The effects of flankers on contrast detection and discrimination in binocular, monocular, and dichoptic presentations

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We investigated how two co-aligned adjacent stimuli (flankers) influence threshold versus pedestal contrast (TvC) functions in binocular, monocular, and dichoptic presentations. Targets were presented to the two eyes or to only one eye. pedestals and flankers were presented to the same eye to which the target was presented (binocular or monocular presentations) or to the other eye (dichoptic presentation). In the binocular presentation of targets and pedestals, the binocular flankers lowered thresholds at low pedestal contrasts. The monocular flankers had a similar effect to the binocular flanker, although the threshold reduction was smaller. In the dichoptic presentation of a target and a pedestal, flankers lowered thresholds when flankers were presented to the eye where targets were presented. In contrast, dichoptic flankers elevated thresholds at intermediate pedestal contrasts when a pedestal was also dichoptically presented. We fitted binocular contrast gain control models to the data. It follows from the fitting results that flankers modulate outputs from spatial filters in the monocular processing stage of contrast gain control.

Keywords: flanker, collinear facilitation, binocular vision, TvC function


**Introduction**

It is well accepted that cells in the primary visual cortex works as multi-orientation and multiscale filters, which respond to the luminance contrast of spatial patterns at specific retinal positions (De Valois & De Valois, 1980; Legge & Foley, 1980; Macleod & Rosenfeld, 1974; Stromeyer & Klein, 1974; Thomas, 1970; Wilson & Bergen, 1979). However, psychophysical studies have shown that the presence of co-aligned adjacent stimuli (flankers) lower the contrast detection threshold of flanked test stimuli (Cass & Alais, 2006; Chen & Tyler, 2001, 2008; Polat & Sagi, 1993, 1994; Williams & Hess, 1998; Woods, Nugent, & Peli, 2002; Yu, Klein, & Levi, 2002). Moreover, physiological studies have reported that the neural firing rate can be modulated by a stimulus presented outside the receptive field when a neuron is simultaneously stimulated (Gilbert, Das, Ito, Kapadia, & Westheimer, 1996; Kapadia, Westheimer, & Gilbert, 2000; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995; Yao & Li, 2002). These findings suggest that the response of a spatial filter changes not only due to its direct input but also due to luminance contrast outside but adjacent to its receptive field.

Huang, Hess, and Dakin (2006) compared the flanker effect among four different viewing conditions. There was a reduction in threshold when a target and flankers were presented to two eyes (binocular flanker) or to one eye (monocular flanker). In contrast, flankers produced no significant effect when flankers were presented to one eye while the target was presented to the other eye (dichoptic flanker), and when a target and flankers were presented in different depth planes (stereoscopic flanker). Based on these results, they concluded that the flanker effect is a monocular phenomenon and occurs at the earliest stage of cortical processing. They also found that contour integration is a
binocular process and occurs after the encoding of relative disparity, suggesting that the flanker effect and contour integration do not share a common mechanism, contrary to Polat’s (1999) view that the flanking interaction between spatial filters has an important role to play in grouping local edges into a smooth contour. However, Huang et al. (2006) found no significant difference in threshold reduction between the binocular and monocular flankers. Rather, the monocular flankers produced a slightly larger threshold reduction. This is an odd result because the binocular flankers are expected to have the larger threshold reduction due to binocular summation, if flankers modulate outputs of spatial filters at a monocular processing stage.

We used a pattern masking paradigm to examine the effects of binocular, monocular, and dichoptic flankers on contrast detection and discrimination. The pattern masking paradigm has been widely used to estimate the nonlinear properties of the visual system. The task of the observer is to discriminate the contrast difference between target alone and target plus pedestal stimulus. Results are plotted as discrimination thresholds of the target against the pedestal contrast, a so-called threshold versus pedestal contrast (TvC) function. Although several researchers have reported that binocular flankers elevate contrast discrimination thresholds (Chen & Tyler, 2001; Zenger-Landolt & Koch, 2001), it is still unclear how they change in the presence of monocular or dichoptic flankers. These experiments address three issues that need to be resolved to better understand the mechanisms underlying flank facilitation. First, is there a difference in threshold reduction between the binocular and monocular flankers? Second, how does dichoptic presentation modulate sensitivity for discrimination? Third, using the two current models (Maehara & Goryo, 2005; Meese, Georgeson, & Baker, 2006) of binocular combination, are the facilitative effects of flankers, additive or multiplicative? The answer to these questions bears upon the nature and site of interactions between spatial filters that occur in early visual processing.

