Distinguishing lateral interaction from uncertainty reduction in collinear flanker effect on contrast discrimination

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To clarify the role of lateral interaction and uncertainty reduction in collinear flanker facilitation of contrast discrimination, we investigated the effect of flankers and spatial cueing on the contrast discrimination threshold. The task of the observers was to detect a 1.3 cyc/deg vertical Gabor target superimposed on one of the Gabor pedestals presented at 3° to the left and right of the fixation point. We measured the target threshold vs. pedestal contrast (TvC) functions in four (2 × 2) conditions: With or without the presence of collinear flankers and with or without a spatial cue that indicated the location of the target. The presence of the flankers lowered the target threshold at low pedestal contrasts, but increased the threshold at high contrasts. The presence of spatial cues lowered the target threshold at all pedestal contrasts regardless of the presence of flankers. The flanker effect was similar in cued and non-cued conditions, suggesting that the effect was similar regardless of cues. The TvC functions are well fit by a divisive inhibition model in which the presence of collinear flankers increases both the excitatory and inhibitory terms of a divisive inhibition response function, while cueing increases only the excitatory term.

Keywords: sensitivity modulation, spatial cue, signal enhancement, masking, TvC function


Introduction

The visual performance for a stimulus can be modulated by its context. One of the most well-established phenomena demonstrating this effect is collinear flanker facilitation, in which the detection threshold of a target Gabor pattern decreases significantly with the presence of collinear Gabor flankers (Chen & Tyler, 2001, 2002; Polat & Sagi, 1993; Solomon, Watson, & Morgan, 1999; Zenger & Sagi, 1996). While this flanker effect is robust and has been repeated by numerous researchers, there is still debate about its mechanisms. Here, we consider two hypotheses that have been proposed in the literature.

The first, the long-range interaction hypothesis, suggests that the flanker effect is due to the interaction between neurons having non-overlapping receptive fields (Chen, Kasamatsu, Polat, & Norcia, 2001; Chen & Tyler, 2001; Polat, 1999; Xing & Heeger, 2001). While V1 neurons are often characterized by their localized classic receptive fields, they extend their axon collaterals or intrinsic fibers horizontally up to 4 mm to contact neurons with CRFs far away from their own (Fisken, Garey, & Powell, 1975; Gilbert & Wiesel, 1983; Rockland & Lund, 1982, 1983). Electrophysiology experiments also show that the response (spike rate) of a V1 neuron to a periodic stimulus (a target, usually a Gabor patch) located within its classical receptive field can be modulated by another periodic stimulus (the context, usually a sinusoid grating or a Gabor patch) projected outside its classical receptive field (Blakemore & Tobin, 1972; Chen et al., 2001; Kapadia, Ito, Gilbert, & Westheimer, 1995; Kapadia, Westheimer, & Gilbert, 2000; Knierim & Van Essen, 1992; Mizobe, Polat, Pettet, & Kasamatsu, 2001; Nelson & Frost, 1985; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Sengpiel, Baddeley, Freeman, Harrad, & Blakemore, 1998; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995). In psychophysics, Chen and Tyler (2001, 2002, 2008) measured the flanker effect on contrast discrimination. They showed that flankers reduce the target threshold at low pedestal contrasts, and increase it at high contrasts. Similar effects were also observed by Morgan and Dresp (1995) with lines. These results imply a crossover flanker effect on the internal response function of the target detector that is similar to that observed in electrophysiology (Chen et al., 2001). They concluded that the presence of the flankers affects both the excitatory and inhibitory sensitivity of the target mechanisms.

The second, the uncertainty reduction hypothesis, suggests that the presence of flankers serves as a spatial cueing function to the target location which reduces spatial uncertainty, thus facilitating target detection (Petrov, Verghese, & Mckee, 2006). Petrov et al. (2006) showed that cueing the target location produced a
facilitation effect in threshold detection similar to that produced by the presence of collinear flankers. They thus argued that uncertainty reduction alone accounted for most of the collinear facilitation. Their argument, however, is not complete. First, similar facilitation effects do not necessarily mean that the same mechanism underlies these two phenomena. It is possible that flankers and cues act on different mechanisms and that these two facilitation effects are unrelated to each other. Second, their key argument of “collinear facilitation is largely uncertainty reduction” was based on a comparison of the percentage of threshold reduction produced by cues alone to the percentage produced by both cues and flankers together. Specifically, the facilitation produced by the cue alone was more than 65% of that produced by the cue and flankers together. This argument is valid only when the effects of the flanker and the cue are additive. For instance, suppose that total facilitation effect in the cue-plus-flanker condition is determined by the Minkowski summation (with the power parameter being 2) of the effects from the cue and the effect from a factor A. That is, the total facilitation is \( (E_c^2 + E_A^2)^{1/2} \) where \( E_c \) is the effect of the cue and \( E_A \) is the effect of the factor A. Thus, given that the cue alone can account for 65% of the total facilitation effect in the cue-plus-flanker condition, the other factor \( A \), when presented alone, should be able to account for 76% of total facilitation. Since neither the nonlinearity nor the effect of other factors was assessed in Petrov et al. (2006), it remains inconclusive whether the collinear flanker effect is a cueing effect. Third, their evidence for uncertainty reduction came from the cueing effect. While it is common to explain the cueing effect in terms of uncertainty reduction (Foley & Schwarz, 1998), this notion is at odds with some recent studies which consider the cueing effect as a change in sensitivity of the system (Lu & Dosher, 1998). Hence, the nature of the cueing effect in collinear facilitation requires further scrutiny.

