Lateral modulation of contrast discrimination: Flanker orientation effects

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We used a dual-masking paradigm to study how contrast discrimination is influenced by the presence of adjacent stimuli differing in orientation. The task of the observer was to detect a vertical Gabor target superimposed on a vertical Gabor pedestal in the presence of flankers. The Gabor flankers had orientations ranging from 0° (parallel to the target) to 90° (orthogonal). The flankers had two different facilitatory effects: (a) Threshold facilitation. The flankers facilitated target detection at low pedestal contrasts. This facilitation was narrowly tuned to flanker orientation. (b) Pedestal enhancement. The flankers at high contrast enhanced the masking effectiveness of the pedestal. This pedestal enhancement changed little with flanker orientation. We fitted the data with a sensitivity modulation model in which the flanker effects were implemented as multiplicative factors modulating the sensitivity of the target mechanism to both excitatory and inhibitory inputs. The model parameters showed that, (a) pedestal enhancement occurs when flanker facilitation to the pedestal is greater than to the target; (b) while the sensitivity modulation was tuned sharply with flanker orientation, the ratio between the excitatory and the inhibitory factors remained constant. The explanation of the flanker orientation effect requires the both the values of each factor and the ratio between them.

Keywords: long-range interaction, divisive inhibition, lateral masking, orientation, threshold

1. Introduction

Visual performance for a stimulus projecting to one location on the retina can be modified by the presence of other stimuli at different locations. By measuring detection thresholds for a target Gabor pattern at the fovea flanked by two other high-contrast Gabor patterns (flankers), Polat and Sagi (1993, 1994) reported that the target threshold decreased from the absolute threshold when a pair of collinear flankers (with the same orientation as the target) was presented in synchrony with the target (facilitation). The amount of facilitation varied with the distance between the flankers and the target. with the greatest facilitation occurring when the distance was about three times the target wavelength. Similar flanker facilitation effects were also reported by Zenger and Sagi (1996) and Solomon, Watson, and Morgan (1999).

The flanker effect is orientation-specific. Polat and Sagi (1993) showed that flanker facilitation was reduced as the orientation of the collinear flankers deviated from the target orientation. They reported a complete loss of facilitation when the flankers were orthogonal to the target.

Other lateral context effects also show orientation specificity. For instance, Field, Hayes, and Hess (1993) reported a contour integration phenomenon in which observers can detect a contour consisting of Gabor patches in a background of otherwise randomly

distributed and oriented Gabor patches. To achieve contour integration, the orientation difference between neighboring Gabor elements in the contour had to be smaller than a certain amount. Theories of contour integration (Field et al., 1993; Li, 1998) postulate that detectors responsive to neighboring contour elements would facilitate with each other if they were similar in orientation, and inhibit each other, or at least fail to facilitate, if their orientations were sufficiently different.

Current studies on lateral context effects focus on the facilitation of a target mechanism produced by flanking stimuli. This facilitative effect may not reveal the true nature of the lateral context effect. Both psychophysical (Chen & Tyler, 2000, 2001) and neurophysiological (Chen, Kasamatsu, Polat, & Norcia, 2001; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Sengpiel, Baddeley, Freeman, Harrad, & Blakemore, 1998) evidence shows that even the same collinear flankers at the same location can have different effects on the response to the target. Polat et al. (1998; also see Chen et al., 2001) measured the flanker effect on the responses of striate cortical neurons to target Gabor patches located within their classical receptive fields. In more than 50% of cells, while the flankers themselves produced no response in the cell, their presence increased cell responses at low contrast and decreased the responses at high contrast. That is, depending on the target contrast, the same flanker can have either facilitative or suppressive effect on a given cell response. The facilitation at low target contrast is

consistent with the flanker effect reported by Polat & Sagi (1993). The high contrast suppression, however, cannot be revealed psychophysically with the detection paradigm.

Chen and Tyler (2000, 2001) employed a dualmasking paradigm in which the observer had to detect a target superimposed on a pedestal (first mask) in the presence of two collinear flankers (second mask). Detection of a target superimposed on a pedestal – called a masking experiment in the literature – has been a wellestablished paradigm for studying the visual detection mechanisms (Breitmeyer, 1984; Foley, 1994; Foley & Chen, 1999; Kontsevich & Tyler, 1999a; Legge & Foley, 1980; Ross & Speed, 1991; Wilson, McFarlane, & Philips, 1983). If the target and the pedestal are the same in all spatiotemporal parameters except contrast, as in Chen and Tyler (2000, 2001), this experiment is equivalent to contrast discrimination. Without flankers, the target threshold versus pedestal contrast (TvC) function had a dipper shape: Relative to the detection threshold measured with no pedestal, the target threshold first decreases (facilitation) and then increases as the pedestal contrast is increased. When flankers are present, they can facilitate target detection at zero pedestal contrast as reported by previous authors (Polat & Sagi, 1993, 1994; Solomon, Watson, & Morgan, 1999; Zenger & Sagi, 1996). However, the amount of lateral facilitation decreases as the pedestal contrast is increased. Thus, compared with the no flanker condition, the TvC function for the flanker condition shows a shallower dip. As the pedestal contrast further increases, the target threshold for flanker condition rises above the target threshold for the no-flanker condition. As a result, the flanker and no-flanker TvC functions shows a cross-over phenomenon: The flanker TvC function has lower thresholds at low pedestal contrasts and higher thresholds at high contrast. This result is consistent with the behavior of striate cortical neurons. Subsequently, Adini & Sagi (2001) and Zenger-Landbolt & Koch (2001) also reported similar phenomenon.

