models (Li, 1998; Pettet *et al.*, 1998; Ross *et al.*, 2000; Ursino and La Cara, 2004; Yen and Finkel, 1998) predict the dual effect of lateral interactions (both collinear facilitation

and non-collinear suppression), none predicts simultaneously the opposing context effects of collinear facilitation and the induction effects.

CONCLUSIONS

Contour integration and collinear facilitation are prominent properties of form perception. We found magnitude and spatial properties for collinear facilitation similar to those found in achromatic luminance paradigms. This supports the notion that the chromatic mechanisms are not impaired when compared to the achromatic mechanism with respect to form perception. Support for these findings appeared recently in several studies on chromatic neurons in V1 and V2 (Friedman *et al.*, 2003; Gegenfurtner *et al.*, 1996; Leventhal *et al.*, 1995; Shapley and Hawken, 2002) and were expressed candidly in the recent paper of Friedman *et al.* (2003). In their words: ‘these findings suggest that the cortical mechanisms of orientation and edge selectivity process chromatic and non-chromatic signals in exactly the same way’.

Acknowledgement

This research was partly supported by the Ela Kodesz grant (HS) and Israel Science Foundation (UP).

REFERENCES

- Adini, Y. and Sagi, D. (2001). Recurrent networks in human visual cortex: psychophysical evidence, *J. Opt. Soc. Amer. A* **18**, 2228–2236.
- Adini, Y., Sagi, D. and Tsodyks, M. (1997). Excitatory-inhibitory network in the visual cortex: psychophysical evidence, *Proc. Natl. Acad. Sci. USA* **94**, 10426–10431.
- Anstis, S. M. and Cavanagh, P. (1983). A minimum motion technique for judging equiluminance, in: *Colour Vision: Psychophysics and Physiology*, Mollon, J. D. and Sharpe, L. T. (Eds), pp. 66–77. Academic Press, London.
- Beaudot, W. H. A. and Mullen, K. T. (2003). How long range is contour integration in human color vision? *Vision Neuroscience* **20**, 51–64.
- Beaudot, W. H. A. and Mullen, K. T. (2005). Orientation selectivity in luminance and color vision assessed using 2-d band-pass filtered spatial noise, *Vision Research* **45**, 687–696.
- Bolz, J. and Gilbert, C. D. (1989). The role of horizontal connections in generating long receptive fields in the cat visual cortex, *J. Neurosci.* **1**, 263–268.
- Bonnehh, Y. and Sagi, D. (1998). Effects of spatial configuration on contrast detection, *Vision Research* **38**, 3541–3543.
- Brainard, D. H. (1997). The psychophysics toolbox, *Spatial Vision* **10**, 433–436.
- Cass, J. R. and Spehar, B. (2005). Dynamics of collinear contrast facilitation are consistent with long-range horizontal striate transmission, *Vision Research* **45**, 2728–2739.
- Cavanagh, P. and Anstis, S. (1991). The contribution of color to motion in normal and color-deficient observers, *Vision Research* **31**, 2109–2148.
- Chen, C. C. and Tyler, C. W. (1999). Spatial pattern summation is phase-insensitive in the fovea but not in the periphery, *Spatial Vision* **12**, 267–285.

