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Lateral sensitivity modulation explains the flanker effect in contrast discrimination

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We used a dual-masking paradigm to study how contrast discrimination can be influenced by the presence of adjacent stimuli. The task of the observer was to detect a target superimposed on a pedestal in the presence of flankers. The flankers (i) reduce the target threshold at zero pedestal contrast, (ii) shift the target threshold versus pedestal contrast (TvC) function horizontally to the left on a log–log plot at high pedestal contrasts, and (iii) reduce the size of pedestal facilitation at low pedestal contrasts. The horizontal shift at high pedestal contrasts suggests that the flanker effect is a multiplicative factor that cannot be explained by previous models of contrast discrimination. We extend the divisive inhibition model of contrast discrimination by implementing the flanker effect as a lateral multiplicative sensitivity modulation. This extended model provides a good account of the data.

Keywords: long-range interaction; divisive inhibition; lateral masking; pedestal; threshold

1. INTRODUCTION

Visual performance for a stimulus presented at one location on the retina can be modified by the presence of other stimuli at different locations. For instance, Polat & Sagi (1993, 1994) (also see Zenger & Sagi 1996) measured detection thresholds for a target Gabor pattern at the fovea flanked by two other high-contrast Gabor patterns (flankers). The target threshold decreased up to about 50% of the absolute threshold (facilitation) when a pair of collinear flankers (with the same orientation as the target) was presented at about three units of target wavelength away. Conversely, flankers with an orientation orthogonal to the target had no effect on target detection. This control result establishes that the effects of the flankers are not generic attention or uncertainty effects but are local or long-range interactions specific to the receptive field structure and orientation selectivity. Adini *et al*. (1997) have reported similar effects of flanker orientation on target detection.

(a) *Relationships between long-range collinear interactions and pattern masking*

There are numerous studies of how the threshold of a target pattern changes with the presence of other patterns (masks) (Legge & Foley 1980; Wilson *et al*. 1983; Breitmeyer 1984; Ross & Speed 1991; Foley 1994; Kontsevich & Tyler 1999; Foley & Chen 1999). These experiments, called masking experiments in the literature, usually concern conditions where the target pattern occupies the same location as a context pattern. In this paper, we refer to a mask with the same spatio-temporal properties as the target pattern as a pedestal. The best-known pedestal effect is the 'dipper'-shaped function of target threshold versus pedestal contrast (TvC) (Legge & Foley 1980; Ross & Speed 1991; Foley 1994; Kontsevich & Tyler 1999; Foley & Chen 1999). If the pedestal is the same as the target in all spatio-temporal dimensions except contrast, the target threshold first decreases (facilitation) and then increases above the absolute threshold (masking) as the pedestal contrast increases.

A widely accepted model of pattern masking is the divisive inhibition or contrast normalization model (Ross & Speed 1991; Wilson & Humanski 1993; Foley 1994; Watson & Solomon 1997; Teo & Heeger 1997; Snowden & Hammett 1998). Although there are variations in detail, all versions of the divisive inhibition models share the same two elements.

The change in target threshold with mask contrast reflects the response properties of the target detection mechanisms. The mask produces a response in the target detection mechanism. In order to be detected, the target should have the strength (e.g. contrast of periodic pattern or light intensity of a spot) to increase the response by a certain amount, defined as one unit. Figure 1 illustrates the relationship between the TvC function and the hypothetical mechanism response function for a special case where the mask is a pedestal with the same spatio-temporal properties as the target except contrast. Suppose that the pedestal (with contrast C_1 in figure 1) pushes the response of the detection mechanism to an accelerating part of the response function. It would require a smaller target contrast (ΔC_1) to increase the response by one unit. On the other hand, if the pedestal pushes the response to a decelerating part of the response function, it will require a greater target contrast (ΔC_2) to increase the response by the same amount. Thus, the change of target threshold reflects nonlinearities in the response of the detection mechanism.

The nonlinear response is a result of contrast normalization or divisive inhibition. Most current theories of pattern masking (Ross & Speed 1991; Wilson & Humanski 1993; Foley 1994; Watson & Solomon 1997; Teo & Heeger 1997; Snowden & Hammett 1998) postulate a multiple-stage model that involves at least a linear operator followed by a nonlinear divisive inhibition operator. The nonlinear operator raises the linear operator excitation by a power and then divides it by an inhibitory