Methods

The present experiment measured contrast thresholds of targets presented on the identical pedestals with or without flankers. Similar to the flanker conditions, there were three presentation conditions for targets and pedestals. For the binocular presentation, targets and pedestals were presented to both eyes. For the monocular presentation, they were presented to one eye. For the dichoptic presentation, a target was presented to one eye while a pedestal was presented to the other eye. By combining the flanker conditions and the pedestal condition, there were five viewing conditions with flankers (Figure 1b) and three viewing conditions without flankers.

Observers

There were three observers, GM, PCH, and JB. All had corrected-to-normal visual acuity. GM and PCH are authors.

Apparatus

Stimuli were generated using a VSG 2/5 (Cambridge Research System, Kent, UK), which produces 15-bit gray-level resolution, and presented on a video monitor (Compaq P1210). The display resolution was set to 1024 × 768 pixels. The refresh rate of the monitor was set to 120 Hz. However, stimuli were presented at a rate of 60 Hz due to frame interleaving of stimuli. One series of frames showed targets whereas the other showed pedestals and flankers. The frame-interleaving method halves luminance contrast of the stimuli. We report methods and results using the halved effective luminance contrast. Observers viewed the display through a mirror stereoscope. A single monitor was used to present stimuli. The image on one half of the screen was directed to one eye while the image on the other half was directed to the other eye, by means of a mirror stereoscope. Presentation regions on the monitor subtended a visual angle of 10° × 8.5° for each eye. Their mean luminance was 30 cd/m². The viewing distance was 57 cm.

Stimuli

There were three types of stimuli: targets, pedestals, and flankers. Their spatial patterns were Gaussian-windowed sinusoidal gratings (Gabor patterns). The underlying gratings had a spatial frequency of 1.1 cpd (wavelength = 0.9° of visual angle) and were oriented at 0° in 0° sine phase at the center of the Gaussian window. The standard deviation of the Gaussian window function was 0.5° of visual angle. The mean luminance of the stimuli was 30 cd/m². Vertical Gabor patterns were used for GM and PCH. Because it was possible that the interocular alignment was not perfect for vertical Gabor patterns, horizontal Gabor patterns were used for JB. Horizontal patterns are less affected by misalignment issues.

Targets and pedestals were simultaneously presented for 150 ms at the center of a presentation region (Figure 1a). This means that the target and pedestal contrasts sum because these spatial patterns were the same. Pedestal contrast was one of the independent variables. Luminance contrast was defined as the peak luminance of a Gabor pattern minus the background luminance and divided by the background luminance. We expressed luminance contrast in dB re 1, where 1 dB is 1/20 of a log unit of contrast.
Flankers were presented 2.7° of visual angle apart from targets and pedestals and were collinear with the target. The separation between targets and flankers was 3 times the wavelength of the Gabor pattern. It is known that flanker effects are largest at this separation distance (Polat & Sagi, 1993). Flankers were presented for 150 ms at the same time as a presentation of targets and pedestals. Luminance contrast of flankers was 12.7 dB (23%).

Four black oblique lines (nonius lines) were presented around a target and a pedestal during a stimulus presentation for precise binocular alignment. One eye saw the top-left and bottom-right lines, whereas the other eye saw the top-right and bottom-left lines. Observers were instructed that the four lines must make a square cross with a missing central part. If the nonius lines did not align properly, prisms were used to correct the stimulus positions. There was always a black square frame (8.2° × 8.2° visual angle) on each image for the right and left eyes. These frames aided peripheral fusion.