- Cottaris, N. P. (2003). Artifacts in spatiochromatic stimuli due to variations in preretinal absorption and axial chromatic aberration: implications for color physiology, *J. Opt. Soc. Amer. A* **20**, 1694–1713.
- Crook, J. M., Engelmann, R. and Lowel, S. (2002). GABA-inactivation attenuates colinear facilitation in cat primary visual cortex, *Experimental Brain Research* **143**, 295–302.
- Dahari, R. and Spitzer, H. (1996). Spatiotemporal adaptation model for retinal ganglion cells, *J. Opt. Soc. Amer. A* **13**, 419–435.
- Delahunt, P. B., Hardy, J. L., Okajima, K. and Werner, J. S. (2005). Senescence of spatial chromatic contrast sensitivity. II. Matching under natural viewing conditions, *J. Opt. Soc. Amer. A* **22**, 60–67.
- Dresp, B. and Grossberg, S. (1999). Spatial facilitation by color and luminance edges: boundary, surface and attentional factors, *Vision Research* **39**, 3431–3443.
- D’Zmura, M. and Singer, B. J. (1996). Spatial pooling of contrast in contrast gain control, *J. Opt. Soc. Amer. A* **13**, 2135–2140.
- Fitzpatrick, D. (1996). The functional organization of local circuits in visual cortex: insights from study of tree shrew striate cortex, *Cerebral Cortex* **6**, 329–341.
- Friedman, H. S., Zhou, H. and von der Heydt, R. (2003). The coding of uniform colour figures in monkey visual cortex, *J. Physiol.* **2**, 593–613.
- Gegenfurtner, K. R. and Kiper, D. C. (1992). Contrast detection in luminance and chromatic noise, *J. Opt. Soc. Amer. A* **9**, 1880–1888.
- Gegenfurtner, K. R., Kiper, D. C. and Fenstemaker, S. B. (1996). Processing of color, form, and motion in macaque area V2, *Visual Neuroscience* **13**, 161–172.
- Gilbert, C. D. and Wiesel, T. N. (1983). Clustered intrinsic connections in cat visual cortex, *J. Neurosci.* **3**, 1116–1133.
- Gilbert, C. D. and Wiesel, T. N. (1985). Intrinsic connectivity and receptive field properties in visual cortex, *Vision Research* **25**, 365–374.
- Gilbert, C. D. and Wiesel, T. N. (1989). Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex, *J. Neurosci.* **9**, 2432–2442.
- Grinvald, A., Lieke, E. E., Frostig, R. D. and Hildesheim, R. (1994). Cortical point-spread function and long range interactions revealed by real-time optical imaging of macaque monkey primary visual cortex, *J. Neurosci.* **14**, 2545–2568.
- Hubel, D. H. and Livingstone, M. S. (1987). Segregation of form, color, and stereopsis in primate area 18, *J. Neurosci.* **7**, 3378–3415.
- Johnson, E. N., Hawken, M. J. and Shapley, R. (2001). The spatial transformation of color in the primary visual cortex of the macaque monkey, *Nature Neuroscience* **4**, 409–416.
- Kapadia, M. K., Ito, M., Gilbert, C. D. and Westheimer, G. (1995). Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in VI of alert monkeys, *Neuron* **15**, 843–856.
- Kapadia, M. K., Westheimer, G. and Gilbert, C. D. (2000). Spatial distribution of contextual interactions in primary visual cortex and in visual perception, *J. Neurophysiol.* **84**, 2048–2062.
- Krauskopf, J., Zaidi, Q. and Mandler, M. (1986). Mechanisms of simultaneous color induction, *J. Opt. Soc. Amer. A* **3**, 1752–1757.
- Landisman, C. E. and Ts’o, D. Y. (2002a). Color processing in macaque striate cortex: relationships to ocular dominance, cytochrome oxidase, and orientation, *J. Neurophysiol.* **87**, 3126–3137.
- Landisman, C. E. and Ts’o, D. Y. (2002b). Color processing in macaque striate cortex: electrophysiological properties, *J. Neurophysiol.* **87**, 3138–3151.
- Lennie, P. (2000). Color vision, in: *Principles of Neural Science*, Kandel, E. R., Schwartz, J. H. and Jessell, T. M. (Eds), McGraw-Hill, New York.
- Leventhal, A. G., Thompson, K. G., Liu, D., Zhou, Y. and Ault, S. J. (1995). Concomitant sensitivity to orientation, direction, and color of cells in layers 2, 3, and 4 of monkey striate cortex, *J. Neurosci.* **15**, 1808–1818.
- Levi, D. M. (1999). Long-range interactions in vision, *Spatial Vision* **12**, 125–127.