Chen & Tyler (2000, 2001) also revealed a mathematical property of the flanker effect. When plotted on log-log coordinates, at high contrasts the flanker TvC function looked like a horizontally left-shifted version of the no-flanker TvC function. Since the flanker contrast was constant throughout the experiment, this horizontal shift on logarithmic coordinates implies that the flanker effect is multiplicative on the effective contrast of the pedestal. If the flanker effect were additive rather than multiplicative, as the pedestal contrast increased by two log units in the measured range, the added constant effect from the flankers would be swamped by the effect from pedestal and would be negligible at high pedestal contrast. Empirically, we would see the two TvC functions merging at high contrast rather than a horizontal shift.

The dual-masking paradigm offers a means of studying the lateral effect on contrast discrimination. It provides much information not available with the traditional lateral masking paradigm (e.g., Polat & Sagi, 1993) for the study of the lateral effect on detection. We employed the dual masking paradigm to investigate the orientation specificity of the lateral effect. Since flanker stimuli can have both facilitatory and masking effects on the target mechanism, the absence of lateral facilitation by an orthogonal flanker can be seen as either a decrease in facilitation or an increase in masking. We attempt to resolve this distinction by comparing how the TvC functions change with the flanker orientation and by fitting the data to a quantitative model to observing how model parameters change with the flanker orientation.

2. Methods

2.1. Stimuli

The target, pedestal and flankers were all Gabor patches defined by the equations

$$G(x,y) = B + BC\cos(2\pi f x')\exp\left(\frac{-x'^2 - (y' - u_y)^2}{2\sigma^2}\right)$$

and

$$x' = x\cos\theta + y\sin\theta$$
$$y' = -x\sin\theta + y\cos\theta$$

where B was the mean luminance, C was the contrast of the pattern ranging from 0 to 1, f was the spatial frequency, σ was the scale parameter (standard deviation) of the Gaussian envelope, u_{ν} was the vertical displacement of the pattern, and θ was the orientation of the Gabor patch. All patterns had a spatial frequency (f) of 4 cycles per degree and a scale parameter (σ) of 0.1768°. The target and the pedestal were centered at the fixation point; hence the displacement $u_{\rm v}$ was zero. The two flankers were placed above and below the target with a displacement (u_v) of 0.75°. The target and the pedestal were vertically oriented with $\theta = 0^{\circ}$. The flankers had orientations ranged from 0° (vertical) to 90°. The flanker orientation deviated from the target by values of 11°, 23°, 30°, 45°, 60°, and 90°. The contrasts of the flankers (C) were -6dB or 0.5. All stimuli were presented concurrently with the temporal waveform of the stimuli was a 90 ms pulse.

2.2. Procedures

We used a temporal two-interval forced-choice (2IFC) paradigm to measure the target threshold. On each trial, the pedestal and the flankers were presented in both intervals. The target was presented randomly in either of the intervals. The task of the observer was to determine which interval contained the target. We used the Ψ threshold-seeking algorithm (Kontsevich & Tyler, 1999b)

to measure the threshold at 75% correct response level. There were 40 trials for each threshold measurement. Each reported datum point reported was an average of 4 to 8 repeated measures. We randomized the sequence by which pedestal contrast and flanker orientations were presented in each threshold measurement.

Two observers participated in this study. CCC is an author of this paper and SAS was a paid observer naive to the purpose of the study. Both observers had corrected to normal (20/20) visual acuity.

2.3. Apparatus

The stimuli were presented on two Mitsubishi Diamond Scan 15 inch monitors driven by IXMicro in 3D ProRez graphic boards. A Macintosh-compatible StarMax computer controlled the graphic boards. Light from the two monitors was combined by a beam splitter. This twomonitor setup allowed us to present the target on one monitor and the context (the pedestal and the flankers) on the other. This arrangement gave us an advantage for independently controlling the contrast of the target while ensuring that the context remained the same in two intervals of a trial. The viewing field was 10.7° (H) by 8° (V). The resolution of the monitors was 640 horizontal by 480 vertical pixels, giving 60 pixel per degree at the viewing distance used (128 cm). The refresh rate of the monitor was 66 Hz. We used the LightMouse photometer (Tyler & McBride, 1997) to measure the full-detailed input-output intensity function of the monitor. This

information allowed us to compute linear lookup table settings to linearize the output within 0.2%. The mean luminance of the display was set at 51 cd/m^2 .

3. Results

Figure 1 shows the TvC functions for observer SAS. Panel (a) contains the functions for no flanker parallel (0°) flanker and orthogonal (90°) flanker conditions. Panel (b) contains two intermediately oriented flanker conditions: the 30° and 60° orientation. The no-flanker condition is replotted here as a reference (blue circles).

Figure 2 shows the TvC functions for observer CCC. Panel (a) plots the same functions as in Figure 1 Panel (a). Panel (b) contains three intermediately-oriented flanker conditions: the 11° , 22° and the 45° flankers. Again, the no-flanker condition is plotted for comparison. The error bars are ± 1 standard error of the mean values. The smooth curves in both Figures 1 and 2 are the fits of the sensitivity modulation model discussed later.

The no-flanker condition showed a dipper shape: The threshold first decreased and then increased as the pedestal contrast was increased. The greatest threshold reduction occurred when the pedestal contrast was at about its own detection threshold. This dipper-shaped TvC function is well established (Bradley & Ohzawa, 1986; Foley, 1994; Foley & Chen, 1999; Kontsevich & Tyler, 1999a; Legge & Foley, 1980; Ross & Speed, 1991).