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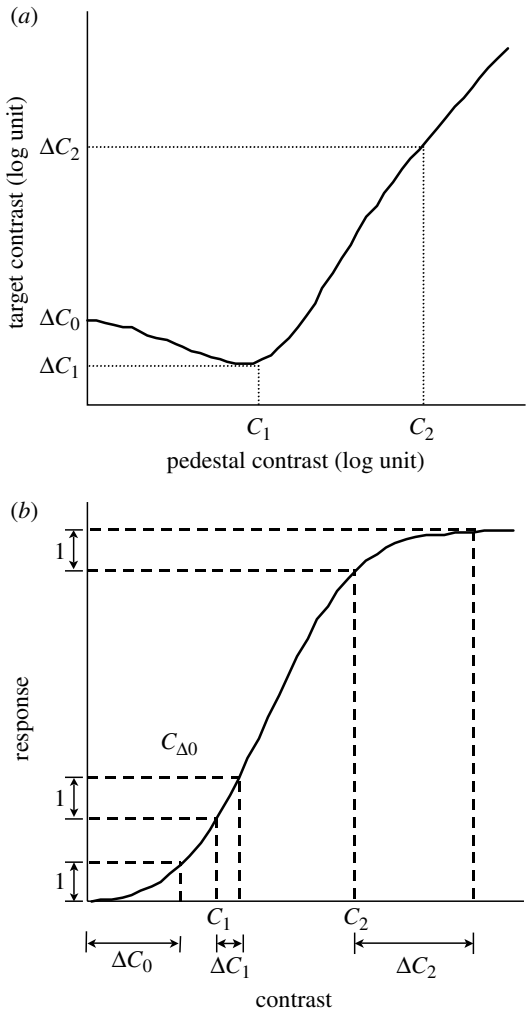

Figure 1. The relationship between the target threshold versus pedestal contrast (TvC) function (*a*) and the underlying contrast response function that could generate it (*b*). ΔC_0 is the target absolute (unmasked) threshold. ΔC_1 and ΔC_2 are target thresholds measured with the presence of pedestal contrast C_1 and C_2, respectively. At threshold, the target increases the response to pedestal alone by one unit. As a result, the target contrast threshold is inversely proportional to the slope of the response function.

input. This inhibitory input is a nonlinear combination of the excitations of all relevant (e.g. adjacent) linear operators.

Although current theories of pattern masking are developed with pedestals as maskers, it has been argued that the same model can account for the effects of non-coincident flankers (Morgan & Dresp 1995; Snowden & Hammett 1998; Solomon *et al.* 1999). Solomon *et al.* (1999) suggested that, in collinear long-range interaction experiments, the receptive field of the target detection mechanism might extend beyond the size of the target. The so-called lateral interaction effect occurs when the receptive field overlaps both the target and the flankers. When the flankers are moved away from the target, the overlap between the receptive field and the flankers decreases. As a result, a high-contrast flanker away from the target could mimic the effect of a low-contrast pedestal on target detectability. Thus, the flanker facilitation effect might occur because the flankers partially overlap the receptive field of the target detection mechanism. Morgan & Dresp (1995) and Snowden & Hammett (1998) also offered an explanation of the long-range interaction that shared many assumptions and a similar conclusion with that of Solomon *et al.* (1999).

(b) *Physiological evidence is inconsistent with divisive inhibition models*

In this paper, we show evidence that the divisive inhibition model in its current form is inappropriate for long-range interactions. Instead, we propose a sensitivity modulation to account for long-range interactions. This model is inspired by recent electrophysiological studies.

Polat *et al.* (1998; also see Chen *et al.* 2001) measured the contrast response functions of striate cortical cells to a target Gabor pattern with and without the presence of two collinear and parallel flanking Gabor patterns located outside the classical receptive field of the cell under study. The majority of the cells exhibited two kinds of flanker effects: (i) increase in target response at low target contrast (facilitation); and (ii) decrease in target response at high target contrast (suppression). Sengpiel *et al.* (1998) and Somers *et al.* (1998) also reported similar effects. Chen *et al.* (2001) also reported another flanker effect in which the flankers increased cell response at all target contrasts and the amount of facilitation actually increased with target contrast. Notice that, in all these studies, flanker contrast was kept constant for each cell while the flanker effect increased with target contrast. These data suggest that the long-range interaction is a multiplicative process such that the flanker effect can be amplified according to the target contrast.

The divisive inhibition model in its current form, on the other hand, assumes that a spatial context, such as a flanker, can have an effect on target response through a normalization process. That is, the effect of the flankers, either excitatory or inhibitory, is simply added to the effect of the target. Thus, at high target contrast, where the relative contribution of the flanker is smaller than at low target contrast, the response functions with and without flankers should converge towards each other. This prediction is contradicted by the physiological data.

(c) *The lateral sensitivity modulation model*

Figure 2 shows a diagram of an alternative model. This model proposes two different inter-mechanism interactions. Between hypercolumns (or other local subdivisions), the interaction is in the form of a lateral sensitivity modulation (shown outside the dotted box in figure 2). Within the same 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 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

$$E'_j = \sum_x \sum_y f_j(x, y) \cdot g(x, y), \qquad (1a)$$

where the centred dot denotes the dot product of the image with the sensitivity profile. We assume that the