- Levi, D. M., Klein, S. A. and Hariharan, S. (2002). Suppressive and facilitatory spatial interactions in foveal vision: Foveal crowding is simple contrast masking, *J. Vision* **2**, 140–166.
- Levitt, H. (1971). Transformed up-down methods in psychoacoustics, *J. Opt. Soc. Amer.* **70**, 1458–1471.
- Li, W. and Gilbert, C. D. (2002). Global contour saliency and local collinear interactions, *J. Neurophysiol.* **88**, 2846–2856.
- Li, Z. (1998). A neural model of contour integration in the primary visual cortex, *Neural Computation* **10**, 903–940.
- Livingstone, M. S. and Hubel, D. H. (1984). Anatomy and physiology of a color system in the primate visual cortex, *J. Neurosci.* **4**, 309–356.
- Livingstone, M. S. and Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth, *J. Neurosci.* **7**, 3416–3468.
- Livingstone, M. S. and Hubel, D. H. (1988). Segregation of form, color, movement and depth: anatomy, physiology and perception, *Science* **240**, 740–749.
- Malach, R., Amir, Y., Harel, M. and Grinvald, A. (1993). Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primate striate cortex, *Proc. Natl. Acad. Sci. USA* **90**, 10469–10473.
- Malach, R., Tootel, R. B. and Malonek, D. (1994). Relationship between orientation domains, cytochrome oxidase stripes, and intrinsic horizontal connections in squirrel monkey area V2, *Cerebral Cortex* **4**, 151–165.
- Mizobe, K., Polat, U., Pettet, M. W. and Kasamatsu, T. (2001). Facilitation and suppression of single striate-cell activity by spatially discrete pattern stimuli presented beyond the receptive field, *Visual Neuroscience* **18**, 377–391.
- Mullen, K. T., Beaudot, W. H. A. and Møllhagga, W. H. (2000). Contour integration in color vision: a common process for the blue-yellow, red-green, and luminance mechanisms? *Vision Research* **40**, 639–655.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies, *Spatial Vision* **10**, 437–442.
- Peterhans, E. and von der Heydt, R. (1989). Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps, *J. Neurosci.* **9**, 1749–1763.
- Pettet, M. W., McKee, S. P. and Grzywacz, N. M. (1998). Constraints on long-range interactions mediating contour detection, *Vision Research* **38**, 865–879.
- Polat, U. (1999). Functional architecture of long-range perceptual interactions, *Spatial Vision* **12**, 143–162.
- Polat, U. and Bonnef, Y. (2000). Collinear interactions and contour integration, *Spatial Vision* **13**, 393–401.
- Polat, U. and Norcia, A. M. (1998). Elongated physiological summation pools in the human visual cortex, *Vision Research* **38**, 3735–3741.
- Polat, U. and Sagi, D. (1993). Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments, *Vision Research* **33**, 993–999.
- Polat, U. and Sagi, D. (1994a). The architecture of perceptual spatial interactions, *Vision Research* **34**, 73–78.
- Polat, U. and Sagi, D. (1994b). Spatial interactions in human vision: from near to far via experience dependent cascades of connections, *Proc. Natl. Acad. Sci. USA* **91**, 1206–1209.
- Polat, U. and Sagi, D. (1995). Placticity of spatial interactions in early vision, in: *Maturational Windows and Adult Cortical Plasticity*, Julesz, B. and Kovacs, I. (Eds), Vol. XXIV, pp. 1–15. Addison-Wesley, Reading, MA.
- Polat, U. and Tyler, C. W. (1999). What pattern the eye sees best, *Vision Research* **39**, 887–895.
- Polat, U., Mizobe, K., Pettet, M. W., Kasamatsu, T. and Norcia, A. M. (1998). Collinear stimuli regulate visual responses depending on cell's contrast threshold, *Nature* **391**, 580–584.