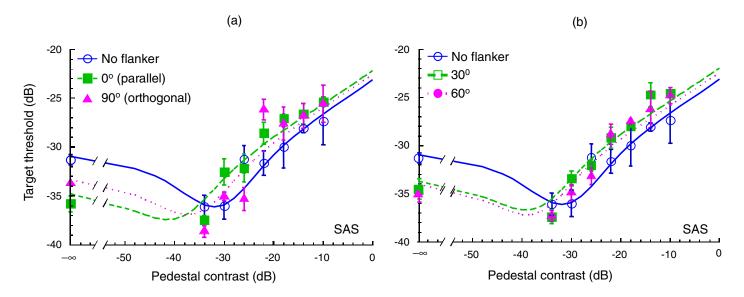


Figure 1. The TvC (target threshold vs. pedestal contrast) functions for observer SAS. Panel (a) shows the functions for the no-flanker (blue open circles, solid curve), 0° (parallel) flanker (green solid squares, dashed curve) and 90° (orthogonal) flanker (magenta up triangles, dotted curve) conditions. Panel (b) shows two intermediately oriented flanker conditions: the 30° (green open squares, dashed curve) and 60° (magenta solid circles, dotted curve). The blue solid circles and curve represent the no-flanker condition as in Panel (a), which is replotted here for a reference. The error bars are 1 standard error of the mean. The smooth curves are fits of the sensitivity modulation model.

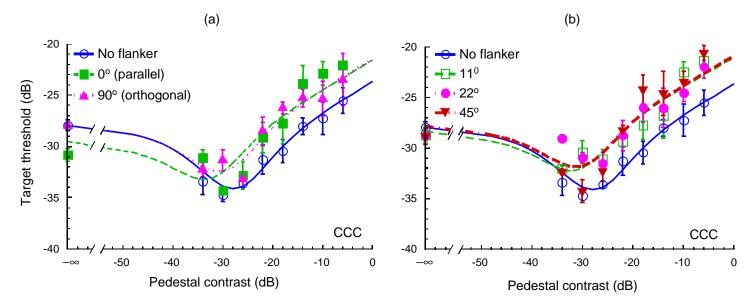


Figure 2. The TvC functions for observer CCC. Panel (a) shows the functions for the no-flanker (blue open circles, solid curve), 0° (parallel) flanker (green solid squares, dashed curve) and 90° (orthogonal) flanker (magenta up-triangles, dotted curve) conditions. Panel (b) shows three intermediately oriented flanker conditions: the 11° (green open squares, dashed curve), 22° (magenta solid circles, dotted curve) and the 45° (red solid down triangles, dashed curve) flankers. The no-flanker condition is replotted for comparison. The error bars represent 1 standard error of the mean. The smooth curves are the fits of the sensitivity modulation model.

When the parallel flankers were presented, they had two major effects on the TvC functions. First, without the pedestal (denoted as $-\infty$ dB contrast pedestal condition in the figures), the flankers reduced the target threshold by 2.9-4.2 dB. This result is comparable with that reported by Polat and Sagi (1993, 1994) in a similar condition. Second, the flankers increased target threshold at high pedestal contrasts. This increase could be as large as 4.5dB (or about a 70% increase in linear contrast) and facilitation was about the same for every contrast. Thus, a given pedestal contrast in the flanker condition had the same effect as a higher pedestal contrast in the no-flanker condition. This effect can be viewed as shifting the TvC function horizontally to low contrasts. Up to the highest pedestal contrast we measured, the two TvC functions show no sign of convergence. These three effects were consistent with those previously reported with different observers (Chen & Tyler, 2001).

The orthogonal flankers produced much less facilitation than the parallel flankers. Without a pedestal, the flanker facilitation significantly dropped from 4.2 to 2.5 dB for observer SAS (t(6.31)=2.5046, p=0.023 < 0.05), and from 2.9 to 0.2 dB for CCC (t(3)=4.79, p=0.0086 < 0.05). Polat and Sagi (1993) also reported a reduction of facilitation in similar conditions. At high pedestal contrasts, however, the orthogonal flankers showed similar effects to the parallel flankers. The TvC function was shifted to the left with little, if any, difference from the effect of the parallel flankers.

The intermediately-oriented flankers produced effects similar to those of the orthogonal flankers. They produced less facilitation than the parallel flankers at low pedestal contrast but slightly greater than the orthogonal ones. At high pedestal contrasts, all the different flankers produce similar suppression effects. That is, they increased target thresholds by about the same amount as did the parallel flankers. Again, these effects looked like a leftward shift of the TvC function by a fixed amount.

The data show that there were two different kind of flanker orientation effects:

- 1. At low contrast, the flanker facilitation decreased as the flanker orientation deviated from the target.
- 2. At high contrast, the flanker masking was about the same for all flanker orientations.

Figure 3 illustrates these relationships. In this figure, we take two slices from Figure 1 and 2 and plot the threshold difference between the flanker conditions and the no flanker condition as a function of flanker orientation at $-\infty$ dB and -10 dB At $-\infty$ dB, the flanker facilitation (decrement in threshold, hence the negative dB value) dropped rapidly as the flanker orientation deviated from the target orientation. The greatest change occurred between 0° and 11° (CCC) and between 0° and 30° (SAS). Subsequently, the threshold stayed about the same for all orientations. At -6dB, however, the flanker masking (increments in threshold, hence the positive dB value) showed no change for all the flanker orientations (for CCC, the difference between thresholds at 0° and 90° flankers, t(5.25)=1.2292, p=0.1368>0.1; for SAS, t(6.84)=0.1063, p=0.4594 > 0.1). Every flanker produced a similar masking effect. Thus, the flanker masking either has no orientation tuning or is very broadly tuned to orientation.

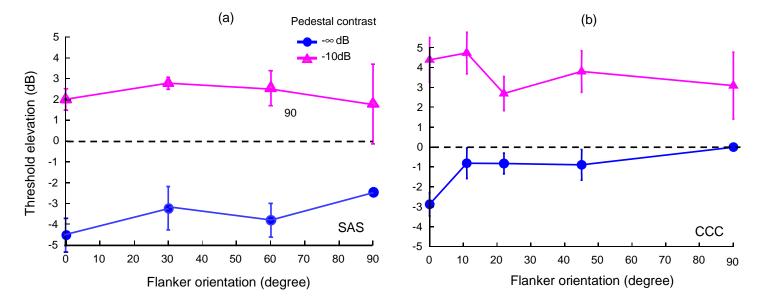


Figure 3. The target threshold at $-\infty$ dB (blue circles) and -6 dB (magenta triangles) contrast pedestal s against flanker orientation. Panel (a) shows the data for observer SAS, and Panel (b) for CCC.