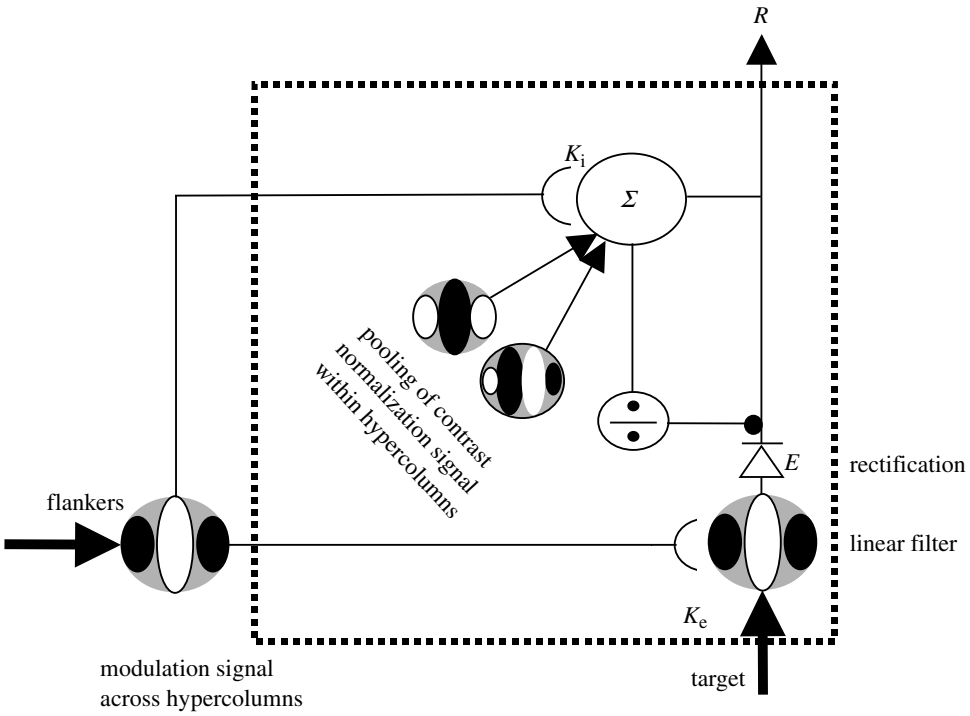

Figure 2. A diagram of the sensitivity modulation model. Inside the dotted box representing a hypercolumn, all linear filters respond to image components presented at the same location. Their behaviours are described by the divisive inhibition models. The initial excitation (E) of a linear filter is 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 § 1(c) for further details.

sensitivity profile of the linear filter is defined by a Gabor function (see § 2). If the image $g(x,y)$ is a periodic pattern with a contrast C as we used in our experiment, equation (1*a*) can be simplified as

$$E'_j = S_{ej} \cdot C, \tag{1b}$$

where $S_{e,j}$ is a constant called the excitatory sensitivity of the mechanism. Detailed derivation from equation (1*a*) to (1*b*) has been discussed elsewhere (Chen *et al.* 2000).

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

$$E_j = \max(E'_j, 0), \tag{2}$$

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

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

$$R_i = E_i^p / (I_j + \sigma). \tag{3}$$

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

$$I_i = \sum_n w_n E_n^q = S_{ij} \cdot C^q, \tag{4}$$

where $S_{i,j} = \sum_n (w_n S_{e,n}^q)$ is the sensitivity of the jth mechanism to the divisive inhibition input.

When the flankers are presented and produce responses in the flanking mechanisms, these mechanisms send a lateral signal that modulates the sensitivity of both the excitatory and divisive inhibitory inputs to the target mechanism. If K_e and K_i are the sensitivity modulation factors to the excitatory and the inhibitory inputs respectively. The response function with the presence of flankers becomes

$$R'_i = (K_e \cdot E_i^p) / (K_i \cdot I_j + \sigma). \tag{5}$$

Both K_e and K_i 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 K_e and K_i to be 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%.

To test whether long-range interactions conform to the divisive inhibition model or the sensitivity modulation model, we measured the contrast discrimination threshold with and without the flankers present. Without a flanker, in a two-alternative forced-choice (2AFC) task, the observer has to discriminate a target superimposed on a pedestal from the pedestal alone. Suppose the decision is made by the local mechanism that gives the greatest response difference between the two intervals. The difference in response is given as

$$\begin{aligned} D &= R_{i,b+t} - R_{i,b} \\ &= E_{i,b+t}{}^p / (\textstyle\sum_j w_j E_{j,b+t}{}^q + \sigma) - E_{I,m}{}^p / (\textstyle\sum_j w_j E_{j,b}{}^q + \sigma), \end{aligned} \tag{6}$$