Procedure

We measured target contrast thresholds at different pedestal contrasts with or without flankers. As mentioned in the Introduction section, there were five presentation conditions with flankers (Figure 1b) and three presentation conditions without flankers (no-flanker conditions). Flankers were presented to the two eyes for the binocular presentation. On the other hand, flankers were presented to only one eye for the monocular pedestal and dichoptic pedestal conditions. We use the term dichoptic flankers when a target and flankers were presented to different eyes. The no-flanker condition was tested for each presentation conditions of targets and pedestals. There were 12 levels of pedestal contrast (−12.0, −16.0, −20.1, −24.2, −28.3, −32.4, −36.4, −40.7, −44.5, −48.7, −52.8, and −∞ dB). That is, the experimental design was defined by a combination of the pedestal presentation (3), the flanker presentation (2 or 3), and the pedestal contrast (12).

On each trial, the target was presented in either the first or the second of two observation intervals (two-alternative forced-choice procedure) while the pedestal and flankers were presented in both intervals. Observers were instructed to press a response as soon as they perceived the target. A one-up/two-down staircase was used to adjust the target contrast. The step size of staircase was initially set at 1.9 dB for upward and downward, respectively. The
Results

The top panels of Figure 2 show mean target contrast thresholds as a function of the contrast of pedestals (TVC function). The middle and bottom panels plot the same data but different fitting curves. Later, we will describe fits of contrast gain control models to the data. The red circles in the figure represent the discrimination threshold for the no-flanker conditions. For binocular (left panels) and monocular (center panels) pedestal conditions, the data showed a typical dipper shape where thresholds decreased and then increased with pedestal contrast. The lowest thresholds were found when the pedestal contrast is near the target detection threshold. The results for the dichoptic pedestal condition showed threshold elevation at higher pedestal contrasts and very small threshold reduction at middle pedestal contrasts (right panels). The individual data (Figure 3) also showed the same trend. These results are consistent with previous findings (Legge, 1979; Maehara & Goryo, 2005; Meese et al., 2006).

To test whether flankers changed the shape of TVC functions, we subjected thresholds to two-way repeated measures ANOVAs (Flanker × Pedestal Contrast). Three ANOVAs were done separately for three presentation conditions of targets and pedestals. For the binocular presentation, the binocular flankers lowered thresholds at low pedestal contrasts (left panels of Figure 2), producing a significant Flanker × Pedestal Contrast interaction, $F(11, 22) = 3.54, p = 0.006$. As a whole, thresholds were not significantly different between the no-flanker and binocular-flanker conditions, $p > 0.05$. The TVC functions had the typical dipper shape, as reflected in the significant quadratic main effect of Pedestal Contrast, $F(1, 2) = 3837, p < 0.001$. Although Chen and Tyler (2001) also reported the threshold reduction in the presence of binocular flankers, their results were different from ours in that flankers elevated thresholds throughout the high pedestal contrast range ($-30$ to $-10$ dB).

Thresholds were significantly different among the flanker conditions for the monocular presentation of a target and a pedestal, $F(2, 4) = 12.4, p = 0.019$. We can see from the center panels of Figure 2 that the flankers lowered thresholds. On the other hand, data points almost overlap between the no-flanker and dichoptic-flanker conditions (red circles and cyan diamonds). That is, the dichoptic flankers were not effective. The Flanker main effect was qualified by the significant Flanker × Pedestal Contrast interaction that the monocular flankers lowered thresholds at low pedestal contrasts but not at high pedestal contrasts, $F(22, 44) = 3.68, p < 0.001$. The threshold reduction looks smaller for the monocular flankers than for the binocular flankers. Actually, the monocular flankers lowered the mean detection thresholds by 2.1 dB while the binocular flankers lowered it by 3.4 dB, although the t-test showed no significant difference between them, $p > 0.05$. The TVC functions had the dipper shape in the monocular presentation, as reflected in the significant quadratic main effect of Pedestal Contrast, $F(1, 2) = 581, p = 0.002$, as well as in the binocular presentation, as reported previously.

For the dichoptic presentation of a target and a pedestal (right panels of Figure 2), the flankers lowered thresholds, $F(2, 4) = 15.5, p = 0.013$. This threshold reduction was limited to low pedestal contrasts, producing a significant Flanker × Pedestal Contrast interaction, $F(22, 44) = 4.29, p < 0.001$. The right panels of Figure 2 show that the dichoptic flankers elevated thresholds at middle pedestal contrasts. This would also contribute to the significant interaction. The TVC functions showed threshold elevation at high pedestal contrasts with a very small dip, as reflected in the significant quadratic main effect of Pedestal Contrast, $F(1, 2) = 55.1, p = 0.018$.