4. Discussion

4.1. The Sensitivity Modulation Model

We fit the sensitivity modulation model of Chen & Kasamatsu (1998; Chen et al., 2001; also see Chen & Tyler, 2000, 2001) sensitivity modulation model to the data for flanker effects on the TvC function. This model proposes two different inter-mechanism interactions, as diagramed in Figure 4. Between hypercolumns (or other local subdivisions), the interaction is in the form of a lateral sensitivity modulation (shown outside the dotted box in Figure 4). Within each hypercolumn, the mechanism response is influenced by other mechanisms in the same hypercolumn through a subsequent process of contrast normalization or divisive inhibition (shown within the dotted box). The original version of this model was developed to explain the variety of flanker effects on response functions of striate cortical cells (Chen & Kasamatsu, 1998; Chen et al. 2001) and the same mathematical form was later discovered to explain the psychophysical data as well (Chen & Tyler, 2001). Xing & Heeger (2001) also proposed a model of a similar form to account for lateral effects.

The first stage of each local mechanism j is a linear operator within a spatial sensitivity profile $f_j(x,y)$. The excitation of this linear operator to an image g(x,y) is given as

$$E'_{j} = \sum_{x} \sum_{y} f_{j}(x, y) \bullet g(x, y)$$
 (1)

where the linear filter $f_j(x,y)$ is defined by a Gabor function (see Methods section). If the image g(x,y) is a periodic pattern with contrast C, as was used in our experiment, Equation 1 can be simplified to

$$E_{i}' = Se_{i} \bullet C \tag{1'}$$

where Se_j is a constant defining the excitatory sensitivity of the mechanism. Detailed derivation of Equation 1' from Equation 1 has been discussed elsewhere (Chen, Foley & Brainard, 2000).

The excitation of the linear operator is halfwaverectified (Chen & Tyler, 1999; Foley, 1994; Foley & Chen, 1999; Teo & Heeger, 1994) to produce the rectified excitation E_j

$$E_{i} = \max\left(E_{i}^{\prime}, 0\right) \tag{2}$$

where max denotes the operation of choosing the greater of the two numbers.

If there is no flanker present, the response of the j-th mechanism is given by its rectified excitation raised to the power p and then divided by a divisive inhibition term I, limited at low levels by an additive constant σ . That is,

$$R_{j} = \frac{E_{i}^{p}}{\left(I_{j} + \sigma\right)} \,. \tag{3}$$

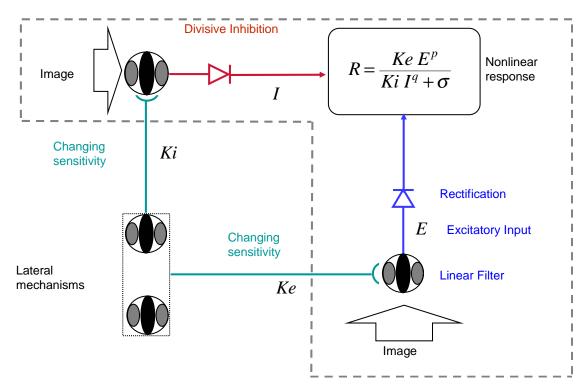


Figure 4. A diagram of the sensitivity modulation model. Inside the dotted box, all linear filters respond to image components presented at the same location. Their behaviors are described by typical divisive inhibition models. The initial excitation (E) of a linear filter is the contrast of the target pattern weighted by the filter's sensitivity to that pattern. The initial excitations of all relevant filters are pooled together to form the divisive inhibitory signal (I). The final response is the initial excitation raised by a power and then divided by the divisive inhibitory signal plus a constant. The flanking filters send signals that change the sensitivities of the contacted filters (see text for further details).

The divisive inhibition input is a nonlinear combination of the rectified excitations of all relevant mechanisms within the same hypercolumn, given by

$$I_{j} = \sum_{n} w_{n} E_{n}^{q} = Si_{j} C^{q}$$

$$\tag{4}$$

where $Si_j = \Sigma_n (w_n Se_j^q)$ is the sensitivity of the *j*-th mechanism to the divisive inhibition input.

So far, without the presence of the flankers, this model has the same form as other divisive inhibition or contrast normalization models (Foley, 1994; Ross & Speed, 1991; Teo & Heeger, 1994; Watson & Solomon, 1997; Wilson & Humanski, 1993). When the flankers are presented and produce responses in the flanking mechanisms, however, our model assumes that these mechanisms send a lateral signal that modulates the sensitivity of both the excitatory and divisive inhibitory inputs to the target mechanism. Let *Ke* and *Ki* denote the sensitivity modulation factors to the excitatory and the inhibitory inputs respectively. Therefore, the response function with the presence of flankers becomes

$$R'_{j} = \frac{Ke \bullet E_{j}^{p}}{Ki \bullet I_{j} + \sigma} \tag{5}$$

Both *Ke* and *Ki* are functions of flanker contrast. However, in the experiment reported in this paper, only two flanker contrasts (0% and 50%) were used. Therefore, we simply take *Ke* and *Ki* to have a value of 1 when the flanker contrast is 0 (thus reducing Equation 5 to Equation 3) and as free parameters to be estimated when the flanker contrast is 50%. As shown below (see sec. 4.2), both Ke and Ki are required in order to account for different aspects of the flanker effect. In our experiment, we measured the target threshold on a pedestal using a 2AFC paradigm in which the observer has to discriminate a target superimposed on a pedestal from the pedestal alone. Suppose the observer's performance is determined by the local mechanism that gives the greatest response difference between the two intervals. When there are no flankers, the difference in response is given as

$$D = R_{j,b+t} - R_{j,b} (6)$$

where j is the mechanism that gives the greatest response difference, b denotes the pedestal contrast and b+t denotes the target-plus-pedestal contrast. The target reaches the threshold when its contrast increases by a certain amount (Legge & Foley, 1980), designated 1 in our model fitting. When the flanker is presented, we

simply replace R_j (from Equation 3) by R'_j (from Equation 5) in Equation 6.