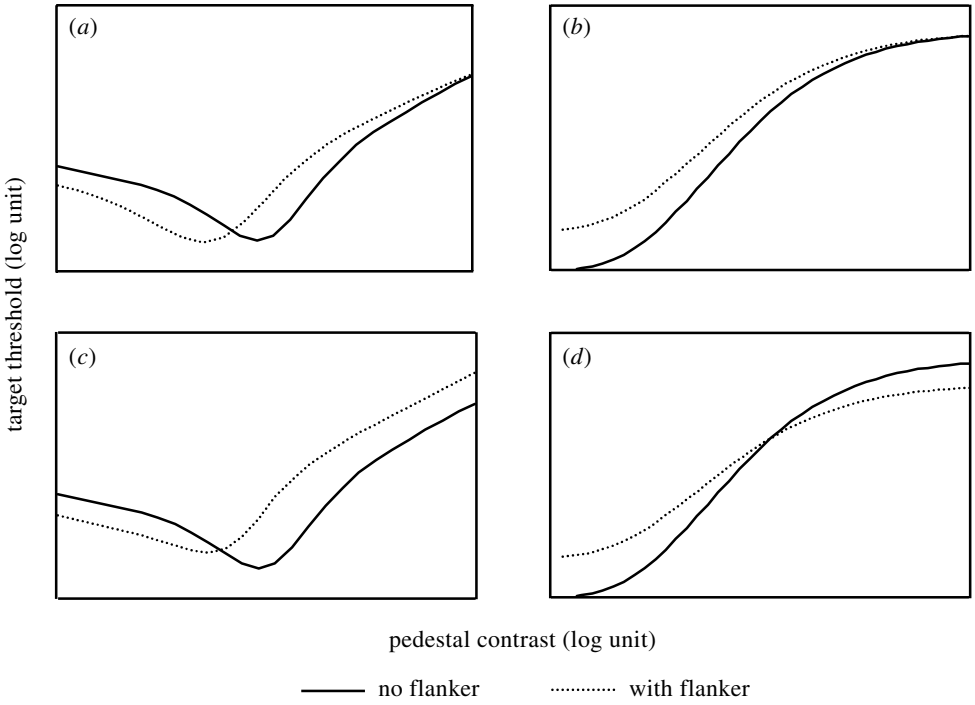

Figure 3. The predictions of the current divisive inhibition models and the lateral sensitivity modulation model on the TvC functions and the theoretical response function that underlies it. Although the exact predictions depend on the parameter values, some salient features will emerge regardless of the parameter values. The current divisive inhibition models suggest that the flanker effect can be implemented as an additive process. They predict that (*a*) the TvC functions and (*b*) the response functions should merge together at high contrasts where the additive flanker effect is negligible compared to the pedestal effect. The lateral sensitivity modulation model suggests that the flanker effect is a multiplicative process. It predicts a parallel shift of the TvC functions on (*c*) a log–log plot and an increasing flanker effect on (*d*) the response function above the cross-over point.

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 D by a certain amount, designated 1 in our model fitting. When the flanker is presented, we simply replace R_j (equation (3)) by R'_j (equation (5)) in equation (6).

(d) *The lateral sensitivity modulation model and the current divisive inhibition model make different predictions for contrast discrimination in the presence of flankers*

Consider a contrast discrimination experiment in which we measure target contrast threshold on various pedestal contrasts. With this experiment, we can plot a target threshold versus pedestal contrast (TvC) function as shown as the solid curves in figure 3*a*. The experiment is then repeated in the presence of flankers. The sensitivity modulation model and the current divisive inhibition model make different predictions as to how the presence of the flankers changes the TvC functions.

In current divisive inhibition models, the inter-mechanism interaction is implemented in the pooling of the divisive inhibition signals (equation (4)). This pooling process sums information from mechanisms that respond both to pedestals and flankers. The presence of a flanker only adds another term in the pooling process. Suppose the flanker contrast is kept constant. The flanker effect is thus a constant in the pooled divisive inhibitory signal and in turn a constant in the response function. On the other hand, the contribution of the pedestal in the response function increases with pedestal contrast. Thus, the relative contribution of the flankers becomes less significant at high pedestal contrasts than at low pedestal contrasts. As a result, the current divisive inhibition model predicts that the TvC function in the presence of the flankers will converge towards the TvC function without any flankers (figure 3*a*) as pedestal contrast increases. Snowden & Hammett (1998) derived the same prediction for contrast discrimination in the presence of a patterned surround. In addition, with equation (6), we can infer the hypothetical contrast response function of the mechanism predicted by the model. Although the exact prediction depends on the parameter values, the divisive inhibition model should always predict a convergence of the two response functions with and without the presence of flankers (figure 3*b*).

In the lateral sensitivity modulation model, on the other hand, the presence of flankers changes the sensitivity of the target mechanism. This change is a multiplicative factor for both the target and the pedestal contrasts. At high pedestal contrast, where the additive constant (σ in equation (3)) is negligible compared with the size of the divisive inhibitory signal (I in equation (3)), the whole response function can be simplified as a ratio between the excitatory signal and the divisive inhibitory signal. The effect of the flanker is then to multiply the response function by a factor (which will be an additive constant in logarithmic coordinates). When this effect is played through the generation of the TvC function, therefore, the flanker effect should be to shift the high-contrast portion of the TvC function horizontally to the left on a

log–log plot (figure 3*c*). With different parameters, the lateral sensitivity model can predict several different types of lateral effects (Chen *et al*. 2001). All of the predictions share the common feature that the flanker effect, and thus the difference between the response functions with and without flankers, increases with contrasts. Figure 3*d* shows an example where the flankers have substantial effects both on the excitatory (numerator in equation (5)) and the inhibitory inputs (denominator in equation (5)) with the effect on the inhibitory inputs being stronger. This special case shows an initial facilitation in the response function being taken over by the suppression and the suppression increases with contrast. A detailed discussion is given in § 4(a,b).