- Roe, A. W. and Ts'o, D. Y. (1999). Specificity of color connectivity between primate V1 and V2, *J. Neurophysiol.* **82**, 2719–2730.
- Ross, W. D., Grossberg, S. and Mingolla, E. (2000). Visual cortical mechanisms of perceptual grouping: interacting layers, networks, columns, and maps, *Neural Networks* **13**, 571–588.
- Schmidt, K. E., Geobel, R., Lowel, S. and Singer, W. (1997). The perceptual grouping criterion of colinearity is reflected by anisotropies of connections in the primary visual cortex, *Europ. J. Neurosci.* **9**, 1083–1089.
- Semo, S., Rosenbluth, A. and Spitzer, H. (1998). Remote adaptation in color vision-experimental study, *Perception* **27** (Suppl. 43).
- Shapley, R. and Hawken, M. (2002). Neural mechanisms for color perception in the primary visual cortex, *Current Opinion Neurobiology* **12**, 426–432.
- Singer, B. and D'Zmura, M. (1994). Color contrast induction, *Vision Research* **34**, 3111–3126.
- Solomon, J. A. and Morgan, M. J. (2000). Facilitation from collinear flanks is cancelled by non-collinear flanks, *Vision Research* **40**, 279–286.
- Solomon, J. A., Watson, A. B. and Morgan, M. (1999). Transducer model produces facilitation from opposite-sign flanks, *Vision Research* **39**, 987–992.
- Spitzer, H. and Barkan, Y. (2005). Computational adaptation model and its predictions for color induction of first and second orders, *Vision Research* **45**, 3323–3342.
- Spitzer, H. and Hochstein, S. (1985). Simple- and complex-cell response dependences on stimulation parameters, *J. Neurophysiol.* **53**, 1244–1265.
- Spitzer, H. and Semo, S. (2002). Color constancy: a biological model and its application for still and video images, *Pattern Recognition* **35**, 1645–1659.
- Ts'o, D. Y. and Gilbert, C. D. (1988). The organization of chromatic and spatial interactions in the primate striate cortex, *J. Neurosci.* **8**, 1712–1727.
- Ts'o, D. Y., Gilbert, C. D. and Wiesel, T. N. (1986). Relationships between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlation analysis, *J. Neurosci.* **6**, 1160–2117.
- Ursino, M. and La Cara, G. E. (2004). A model of contextual interactions and contour detection in primary visual cortex, *Neural Networks* **17**, 719–735.
- Webster, M. A. and Mollon, J. D. (1995). Colour constancy influenced by contrast adaptation, *Nature* **373**, 694–698.
- Wesner, M. F. and Shevell, S. K. (1992). Color perception within a chromatic context: changes in red/green equilibria caused by noncontiguous light, *Vision Research* **32**, 1623–1634.
- Williams, C. B. and Hess, R. F. (1998). Relationship between facilitation at threshold and suprathreshold contour integration, *J. Opt. Soc. Amer. A* **15**, 2046–2051.
- Woods, R. L., Nugent, A. K. and Peli, E. (2002). Lateral interactions: size does matter, *Vision Research* **42**, 733–745.
- Yen, S. and Finkel, L. H. (1998). Extraction of perceptually salient contours by striate cortical networks, *Vision Research* **38**, 719–741.
- Yoshioka, T., Blasdel, G. G., Levitt, J. B. and Lund, J. S. (1996). Relation between patterns of intrinsic lateral connectivity, ocular dominance, and cytochrome oxidase-reactive regions in macaque monkey striate cortex, *Cerebral Cortex* **6**, 297–310.
- Yu, C., Klein, S. A. and Levi, D. M. (2002). Facilitation of contrast detection by cross-oriented surround stimuli and its psychophysical mechanisms, *J. Vision* **2**, 243–255.
- Zeki, S. (1983). Colour coding in the cerebral cortex: the responses of wavelength-selective and colour-coded cells in monkey visual cortex to changes in wavelength composition, *Neuroscience* **9**, 767–781.