Binocular summation ratios were calculated by dividing the monocular detection threshold by the binocular detection threshold. A binocular summation ratio is typically between 1.4 and 2 (Legge, 1984a; Maehara & Goryo, 2005; Meese et al., 2006). Although the mean data showed a binocular summation ratio of 1.44, GM and PCH showed comparatively smaller ratios (1.27 and 1.28). This might be attributable to an imperfect eye alignment. Even a small misalignment could cause a certain amount of phase shift for the vertical stimuli. According to Legge (1984a), binocular summation ratios are smaller than 1.4 when sinusoidal gratings are not in phase between the two eyes. Actually, the binocular summation ratio of JB (1.81), in whom horizontal Gabor patterns were presented, was comparable with those reported in the previous studies. It is controversial whether the flanker effect is phase sensitive (Solomon, Watson, & Morgan, 1999; Williams & Hess, 1998) or insensitive (Polat & Sagi, 1993). In the present study, the imperfect phase alignment seems not to have changed the flanker effect so much because the flanker effect was quite consistent among observers.

Slopes at the high pedestal contrasts ($-32.4$ dB to $-12.0$ dB) in the mean data were $0.82, 0.78$, and $0.92$ dB for the binocular, monocular, and dichoptic presentations of targets and pedestals, respectively, in the absence of flankers. Dichoptic pedestals produced a steeper slope,
being consistent with the previous findings (Legge, 1984b; Meese et al., 2006). We found that, in the dichoptic-pedestal condition, the slope was less steep for the dichoptic-flanker condition (0.78) than for the monocular-flanker (1.06) and the no-flanker conditions (0.92). This is due to the threshold elevation at the middle pedestal contrasts in the presence of the dichoptic flankers (right panels of Figure 2). The binocular and monocular flankers did not yield a substantial change in slopes.

We can see from Figure 3 that slopes of TVC functions at the high pedestal contrast range are steeper for GM and PCH (0.87 and 1.24 for the no-flanker condition) than for JB (0.64) when targets and pedestals were dichoptically presented (right panels). This resulted in standard errors of the mean data for the dichoptic-pedestal condition being larger. Baker and Meese (2007) reported that slopes in dichoptic masking were shallower when a target and a pedestal were out of phase than when they were in phase. However, this seems unlikely to happen here because horizontal stimuli were presented for JB and he showed substantial binocular summation. Perhaps stimulus orientation affects the slope of TVC functions. Stimuli were horizontal for JB whereas vertical for GM and PCH. However, the previous study did not show such a relationship.
between slope and orientation (Meese et al., 2006). It is unclear what caused the individual difference in slopes.

Modeling

The aim of the present study is to explain the flanker effect on the basis of binocular versions of contrast gain control models. Two such models have been proposed, the twin summation model (Maehara & Goryo, 2005) and the two-stage model (Meese et al., 2006).

Overview of the twin summation model

We first describe the twin summation model because the model has simpler structure than the two-stage model. Figure 4a shows schematic illustration of the twin summation model. A characteristic of this model is that divisive inhibition takes place after summations of signals between two eyes (Maehara & Goryo, 2005). The first stage of processing is linear filtering of stimulus patterns presented to each eye. The linear filters have a linear spatial sensitivity function, expressed as a Gaussian-windowed cosine, and are most sensitive to a pattern with a specific phase, orientation, and spatial frequency.
Responses of the filters are proportional to contrasts of spatial components of stimuli. It is assumed that there are many mechanisms tuned to different phases, orientations, and spatial frequencies. However, we show only one mechanism here because targets, pedestals, and flankers had the same spatial pattern in the present experiment.