2. METHODS

(a) *Apparatus*

The stimuli were presented on two Sony CPD-1425 monitors (Sony, Inc., NJ, USA) each driven by a Radius PrecisionColor graphic board (Radius, Inc., Sunnyvale, CA, USA). A Macintosh Quadra Pro computer (Apple Computer, Inc., Cupertino, CA, USA) controlled the graphic boards. The resolution of the monitor was 640 horizontal by 480 vertical pixels. At the viewing distance we used (128 cm), there were 60 pixels deg^{-1}. The viewing field was then 10.7° (H) by 8° (V). The refresh rate of the monitor was 60 Hz. We used the LightMouse photometer (Smith–Kettlewell Eye Research Institute, San Francisco, CA, USA) (Tyler & McBride 1997) to measure the full input–output intensity function of the monitor. This information allowed us to compute linear look-up table settings to linearize the output within 1%. The mean luminance of the monitor was set at 26 cd m^{-2}.

(b) *Stimuli*

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

$$G(x,y) = B + B \times C \times \cos(2\pi f x) \times \exp(-x^2/2\sigma^2) \times \exp(-(y-u_y)^2/2\sigma^2),$$

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 and u_y was the vertical displacement of the pattern. All patterns had a spatial frequency (f) of 4 cycles deg^{-1} and a scale parameter (σ) 0.1768°. The target and the pedestal were centered at the fixation point, therefore the displacement u_y was zero. The two flankers were placed above and below the target with a displacement (u_y) of 0.75°. All stimuli were presented concurrently. The temporal waveform of the stimuli was a pulse with duration of 100 ms.

(c) *Procedures*

We used a temporal two-alternative forced-choice paradigm to measure the target threshold. In 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 QUEST adaptive threshold algorithm (Watson & Pelli 1983) to measure the threshold at a 91.5% correct response level.

The target contrast threshold was measured on several pedestal contrasts ranging from −34 dB (2%) to −6 dB (50%). On each trial, the two flankers always had the same contrast. The flanker contrast was either 50% −6 dB or 0%. Each target threshold measure is the average of at least four repeats for each observer.

The experimental control software was written in Matlab (MathWorks, Inc, Natick, MA, USA) using the Psychophysics Toolbox (Brainard 1997), which provides high-level access to the C-language VideoToolbox (Pelli 1997).

Two observers served in the study: C.-C.C. (male, early 30s) is an author of this paper, and M.D.L. (female, late 20s) was a paid observer naive to the purpose of the experiment. M.D.L. had a normal and C.-C.C. a corrected-to-normal visual acuity (20/20).

3. RESULTS

We plot our data as target threshold versus pedestal contrast (TvC) functions for both flanker and no-flanker conditions (figure 4). They were fitted by least-squares estimation with the model described in § 1(c). The best-fitting parameters for the two observers are provided in table 1. The smooth curves in figure 4 show the fit of the sensitivity modulation model. When there were no flankers (closed circles and solid curve), the TvC functions showed a typical dipper shape. That is, the target threshold first decreased and then increased above its absolute contrast threshold as pedestal contrast increased. The greatest threshold decrement occurred when the pedestal contrast was approximately at its own detection threshold. This dipper-shaped TvC function is well established in the literature (Legge & Foley 1980; Ross & Speed 1991; Foley 1994; Kontsevich & Tyler 1999; Foley & Chen 1999). A particularly robust facilitation effect of −9 dB is seen for MDL.

The open circles and dashed curve show the TvC function measured in the presence of −6 dB (50%) flankers. The flankers have three major effects on the TvC functions. First, when there was no pedestal (denoted as −∞ dB contrast pedestal in figure 4), the flankers reduced the target threshold by 2.0–3.2 dB. This facilitation is commensurate with that reported by Polat & Sagi (1993, 1994) in a similar condition. Second, as the pedestal contrast increased, the target threshold did not show as much decrement as in the case of no flankers. There was little, if any, low pedestal contrast dip when the flankers were presented. Third, the flanker increased target threshold at high pedestal contrasts. This increment could be as large as 6 dB (or twofold increment in linear contrast) and is about the same for every contrast. This effect can be viewed as shifting the TvC function horizontally to the left. Up to the highest pedestal contrast we measured, the two TvC functions show no sign of convergence. Therefore, the data support the lateral sensitivity modulation model and not the current divisive inhibition model.

The smooth curves in the figure 4 are the fit of the sensitivity modulation model. This goodness-of-fit of the model, represented as the root mean squared error, is 0.98 dB for C.-C.C. and 1.11 dB for M.D.L. These values are close to the mean standard deviation of the measurement error (0.92 dB for C.-C.C., 1.06 dB for M.D.L.) and are significantly smaller than the fits for the normalization model (1.33 dB for C.-C.C., 2.03 dB for M.D.L.).

4. DISCUSSION

(a) *Sensitivity modulation factors*

The two parameters K_e and K_i represent the strength of the lateral effects received by the target mechanism.