The fit of this model is shown as smooth curves in the Figure 1 and 2 and Table 1 gives the parameter values. The goodness-of-fit of the model, represented as the root mean squared error (RMSE), was 1.19 dB for CCC, 1.08 dB for SAS. These values are close to the mean standard deviation of the measurement error (1.02 dB for CCC, 0.99 dB for SAS). Hence, the model gives an excellent description of the data.

Table 1. Fitted Parameters for the Sensitivity Modulation Model

			CCC	SAS
TvC function	Se		100*	100*
parameters	Si		106	95
	Р		2.98	2.80
	Q		2.28	2.15
	σ		35.79	10.18
Lateral	Ke**	0°	2.58	2.72
modulation		11°	1.66	
factors		22°	1.42	
		30°		2.06
		45°	1.33	
		60°		2.11
		90°	1.29	1.75
	Ki**	0°	3.28	3.67
		11°	2.24	
		22°	1.96	
		30°		2.58
		45°	1.83	
		60°		2.56
		90°	1.66	1.99

^{*} Pre-assigned value, not a free parameter.

4.2. The Sensitivity Modulation Factors and the Contrast Dependent Lateral Effects

The empirical results show that flanker facilitation at low contrast reduces quickly as the flanker orientation deviates from target orientation while flanker suppression is almost independent of flanker orientation. How does the sensitivity modulation model explain this result? First consider the nature of the flanker facilitation at low contrast and the flanker suppression at high contrast. The parameters *Ke* and *Ki* represent the strength of the lateral effects received by the target mechanism. The parameter *Ke* is required to account for the facilitation that occurs at zero or low pedestal contrasts (Polat & Sagi, 1993, 1994). Given the parameter values, when the pedestal is not presented and the target is near threshold, the magnitude of the divisive inhibition term I (Equation 5) is negligible compared with the additive constant σ . Thus, in this scenario, Equation 6 can be simplified to

$$1 = \frac{Ke * C_t^p}{\sigma}$$

$$C_t = \left(\frac{\sigma}{Ke}\right)^{\frac{1}{p}}.$$

Thus, the target threshold approximates a ratio between the additive constant and *Ke* raised to a power of 1/*p*. If *Ke* is larger than 1, the target threshold decreases. This result explains the lateral masking effect found by Polat and Sagi (1993, 1994), the in-phase flanker effect of Solomon et al. (1999) and the initial flanker facilitation at lower end of the TvC functions.

The flanker suppression at high pedestal contrasts depends on both Ke and Ki. When the pedestal contrast is sufficiently high, the additive constant (σ) is negligible compared with the inhibition term (*I*) in the response function (Equation 5). Thus, we can simplify the response without the flankers as (E^p/I) and the response with flankers as $(Ke/Ki)*(E^p/I)$. That is, the response function with flankers is the ratio between *Ke* and *Ki* multiplied by the no-flanker response function. Translating the responses to thresholds, the threshold difference between the flanker and the no-flanker conditions is proportional to the ratio Ki/Ke. Since Ke and Ki are independent of pedestal contrast, this ratio gives a parallel shift of TvC functions horizontally on log-log coordinates. The presence of the flankers reduces the responses and increases the thresholds, consistent with Ki being greater than Ke.

Intuitively, one can approximate the change of the TvC functions in Figure 1 and 2 with the concept of equivalent contrast. The flankers have a facilitatory effect on both the target and the pedestal. When there is no pedestal or the pedestal is weak, one only needs to consider the flanker effect on the target. Due to the flanker facilitation, a target with a particular contrast in the flanker condition produces the same response in the system as a target with a higher contrast in the no-flanker condition. Hence, the threshold in the flanker condition is lower than in the no-flanker condition. When the pedestal contrast is high, in addition to the facilitation on the target, which pushes the TvC functions down, it becomes necessary to consider the flanker effect on the pedestal. Empirically, we find that the pedestal is effectively facilitated by the flankers, producing the same effect as a pedestal with a higher contrast in the noflanker condition. This facilitatory effect is essentially the same as pushing the TvC function leftward in logarithmic coordinates. Since the target threshold at this part of TvC functions increases with pedestal contrast, a leftward shift means that the target threshold increases in the flanker condition at the same pedestal contrast relative to the no-flanker condition. The net result of these two processes seen in the data (Figure 1 and 2) is the sum of a

^{**}Each flanker orientation had a pair of *Ke* and *Ki* as free parameters except the no-flanker condition where both *Ke* and *Ki* were set to 1.0.

leftward movement produced by the facilitation of the pedestal and a downward movement by the facilitation of the target.

Figure 5 plots how the parameters *Ke* and *Ki* change with flanker orientation. Both parameters drop quickly as the flanker orientation deviates from the target orientation. This effect is more obvious with the parameters for CCC's data (Panel b), which has more sample values at small orientation differences. The change of parameters can be characterized by a linear combination of two Gaussian functions of flanker orientation (smooth curves). One Gaussian is narrowly tuned with a scale parameter ("standard deviation") for Ke of 2.55° (SAS) or 4.49° (CCC), and for Ki of 2.56° (SAS), or 4.48° (CCC); and the other is broadly tuned with scale parameters for Ke of 72.43° (SAS) or 77.47° (CCC), and for Ki of 63.88° (SAS), or 72.21° (CCC). The similarities in the tuning functions for *Ke* and *Ki* are consistent with the idea that the excitatory and inhibitory lateral modulation effects are from the same source and act on different agents in the target mechanism. We acknowledge that the Gaussian parameters for SAS are less constrained due to the limited number of samples, but they are nevertheless of similar magnitudes to those for CCC. One Gaussian function of flanker orientation cannot capture the behavior of *Ke* and *Ki* as it provides a much poorer fit to the data (F(8,10) = 37.87, p < 0.0001). Thus, it is clear that there must be two components for both the excitatory and inhibitory lateral modulations: one narrowly tuned to flanker orientation and the other broadly tuned.