Outputs of the linear filters are monocular excitation $E_{ij}$ and monocular inhibitory signal $I_{ij}$. The monocular excitation produced by pattern component $i$, which is presented to eye $j$, is

$$ E_{ij}^m = C_{ij}S_E, \quad (1) $$

where $C_{ij}$ is component contrast and $S_E$ is the excitatory sensitivity of the mechanism either to target or pedestal. Since excitation is a linear process, monocular excitation produced by target plus pedestal is the sum of their individual excitations:

$$ E_j = C_{ij}S_E + C_{pj}S_E. \quad (2) $$

The monocular excitations are then half-wave rectified:

$$ E_j = \max(E_j^m, 0). \quad (3) $$

The rectified monocular excitations $E_L$ and $E_R$ originate in the left and right eyes, respectively. These monocular excitations are raised to power $m$ (nonlinear transducer) and then summed to yield binocular excitation $E$:

$$ E = E_L^m + E_R^m. \quad (4) $$

Inhibitory signals are computed in much the same way excitations are. Monocular inhibitory signals are also products of stimulus contrast and sensitivity:

$$ I_j = C_{ij}S_I + C_{pj}S_I, \quad (5) $$

where $S_I$ is an inhibitory sensitivity of mechanism. Then, the monocular inhibitory signals are half-wave rectified. The binocular inhibitory signal $I$ is a sum of the rectified signals raised to power $n$:

$$ I = I_L^n + I_R^n. \quad (6) $$

The model contains the broadband divisive inhibition that Foley (1994) originally incorporated in his contrast processing model. The binocular excitation and binocular inhibitory signals are raised again to power $p$ or $q$ after the summation of monocular signals. Then, the mechanism

Figure 4. Schematic illustrations of binocular versions of contrast gain control models. (a) The twin summation model. (b) The two-stage model.
response \( R \) is computed as the binocular excitation divided by the binocular inhibitory signal plus a semi-saturation constant \( z \). These calculations are expressed as

\[
R = \frac{E^p}{(I^q + z)}.
\]  

(7)

Although the broadband divisive inhibition means that inhibitory signals from different mechanisms are summed up to yield the denominator, this summation is omitted from the calculation here because the present stimuli had the same spatial properties.

A target contrast will be the threshold when the response to the target plus pedestal \((R_{t+p})\) exceeds the response to the pedestal alone \((R_p)\) by a constant value. Stated more specifically, behavioral thresholds depend on the value of the decision variable \( D \):

\[
D = R_{t+p} - R_p.
\]  

(8)

At the threshold, \( D = 1 \).

**Fitting the twin summation model to the data**

Huang et al. (2006) suggested that the flanker effect takes place at the monocular processing stage. According to Polat (1999), each spatial filter receives lateral excitation and lateral inhibition from adjacent filters with the same orientation and spatial frequency selectivity. Therefore, it seems reasonable to assume that flankers modulate monocular excitation and monocular inhibitory signals. Polat (1999) supposed that the inputs from the lateral interaction are added to the filter output. This additive modulation can be expressed in a framework of the twin summation model as follows:

\[
E = (E_L + K_{EL})^m + (E_R + K_{ER})^m,
\]  

(9)

and

\[
I = (I_L + K_{IL})^n + (I_R + K_{IR})^n,
\]  

(10)

where \( K_{EL} \) and \( K_{IL} \) are modulation factors for monocular excitations and monocular inhibitory signals, respectively. The additive modulation factors have positive values when flankers are presented. Although there are different factors for the left and right eyes, their values are the same between two eyes \((K_{EL} = K_{ER}; K_{IL} = K_{IR})\) for the binocular flankers. For the no-flanker condition, all the modulation factors are set to be 0, being ineffective. In the case that flankers are presented to only one eye (monocular or dichoptic flanker), modulation factors are effective only for the eye where flankers are presented whereas they are ineffective for the other eye.

The fitting procedure was given as follows. Parameter values that gave a rough fit to data were found by trial and error. Then, thirty least square fits were computed. Each fit started with a different set of parameter values randomly sampled from normal distributions. Mean values and SDs of the normal distributions were set to be the rough-fit values and 30% of them, respectively. The reported fits are those that achieved the lowest errors. Matlab “fminsearch” function was used to fit the model.