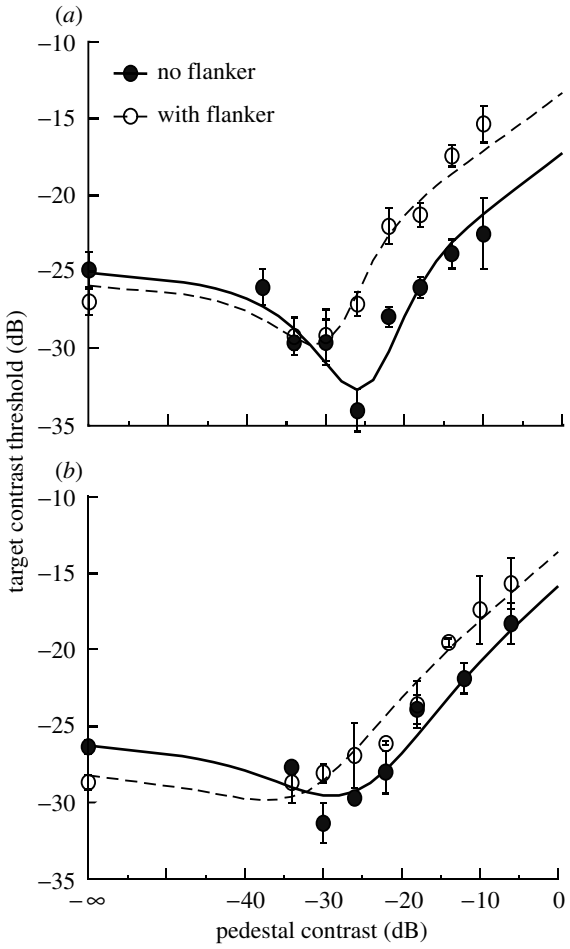

Figure 4. Flanker effect on TvC functions for observer (*a*) M.D.L. and (*b*) C.-C.C. The smooth curves are the fit of the lateral sensitivity modulation model. The closed circles and the solid curve denote the TvC functions measured with no flanker presented. The open circles and the dotted curve denote the TvC function measured with the presence of −6 dB or 50% contrast flankers.

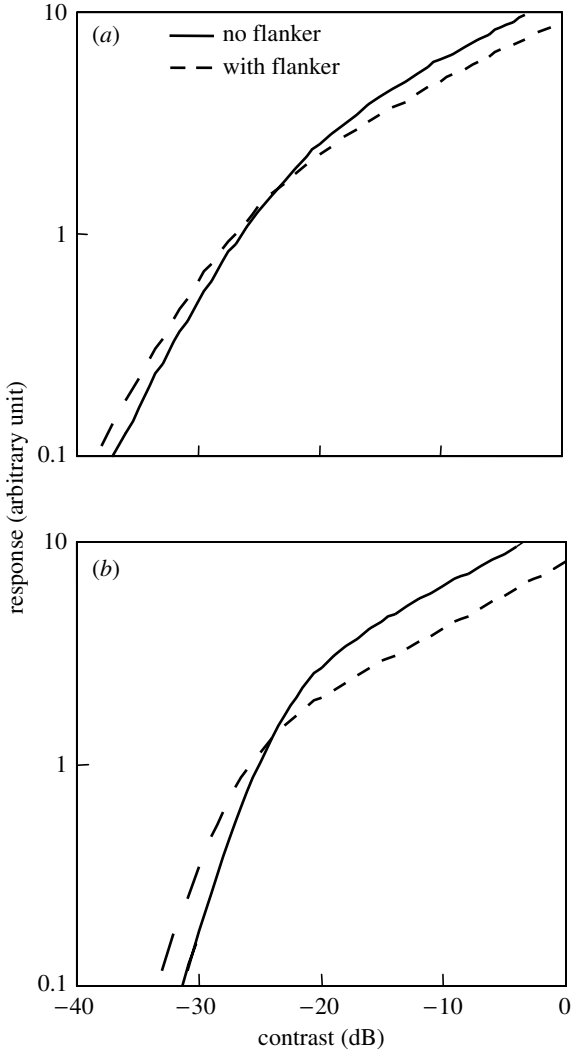

Figure 5. Inferred response functions. This derivation is achieved by plugging the model parameters from table 1 in equation (5). Both observers show a crossover flanker effect on the response function.

The parameter K_e is required to account for the facilitation that occurs at zero or low pedestal contrasts (Polat & Sagi 1993, 1994). Given the parameter values we have, 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 as

$$1 = K_e \times C_t^p/\sigma$$

or

$$C_t = (\sigma/K_e)^{1/p}.$$

There, the target threshold approximates a ratio between the additive constant and K_e raised to a power of $1/p$. Thus, a K_e larger than 1 will boost the response and make the target easier to detect. This result explains the lateral masking effect found by Polat & Sagi (1993, 1994), in-phase flanker effect of Solomon *et al.* (1999) and the initial facilitation at lower end of the TvC functions.

K_i, on the other hand, is required to account for the increment in masking at high pedestal contrasts. 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 $(K_e/K_i) \times (E^p/I)$. That is, the response function with flankers is a constant multiplied by the response function without flankers. Translating the responses to thresholds gives the parallel shift of TvC functions we observed on a log–log coordinate.