When the flanker orientation is close to 0°, or

parallel to the target, the lateral modulation is dominated by the narrowly tuned component. As a result, the values of *Ke* and *Ki* drop rapidly with flanker orientation. Since the target threshold at low pedestal contrast is determined by the value of *Ke*, this dramatic change of Ke reflects the narrow flanker orientation tuning in target thresholds in low pedestal contrast.

While the value of Ki is greater than that of Ke, it decreases with flanker orientation at about the same rate as does Ke. As a result, the ratio Ki/Ke (green open triangles in Figure 5) is roughly constant for all flanker orientations. This constant Ki/Ke ratio is reflected in the data as the flanker suppression that is broadly tuned in orientation.

4.3. Comparison with Contrast Matching Data

Yu, Klein and Levi (2001) compared the apparent contrast of a periodic test pattern with and without a periodic pattern surround. They reported that the cross-orientation surround had a "slight facilitation" effect on test contrast among some of their observers (average 6.3% to 7.1% increment from test contrast at high contrasts, but individually as high as 11% for one observer and suppressive for another). A similar "slight facilitation" effect was also reported for other contrast matching studies (e.g., Xing & Heeger, 2000). At first glance, these results are not consistent with ours, which show discrimination threshold increases at high contrast in a manner that can be explained as a suppressive effect by the flankers. However, contrast discrimination and

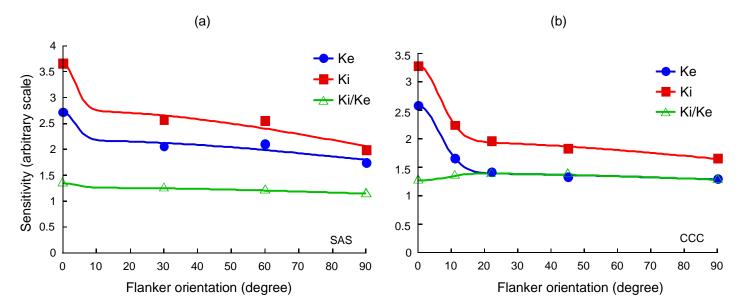


Figure 5. This figure shows the flanker modulation factors plotted against flanker orientation. The blue circles represent the excitatory modulation factor (Ke) and the red circles represent the inhibitory modulation factor (Ki). The ratio Ki/Ke are represented as green open squares. The smooth curves each represents a linear combination of two Gaussian functions of orientation that fit the Ke or Ki values. Panel (a) shows the factors for observer SAS, and Panel (b) for CCC.

contrast matching paradigms measure different aspects of the mechanism responses. A contrast matching experiment, which compares a test contrast to a reference contrast, concerns the magnitude of the response. Contrast discrimination experiments, which measure the increment threshold from a base contrast as shown in section 4.1, concern the slope of the contrast response function in relation to the prevailing noise. Hence, it is meaningless to compare directly the discrimination and matching data. It is possible that, in the same experimental setup, discrimination threshold increases (slope of the response function is flatter) while the apparent contrast also increases (the magnitude of the response to base contrast increases). Yu, Klein, and & Levi (2001) actually reported in the same study that the surround showed different effects on contrast discrimination and contrast matching, and were puzzled by that difference. Nevertheless, it is possible to derive the response function from the discrimination performance, as shown in section 4.1 (Equations 5 & 6). The magnitude of the response is proportional to Ke/Ki (see sec. 4.2). From Table 1, it is easy to determine that, on average, the ratio Ke/Ki between 0° and 90° changes from 0.76 to 0.83 or a 9% increase (for SAS, 0.74 to 0.88; and for CCC, 0.79 to 0.78). This change, though close to zero, is comparable with the "slight facilitation" reported by Yu, Klein, and Levi. It is evident, therefore, that the apparently contradictory prior results are in fact compatible with our model.

4.4. The Uniqueness of Lateral Effects

There are numerous studies on how the target detection threshold changes with context. Usually, those studies have focused on conditions in which the contextual stimuli, or the pedestals, occupy the same location and are of the same size, as the target (Breitmeyer, 1984; Foley, 1994; Foley & Chen, 1999; Kontsevich & Tyler, 1999a; Legge & Foley, 1980; Ross & Speed, 1991; Wilson, McFarlane & Phillips, 1983). The typical pedestal effect is the dipper shaped TvC function as measured in the no-flanker condition. There also have been attempts to explain flanker facilitation as a special case of the pedestal effect (Morgan & Dresp, 1995; Snowden & Hammett, 1998; Solomon, Watson & Morgan, 1999). Snowden & Hammett suggested that, in the flanker facilitation experiments (Polat & Sagi, 1993, 1994; Zenger & Sagi, 1996), the receptive field of the target detection mechanism might extend beyond the size of the target. When the flankers are placed at an appropriate distance away from the target, there is only a small overlap between the receptive field and the flankers. In turn, a high-contrast flanker distant from the target could mimic the effect of a low-contrast pedestal on target detectability. Thus, the mechanism of the flanker

facilitation could be the same as the dip at low pedestal contrasts. Morgan and Dresp and Solomon et al. also offered a similar explanation of the flanker facilitation. None of these authors, however, noted the extremely narrow range of facilitation predicted by this hypothesis for Gaussian stimuli, or its incompatibility with the extended range (up to 9λ) of the measured flanker effects reported by Polat and Sagi.