First, we fitted the twin summation model to the data for the no-flanker condition. Threshold data for model fitting is available as supplementary materials (Table S1). Errors and estimated parameters of the fits are given in Table 1. \( S_E \), \( m \), \( n \), \( p \), \( q \), and \( z \) were free parameters that were not fixed in advance. \( S_E \) was a fixed parameter. The red smooth curves in the top panels of Figure 2 correspond to the best fit for the mean data. The root mean squared errors (RMSEs) of the fits were 0.655 dB for the mean data, 0.810 dB for GM, 1.13 dB for PCH, and 1.25 dB for JB. These errors were close to the mean SEs of thresholds for the no-flanker condition (1.82 dB for the mean, 1.81 dB for GM, 1.35 dB for PCH, and 1.47 dB for JB).
and similar to fitting errors reported in the previous studies (Maehara & Goryo, 2005; Meese et al., 2006). After the first fitting, the model was fitted to the data for the conditions with flankers. The modulation factors were set to be free for the second fit. Other parameters were fixed to the values estimated by the first fit. The blue and cyan curves in the middle row panels of Figure 2 correspond to the best fit to the mean data (see Figure S1 in the supplementary materials for individual fits). The RMSEs of the second fits were 1.01 dB for the mean data, 1.25 dB for GM, 1.33 dB for PCH, and 1.75 dB for JB (Table 2). These errors were close to the mean SEs of thresholds for conditions with flankers (1.50 dB for the mean, 0.773 dB for GM, 1.01 dB for PCH, and 0.925 dB for JB). The fits were reasonably good.

Chen and Tyler (2001) also attributed the flanker effect to the lateral interaction between spatial filters. However, their theory is different from Polat’s (1999) theory in that the lateral interaction multiplicatively, not additively, modulates the outputs of a filter. This process can be expressed as

$$E = K_{E_L}E^m_L + K_{E_R}E^m_R,$$

and

$$I = K_{I_L}I^m_L + K_{I_R}I^m_R.$$  

The multiplicative modulation factors have values more than 1 in the presence of flankers. For the no-flanker condition, all the modulation factors are set to be 1, being ineffective. We fitted this model to the data for the conditions with flankers. The modulation factors were set to be free whereas other parameters were fixed to the values estimated by the first fit. The blue and cyan curves in the bottom panels of Figure 2 and in Figure 3

<table>
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<tr>
<th></th>
<th>Twin summation model with additive modulation</th>
<th>Twin summation model with multiplicative modulation</th>
<th>Two-stage model with additive modulation</th>
<th>Two-stage model with multiplicative modulation</th>
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<tr>
<td>JB</td>
<td>0.600</td>
<td>0.529</td>
<td>183</td>
<td>1.75</td>
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Table 2. Estimated modulation factors and fitting errors for the conditions with flankers. Numbers of data points were 55 for the mean data and 60 for individual data.
correspond to the best fit. The RMSE for conditions with flankers were 0.951 dB for the mean, 1.47 dB for GM, 1.34 dB for PCH, and 1.67 dB for JB (Table 2). The errors were comparable between the additive and multiplicative modulation assumptions.

Overview of the two-stage model

Figure 4b shows the schematic illustration of the two-stage model. A characteristic of this model is that there are two stages of divisive inhibition before and after the interocular summation of signals (Meese et al., 2006). The processing starts with linear filtering and half-wave rectification (Equations 1, 2, and 3). The monocular excitations $E_L$ and $E_R$ are raised to power $m$ and divided by a sum of the two monocular excitations and a constant $s$, yielding the first-stage outputs $F_L$ and $F_R$:

$$ F_j = E_j^m / (E_L + E_R + s). \quad (13) $$

The first-stage outputs are summed between two eyes, raised to power $p$, and then subjected to the second-stage divisive inhibition. This calculation is expressed as

$$ R = \frac{(F_L + F_R)^p}{(F_L + F_R)^q + z}, \quad (14) $$

where $R$ is the mechanism response and $z$ is a constant. The inhibition from other mechanisms is also omitted here. A target contrast will be the threshold when the response to the target plus pedestal ($R_t + p$) exceeds the response to the pedestal alone ($R_p$) by a constant value $d$. That is, $D = d$ at the threshold. The constant $d$ is one of the free parameters, whereas it was fixed to be 1 in the twin summation model.