The value of K_i is greater than K_e for our data set. This explains the decrease of the dip in the TvC function with flankers. As discussed above, at low pedestal contrasts, the divisive inhibition term (I) is negligible compared with the additive constant (σ). As pedestal contrast increases, the divisive inhibitory term begins to catch up. Since K_i is larger than K_e, the flankers have a greater effect in the denominator of the response function than in the numerator. Therefore, the facilitation effect observed

Table 1. *Fitted parameters for the model*

	C.-C.C.	M.D.L.
K_e	1.52	2.63
K_i	1.92	4.09
S_e	100[a]	100[a]
S_i	99	106
p	2.29	3.86
q	1.76	3.27
σ	20.35	436

[a] Pre-assigned value, not a free parameter.

at low contrasts should decrease with the pedestal contrast. At medium contrasts, where the TvC function measured without the flankers shows a dip, the presence of flankers produces less threshold reduction than at lower contrasts. Compared to the initial facilitation, the presence of the flankers has the effect of reducing, if not eliminating, the dip at medium contrasts.

(b) *Inferred response functions*

Figure 5 shows inferred contrast response functions (equation (5)) for the fitted parameters for two observers. For both observers, the flanker effect on the contrast response function has a 'crossover' behaviour: facilitation at low contrasts and suppression at high contrasts. Also, the flanker effect increases with contrast. This 'crossover' effect should not be a surprise. Electrophysiological studies (Polat *et al*. 1998; Chen *et al*. 2001) have shown the crossover effect that is most commonly seen (from 38% to more than 50% in different studies) in the collinear flanker effect on single cell responses.

(c) *Comparison with previous studies*

Snowden & Hammett (1998) measured the contrast threshold of a target pattern on a pedestal surrounded by a sinusoidal background that has the same orientation and spatial frequency as the target and the pedestal. The background affected TvC functions differently from the flankers. First of all, the background produced no facilitation on target threshold in the absence of the pedestal. In our configuration, then, the background is not acting as a weak pedestal. Second, the background increased the target threshold at low contrast and thus eliminated or reduced the facilitation 'dipper' at low pedestal contrasts. But the degree of threshold increment declined as the pedestal contrast further increased and eventually the two TvC functions merged.

Why did the pattern background produce a different result from the collinear flankers? It has been shown that the flanker facilitation is a location-specific effect. Electrophysiological evidence has shown that the flankers facilitate target cell responses only when the flankers are collinear with the target; otherwise, they suppress the cell responses (Kapadia *et al*. 1999). Recently, Solomon & Morgan (2000) showed that the facilitation produced by collinear flankers can be cancelled by adding extra flankers on both sides of the target to form a quartet. Thus, it seems that the effect of non-collinear flankers is inhibitory in nature. The pattern background used by Snowden & Hammett (1998) contained both the collinear and non-collinear parts. It is likely that the inhibitory non-collinear parts in the background produce the discrepancy between their data and ours.

Morgan & Dresp (1995) measured the detection threshold of a small luminance square on a luminance pedestal with and without a neighbouring luminance line (flanker). They reported a reduction of facilitation by the presence of the flanker as the pedestal luminance increased that is consistent with our finding of a reduction of dip at low contrasts. On the other hand, they did not find an increment in threshold at high contrast. Notice that the size of the target (3.6 arcmin) and distance between the target and the flanker (3.6 arcmin) in their experiment were small. Their stimuli might all fall within the receptive field of the same mechanism. Thus, without the multiplicative contribution from the lateral mechanism, the presence of a flanker might just add a constant both in the numerator and denominator of the response function. As argued above (§ 1(b)), this flanker effect reduces with contrast and hence can be explained by both the conventional divisive inhibition model and our model.

In addition to the contrast normalization approach (Snowden & Hammett 1998; Solomon *et al*. 1999) discussed in § 1(a), Stemmler *et al*. (1995) also proposed a neurophysiology-based model of lateral interaction. They recognized that the lateral interaction was contrast dependent, which agrees with our analysis. Their model, however, was based on subtractive inhibition rather than the divisive inhibition that we propose. As a result, in order to explain the contrast-dependent lateral effect, they assumed that the lateral cells were excitatory at low contrast and inhibitory at high contrast. This is different from our model, in which the contrast-dependent effect is achieved by multiplying contrast-independent factors. Their model, as well as other subtractive-inhibition-based models (e.g. Sommers *et al*. 1998) contradicts the recent electrophysiological evidence that the lateral effect can be expansively facilitative or suppressive (Sengpiel *et al*. 1998; Chen *et al*. 2001).

5. CONCLUSION

The tight agreement between the present psychophysical results and previous analyses of responses measured by cortical neurophysiology suggests a new view of long-range interactions among local analysis units in visual cortex. Instead of operating by simple gain control pooling, the lateral interactions appear to operate by a feed-forward multiplicative facilitation at an early level of lateral connectivity. This lateral facilitation produces an expansive effect both in the excitatory and inhibitory pathways in the mechanism with the result of a crossover in the response function. This process provides an explanation for the long-range effects on contrast discrimination reported here and on detection threshold reported by Polat & Sagi (1993, 1994) and subsequent authors.