In the present context, equating the flanker effect to a pedestal effect cannot explain the flanker suppression at high contrast. In current theories of pedestal effects (Foley, 1994; Ross & Speed, 1991; Teo & Heeger, 1997; Watson & Solomon, 1997; Wilson & Humanski, 1993), the presence of the pedestal increases both the direct excitatory and the divisive inhibitory terms (E and I in Equation 5) terms in the response function. Its contribution to the mechanism response is added to that of the target. Suppose that the flanker contrast is constant in the flanker conditions as in our experiments, then equating the flankers to a weak pedestal is equivalent to increasing E and I in Equation 5 by a constant. On the other hand, the contribution of the pedestal to E and I, and in turn the response, increases with pedestal contrast. Thus, the TvC function in the presence of the flankers will converge to the TvC function without any flankers as pedestal contrast increases. Snowden & Hammett (1998) derived the same prediction for contrast discrimination in the presence of a patterned surround.

Although the exact prediction depends on the parameter values, considering the flankers as a weak pedestal should always predict a convergence of the two TvC functions with and without the flanker present. Our data are not consistent with this prediction. At high pedestal contrasts, there is not only a strong flanker masking effect, but also the magnitude of the suppression is roughly uniform. Up to the highest pedestal contrast measured, there is no sign of convergence between the no-flanker TvC function and any of the flanker TvC functions.

The uniqueness of the flanker effect can also be demonstrated empirically by comparing the orthogonal flanker TvC functions with the orthogonal pedestal TvC functions. It is known that an orthogonal pedestal does not facilitate target detection (Foley, 1994; Foley & Chen, 1998). The TvC function no longer has a dipper shape. The orthogonal pedestal has no effect on target threshold in low and medium pedestal contrasts. Thus, if the flankers behaved like a low contrast pedestals, orthogonal flankers should produce no effect on target detection. While the orthogonal flankers failed to show flanker facilitation at low pedestal contrasts for CCC, they did have a facilitatory effect for the other observer. In addition, the orthogonal flanker produces substantial flanker suppression in both observers, contrary to the prediction from the orthogonal pedestal behavior.

The most relevant evidence may be the two-pedestal experiment reported by Foley (1994). He measured the

TvC function for a vertical target on a vertical pedestal superimposed on a horizontal pedestal. This experiment is very similar to ours except that his second contextual stimulus is a pedestal while ours is a flanker. Compared with behavior of the TvC function without the constant horizontal pedestal, the presence of the horizontal pedestal increases the target threshold at low vertical pedestal contrasts but has little, or slightly facilitatory, effect on target detection at higher contrasts. The two TvC functions merge together at high pedestal contrasts. This is exactly the result one would predict if the effects from two pedestals are summed together to determine the target threshold. This result is qualitatively different from our orthogonal-flanker TvC functions, in which the flankers produce little or no facilitatory effect at low pedestal contrasts and a suppressive effect at high pedestal contrasts. This comparison shows that the behavior of flankers is different from that of pedestals. The flankers operate through a multiplicative factor that modulates the responses of the target mechanism.

5. Conclusions

We have shown that there are two flanker effects: (1) a target facilitation that is narrowly tuned to flanker orientation, and (2) a pedestal enhancement that is broadly tuned to flanker orientation. These effects can be explained by the properties of both the excitatory and inhibitory lateral modulations. The magnitude of the lateral modulation varies with orientation giving a target facilitation that has a narrow orientation tuning, and the ratio between the inhibitory and excitatory lateral modulation is independent of flanker orientation giving a pedestal enhancement with a broad orientation tuning.

In conclusion, the sensitivity modulation model of Chen & Kasamatsu (1998; also see Chen et al. 2001) provides a clear and simple interpretation of a wide array of neurophysiological, electrophysiological and psychophysical data in long-range interactions of the neural response to contrast elements, including the present data. It may be noted that that the original divisive inhibition-based gain-control models (Albrecht & Geisler, 1991; Carandini & Heeger, 1994; Foley, 1994; Heeger, 1992; Ross & Speed, 1991), which were designed to account for the interaction among mechanisms, are incompatible with many aspects of the present data, in particular, the parallel shift of TvC functions at high contrast and the strong suppression effect produced by orthogonal flankers. To explain the surround suppression effect of contrast matching, Xing & Heeger (2001) recently revised their original divisive inhibition model. Their revision essentially incorporates the sensitivity modulation factor of Chen and Kasamatsu (1998; also see Chen et al. 2001; Chen & Tyler, 2000, 2001). There is thus converging agreement on the role of

sensitivity modulation as a key mechanism of lateral interactions in visual cortex.

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References

- Adini, Y., & Sagi, D. (2001). Recurrent networks in human visual cortex: Psychophysics evidence. *Journal of the Optical Society of America A*, 18, 2228-2236. [PubMed]
- Albrecht, D. G., & Geisler, W. S. (1991). Motion selectivity and the contrast-response function of simple cells in the visual cortex. *Visual Neuroscience*, 7, 531-546. [PubMed]
- Bradley, A., & Ohzawa, I. (1986) A comparison of contrast detection and discrimination. *Vision Research*, 26, 991-997. [PubMed]
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433-436. [PubMed]
- Breitmeyer, B. G. (1984). Visual masking: An integrative approach. Oxford: Oxford University Press.
- Carandini, M. & Heeger, D. J. (1994). Summation and division by neurons in primate visual cortex. *Science*, 264, 1333-1336. [PubMed]
- Chen, C.-C., Foley, J. M. & Brainard, D. H. (2000). Detection of chromoluminance patterns on chromoluminance pedestals II: Model. *Vision Research*, 40, 789-803. [PubMed]
- Chen, C.-C., & Kasamatsu, T. (1998). A sensitivity modulation model for lateral interaction among striate cells in cat visual cortex [Abstract]. Society for Neuroscience Abstracts, 24, 1979.
- Chen, C.-C., Kasamatsu, T., Polat, U., & Norcia, A. M. (2001). Contrast response characteristics of long-range lateral interactions in cat striate cortex. *Neuroreport*, 12, 655-661. [PubMed]
- Chen, C.-C., & Tyler, C. W. (1999). Spatial pattern summation is phase-insensitive in the fovea but not in the periphery. *Spatial Vision*, 12, 267-285. [PubMed]
- Chen, C.-C., & Tyler, C. W. (2000). Spatial long-range modulation of contrast discrimination. SPIE *Proceedings*, 4080, 87-93.
- Chen, C.-C., & Tyler, C. W. (2001). Lateral sensitivity modulation explains the flanker effect in contrast discrimination. *Proceedings of the Royal Society, Series B Biological Science*, 268, 509-516. [PubMed]