Fitting the two-stage model to the data

The two-stage model was fitted to the data in almost the same way as the twin summation model. However, in the first fits to the mean data, estimated parameters did not always show appropriate values. In such fits, a constant $z$ was close to 0 (e.g., 0.0044) whereas a constant $s$ had an extremely large value (e.g., 907). Since this makes the two-stage model work in a different way from its design, we excluded fits where a constant $z$ was estimated to be smaller than 0.02.

For the first fits to the no-flanker condition, parameters $m, p, q, s, z,$ and $d$ were free to vary. The RMSEs of the fits were 0.742 dB for the mean data, 0.757 dB for GM, 1.31 dB for PCH, and 1.34 dB for JB (Table 1). These errors were comparable with RMSEs of the fits of the twin summation model.

The two-stage model can also adopt the additive modulation factors at the first divisive inhibition stage:

$$ F_j = (K_E j + E_j)^m / (K_{EL} + E_L + K_{IR} + E_R + s). \quad (15) $$

This model was fitted to data for the conditions with flanksers. The RMSEs were 1.01 dB for the mean data, 1.27 dB for GM, 1.31 dB for PCH, and 1.89 dB for JB. The fits were reasonably good (Figure B1 in Appendix B and Figure S2 in the supplementary materials). Note that $K_i$ were estimated to be 0 for GM and JB (Table 1). This means that only the excitatory modulation possibly explains the flanker effect.

We also tested the two-stage model with the multiplicative modulation. The process can be expressed as

$$ F_j = (K_E j E_j^m) / (K_{RL} E_L + K_{IR} E_R + s). \quad (16) $$

The RMSEs for the multiplicative modulation assumption were 1.35 dB for the mean data, 1.90 dB for GM, 1.37 dB for PCH, and 1.83 dB for JB. These errors were also comparable with errors of the previous fits (Figure B1 in Appendix B and Figure S3 in the supplementary materials).

Discussion

The present study examined how TvC functions change with binocular, monocular, or dichoptic flankers. First, we found that binocular flankers lowered thresholds at low pedestal contrasts whereas they were ineffective at very high pedestal contrasts. The monocular flankers had a similar effect, although the threshold reduction was smaller than that found for the binocular flanker. Second, the dichoptic flankers elevated thresholds at middle pedestal contrasts when flankers and pedestal were presented to the same eye while a target was presented to the other eye. However, the dichoptic flankers had little effect when both target and pedestal were presented to one eye and flankers to the other eye. Third, the flanker effect can be explained by assuming that flankers either additively or multiplicatively modulate outputs of spatial filters at the monocular processing stage of contrast gain control. Fitting errors for either of the two current models of binocular combination substantiated this.

The additive modulation means that spatial filters receive input from adjacent region as well as from their receptive field. Since this additional input works as
another pedestal, flankers also lower thresholds at low pedestal contrasts and elevate them at high pedestal contrasts. However, the larger the excitatory and inhibitory signals, the less effective the additive modulation factors. Therefore, the flanker effect is largest at $-\infty$ dB of pedestal contrast and gradually gets smaller as a pedestal contrast increases. We can see this trend from the fits in the middle row panels of Figure 2. The additive modulation is more effective for the binocular flankers than for the monocular flanker because the additive modulation takes place in the monocular processing stage of each eye. In the additive modulation assumption, the dichoptic flankers produce a little threshold reduction in the same way as the dichoptic pedestal (Maehara & Goryo, 2005; Meese et al., 2006).

The multiplicative modulation means that spatial filters become more sensitive to luminance contrast in the presence of flankers. This results in left-downward shifts of TVC functions. The modulation factors cancel each other between numerator and denominator of divisive inhibition when inhibitory signals are large enough to ignore a constant $s$ or $z$. For example, if a semi-saturation constant $z$ was removed, the mechanism response of the twin summation model for the binocular presentation will become

$$R = \frac{K^\circ_E E_L + E^\circ_R}{K_1^0 (I^\circ_L + I^\circ_R)^q}. \quad (17)$$

We can see from the above equation that $K_E$ and $K_I$ cancel mutually. A similar cancellation occurs also in the two-stage model if the constant $s$ is removed from Equation 16. Therefore, the fits show that flankers are not effective at very high pedestal contrasts (bottom panels of Figure 2). The monocular flankers with the dichoptic pedestal shift TVC functions only downward because the dichoptic flankers do not affect the response to a pedestal presented to the other eye. In contrast, the dichoptic flankers with a monocular pedestal shift TVC functions leftward. In both cases, flankers induce no threshold change at very high pedestal contrasts due to the cancellation of modulation factors.