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REFERENCES

Adini, Y., Sagi, D. & Tsodyks, M. 1997 Excitatory–inhibitory network in the visual cortex: psychophysical evidence. *Proc. Natl Acad. Sci. USA* **94**, 10 426–10 431.

Brainard, D. H. 1997 The psychophysics toolbox. *Spat. Vis.* **10**, 433–436.

Breitmeyer, B. G. 1984 *Visual masking: an integrative approach*. Oxford University Press.

Chen, C.-C. & Tyler, C. W. 1999 Spatial pattern summation is phase-insensitive in the fovea but not in the periphery. *Spat. Vis.* **12**, 267–285.

Chen, C.-C., Foley, J. M. & Brainard, D. H. 2000 Detection of chromoluminance patterns on chromoluminance pedestals. II. Model. *Vis. Res.* **40**, 789–803.

Chen, C.-C., Kasamatsu, T., Polat, U. & Norcia, A. M. 2001 Contrast response characteristics of long-range lateral interactions in cat striate cortex. *NeuroReport*. (Submitted.)

Foley, J. M. 1994 Human luminance pattern-vision mechanisms: masking experiments require a new model. *J. Opt. Soc. Am.* A **11**, 1710–1719.

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. *Vis. Res.* **39**, 3855–3872.

Kapadia, M. K., Westheimer, G. & Gilbert, C. D. 1999 Dynamics of spatial summation in primary visual cortex of alert monkey. *Proc. Natl. Acad. Sci. USA* **96**, 12 073–12 078.

Kontsevich, L. L. & Tyler, C. W. 1999 Nonlinearity of near-threshold contrast transduction. *Vis. Res.* **39**, 1869–1880.

Legge, G. E. & Foley, J. M. 1980 Contrast masking in human vision. *J. Opt. Soc. Am.* **70**, 1458–1470.

Morgan, M. J. & Dresp, B. 1995 Contrast detection facilitation by spatially separated targets and inducers. *Vis. Res.* **35**, 1019–1024.

Pelli, D. G. 1997 The Video Toolbox software for visual psychophysics: tranform numbers into movies. *Spat. Vis.* **10**, 437–442.

Polat, U. & Sagi, D. 1993 Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. *Vis. Res.* **33**, 993–999.

Polat, U. & Sagi, D. 1994 The architecture of perceptual spatial interactions. *Vis. Res.* **34**, 73–78.

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.

Ross, J. & Speed, H. D. 1991 Contrast adaptation and contrast masking in human vision. *Proc. R. Soc. Lond.* B **246**, 61–69.

Sengpiel, F., Baddeley, R. J., Freeman, T. C., Harrad, R. & Blakemore, C. 1998 Different mechanisms underlie three inhibitory phenomena in cat area 17. *Vis. Res.* **38**, 2067–2080.

Snowden, R. J. & Hammett, S. T. 1998 The effects of surround contrast on contrast thresholds, perceived contrast and contrast discrimination. *Vis. Res.* **38**, 1935–1945.

Solomon, J. A., Watson, A. B. & Morgan, M. J. 1999 Transducer model produces facilitation from opposite-sign flanks. *Vis. Res.* **39**, 987–992.

Solomon, J. A. & Morgan, M. J. 2000 Facilitation from collinear flanks is cancelled by non-collinear flanks. *Vis. Res.* **40**, 279–286.

Somers, D. C., Todorov, E. V., Siapas, A. G. & Sur, M. 1998 A local circuit integration approach to understanding visual cortical receptive fields. *Cerebr. Cortex* **8**, 204–217.

Stemmler, M., Usher, M. & Niebur, E. 1995 Lateral interactions in primary visual cortex: a model bridging physiology and psychophysics. *Science* **269**, 1877–1880.

Teo, P. C. & Heeger, D. J. 1994 Perceptual image distortion. *SPIE Proc.* **2179**, 127–141.

Tyler, C. W. & McBride, B. 1997 The Morphonome image psychophysics software and a calibrator for Macintosh systems. *Spat. Vis.* **10**, 479–484.

Watson, A. B. & Pelli, D. G. 1983 QUEST: a Bayesian adaptive psychometric method. *Percept. Psychophys.* **33**, 113–120.

Watson, A. B. & Solomon, J. A. 1997 A model of visual contrast gain control and pattern masking. *J. Opt. Soc. Am.* A **14**, 2378–2390.

Wilson, H. R. & Humanski, R. 1993 Spatial frequency adaptation and contrast gain control. *Vis. Res.* **33**, 1133–1149.

Wilson, H. R., McFarlane, D. K. & Philips, G. C. 1983 Spatial frequency tuning of orientation selectivity units estimated by oblique masking. *Vis. Res.* **23**, 873–882.

Zenger, B. & Sagi, D. 1996 Isolating excitatory and inhibitory nonlinear spatial interactions involved in contrast detection. *Vis. Res.* **36**, 2497–2513.

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