Field, D. J., Hayes, A, Hess, R. F. (1993). Contour integration by the human visual system: Evidence for a local "association field." *Vision Research*, *33*, 173-193. [PubMed]

- Foley, J. M. (1994). Human luminance pattern-vision mechanisms: Masking experiments require a new model. *Journal of the Optical Society of America A*, 11, 1710-1719. [PubMed]
- Foley, J. M., & Chen, C. C. (1999). Pattern detection in the presence of maskers that differ in spatial phase and temporal offset: threshold measurements and a model. *Vision Research*, 39, 3855-3872. [PubMed]
- Heeger, D. J. (1992). Normalization of cell responses in cat striate cortex. *Visual Neuroscience*, 9, 181-197. [PubMed]
- Kontsevich, L. L., & Tyler, C. W. (1999a). Nonlinearities of near-threshold contrast transduction. *Vision Research*, 39, 1869-1880. [PubMed]
- Kontsevich, L. L., & Tyler, C. W. (1999b). Bayesian adaptive estimation of psychometric slope and threshold. *Vision Research*, 39, 2729-2737. [PubMed]
- Legge, G. E. & Foley, J. M. (1980). Contrast masking in human vision. *Journal of the Optical Society of America*, 70, 1458-1470. [PubMed]
- Li, Z. (1998). A neural model of contour integration in the primary visual cortex. *Neural Computing*, 10, 903-40. [PubMed]
- The MathWorks, Inc. (1993). *Matlab* [Computer software]. Natick, MA:. [Link].
- Morgan, M. J., & Dresp, B. (1995). Contrast detection facilitation by spatially separated targets and inducers. *Vision Research*, *35*, 1019-1024. [PubMed]
- Pelli, D. G. (1997). The Video Toolbox software for visual psychophysics: Tranform numbers into movies. *Spatial Vision*, 10, 437-442. [PubMed]
- Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. *Vision Research*, 33, 993-999. [PubMed]
- Polat, U., & Sagi, D. (1994). The architecture of perceptual spatial interactions. *Vision Research*, 34, 73-78. [PubMed]
- Polat, U., Mizobe K., Pettet, M. W., Kasamatsu, T., & Norcia A. M. (1998) Collinear stimuli regulate visual responses depending on cell's contrast threshold. *Nature*, 391, 580-584. [PubMed]

- Ross, J., & Speed, H. D. (1991). Contrast adaptation and contrast masking in human vision. *Proceedings of the Royal Society, Series B Biological Science*, 246, 61-69. [PubMed]
- Sengpiel, F., Baddeley, R. J., Freeman, T. C., Harrad, R., & Blakemore, C. (1998). Different mechanisms underlie three inhibitory phenomena in cat area 17. *Vision Research*, 38, 2067-2080. [PubMed]
- Snowden, R. J., & Hammett, S. T. (1998). The effects of surround contrast on contrast thresholds, perceived contrast and contrast discrimination. *Vision Research*, 38, 1935-1945. [PubMed]
- Solomon, J. A., Watson, A. B., & Morgan, M. J. (1999). Transducer model produces facilitation from opposite-sign flanks. *Vision Research*, 39, 987-992. [PubMed]
- Teo, P. C., & Heeger, D. J. (1994). Perceptual image distortion. SPIE Proceeding, 2179, 127-141.
- Tyler, C. W., & McBride, B. (1997). The Morphonome image psychophysics software and a calibrator for Macintosh systems. *Spatial Vision*, 10, 479-484. [PubMed]
- Watson, A. B., & Solomon, J. A. (1997). A model of visual contrast gain control and pattern masking. Journal of the Optical Society of America A, 14, 2378-2390. [PubMed]
- Wilson, H. R., & Humanski, R. (1993). Spatial frequency adaptation and contrast gain control. *Vision Research*, 33, 1133-1149. [PubMed]
- Wilson, H. R., McFarlane, D. K., & Phillips, G. C. (1983). Spatial frequency tuning of orientation selectivity units estimated by oblique masking. *Vision Research*, 23, 873-882. [PubMed]
- Xing, J., & Heeger, D. J. (2001). Measurement and modeling of center-surround suppression and enhancement. *Vision Research*, 41, 571-583. [PubMed]
- Yu, C. Klein, S. A., & Levi, D. M. (2001). Surround modulation of perceived contrast and the role of brightness induction. *Journal of Vision*, 1, 18-31, http://journalofvision.org/1/1/3/, DOI 10.1167/1.1.3. [Article]
- Zenger, B., & Sagi, D. (1996). Isolating excitatory and inhibitory nonlinear spatial interactions involved in contrast detection. *Vision Research*, *36*, 2497-2513. [PubMed]
- Zenger-Landolt B, & Koch C. (2001). Flanker effects in peripheral contrast discrimination—Psychophysics and modeling. Vision Research, 41, 3663-3775. [PubMed]