Threshold reduction was larger for the binocular flankers than for the monocular flanker, though the difference was not statistically significant. The fits of contrast gain control models also show that threshold reduction is larger for the binocular flankers than for the monocular flankers at the low pedestal contrast range. If the modulation factors are assumed to be after the binocular integration so that the binocular and monocular flankers produce the same effect, we face a difficulty to explain the TVC functions with the dichoptic flankers. Therefore, it is reasonable to suppose that the binocular flankers produce a larger effect than the monocular flankers. This difference would be too small to yield a significant statistical value for pair-wise comparison, such as Huang et al. (2006) did.

Fitting errors were comparable between the additive and multiplicative modulations. It is difficult to conclude which assumption is better, based on the fitting errors. However, the fits show a qualitative difference between the two assumptions. The dichoptic flankers produce no threshold reduction for the additive modulation whereas they produce no threshold reduction for the multiplicative modulation. In the present study, the dichoptic flankers produced no significant change in detection thresholds (the 95% confidence interval was between 0.3 and $-0.8$ dB). Huang et al. (2006) also showed that detection thresholds did not significantly change in the presence of the dichoptic flankers. These results suggest that the multiplicative modulation is more appropriate than additive modulation.

Chen and Tyler (2001) reported that the binocular flankers elevated thresholds throughout the high pedestal contrast range, whereas they produced little effect in the same range in the present study. This difference might be due to pedestals not having high enough effective contrasts in Chen and Tyler’s experiment. Actually, binocular detection thresholds were higher for their study (about $-25$ dB) than for the present study ($-40.1$ to $-33.8$ dB), suggesting that the visual system was less sensitive to their stimuli than to our stimuli. We speculate that, also in Chen and Tyler’s experiment, the flankers would become ineffective if a pedestal had a higher contrast or if stimuli had lower spatial frequencies.

Conclusion

This paper has described what mechanism may be responsible for effects of binocular, monocular, and dichoptic flankers on TVC functions. It seems reasonable to assume that the interaction between spatial filters additively or multiplicatively modulates outputs from spatial filters in the monocular processing stage of contrast gain control. This process makes it easier to detect a target below thresholds. On the other hand, contrast discrimination can become more difficult in the presence of flankers. This suggests that the flanking effects, being confined to threshold contrast and monocular processing, may be of limited significance to visual processing that is of a suprathreshold and stereoscopic nature. One such suprathreshold process is contour integration (Field, Hayes, & Hess, 1993), which has been shown to be independent of stimulus contrast (Hess, Dakin, & Field, 1998) and disparity (Hess & Field, 1995). We speculate that the interaction between spatial filters may aid the detection of continuous edges when smeared by blurring or noisy environment.
Appendix A

Summary of symbols

- **$S_E$** Excitatory sensitivity parameters of spatial filters
- **$S_I$** Inhibitory sensitivity parameters of spatial filters
- **$m$** Exponents for monocular excitations
- **$n$** Exponents for monocular inhibitory signals
- **$p$** Exponents for binocular excitations
- **$q$** Exponents for binocular inhibitory signals
- **$z$** Semi-saturation constants
- **$s$** Semi-saturation constants for the first-stage contrast gain control

- **$d$** Response differences necessary to detect a target
- **$K_{Ej}$** Excitatory modulation factors for eye $j$
- **$K_{Ij}$** Inhibitory modulation factors for eye $j$

Appendix B

Additional figures

Figures B1 and B2.

Presentation of targets and pedestals

Figure B1. The mean TvC functions. Smooth curves correspond to the best fits of the two-stage model with the additive or multiplicative modulation factors (middle and bottom panels, respectively). The top panels show the mean data without fitting curves.
Acknowledgments

This work was supported by grants from the Japan Society for Promotion of Science to G. M. and from the Natural Sciences and Engineering Research Council of Canada to R. F. H. (RGPIN 46528-06).

Commercial relationship: none.

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References