In current study, we measured the target contrast discrimination threshold with a combination of four conditions: cue alone, flankers alone, cue plus flankers, and a baseline, in which there was no cue or flanker. In the contrast discrimination paradigm we used, the task of the observers was to detect a target superimposed on a pedestal whose spatiotemporal parameters, with the exception of contrast, were the same as those of the target. It is shown that systematically measuring the contrast discrimination threshold at various pedestal contrasts, that is, the target threshold vs. pedestal contrast (TvC) function, allowed us to estimate the response properties of the target detection mechanisms and thus provided a more comprehensive estimation of flanker effects (Chen & Tyler, 2001, 2008). Similarly, it is also reported that the amount of uncertainty reduction can be estimated by observing the cueing effects on the TvC functions (Foley & Schwarz, 1998). Hence, our design allows us to estimate the effects of both uncertainty reduction and long range interaction on collinear facilitation.

Our experimental design was different from Petrov et al. (2006) in one important aspect. Unlike in their experiments, where cues and targets were always in the center of the screen, the target in our experiment appeared randomly in one of two possible locations. The observers were required to attend to both locations when there was no cue, but just one location when the cue was available. This arrangement has two advantages. First, spatial uncertainty is maintained at any pedestal contrast. In the configuration used by Petrov et al. (2006), if one put a pedestal at the target location, the pedestal would indicate the target location and thus eliminate uncertainty. In our configuration, there were two possible locations for the target. The pedestal provided no indication as to the target location. Thus, the uncertainty is always there regardless of the pedestal contrast. This allowed us to study the cueing effect for the whole TvC function and in turn the response function of the target detection mechanism. Second, only the cue provided information about the target location. Even with flankers, an observer still had to monitor two possible target locations when the cue was not available. Hence, this effectively separated the effects of the cue and the flanker effect per se. The cueing effect provided by the flanker would be negligible compared to that of the cue itself. Thus, it allows us to estimate the effect of factors other than cueing in flanker facilitation.

The flankers could not indicate the target location in our experimental paradigm. Hence, if the collinear effect is mostly due to uncertainty we would expect that (1) the presence of flankers should produce little effect on TvC functions and thus (2) the TvC function for the flanker-plus-cue condition should be similar to that for the cue-alone condition. In addition, even the small flanker effect that may be observed would be abolished as the pedestal contrast increased. On the other hand, if long-range interaction plays a role in collinear effect, we would expect that the flankers should produce a crossover effect, regardless of the cueing conditions. The crossover effect means that the flankers reduce the target threshold at low pedestal contrasts and increase it at high contrasts (Chen & Tyler, 2001, 2002, 2008; Morgan & Dresp, 1995).

Method

Apparatus

The stimuli were presented on two Viewsonic 15” CRT monitors, each driven by a Radeon 7200 graphic board which provided 10-bit digital-to-analog converter depth. A Macintosh computer controlled the graphic board. Lights from the two monitors were combined by a beam.
splitter. This two-monitor setup allowed us to present the target on one monitor and the mask on the other, which gave us the advantage of independent control of the target and the mask. The viewing field was 10.7° (H) by 8° (V). The resolution of the monitors was 640 horizontal by 480 vertical pixels, giving 60 pixels 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 74.9 cd/m².

Stimuli

There were four conditions in this study: cue alone, flankers alone, cue plus flankers, and baseline (without cue or flankers). The target was superimposed on pedestals whose contrast ranged from −∞ to −6 dB.

Examples of the stimuli are shown in Figure 1. The target, pedestal and flankers were all Gabor patches defined by the equation

\[ G(x, y, c, u_x, u_y) = B + B \cdot c \cdot \cos(2\pi f x) \]

\[ \times \exp\left(-\frac{(x - u_x)^2}{2\sigma^2}\right) \times \exp\left(-\frac{(y - u_y)^2}{2\sigma^2}\right), \]

where \( B \) was the mean luminance, \( c \) was the contrast of the pattern ranging from 0 to 1, \( f \) was the spatial frequency, \( \sigma \) was the scale parameter (standard deviation) of the Gaussian envelope, and \( u_x \) and \( u_y \) were the horizontal and vertical displacements of the pattern respectively. All patterns had a spatial frequency \( f \) of 1.3 cycles per degree and a scale parameter \( \sigma \) of 0.35 deg. The pedestal and the target were placed 3 deg to the left and/or right of the central fixation point, with the displacement \( u_x \) of zero. The displacement of flankers \((u_y)\) above and below the target is 2.31 deg, corresponding to 3 times target carrier wavelength. The contrast of the flankers \((c)\) was −6 dB or 50%.

A visual white noise with a contrast of −14 dB served as a cue indicating the location of the target. The pixel size of the cue was 8 and the whole size was the same as the target.

Procedures

Figure 1 also illustrates the procedures of this experiment. A temporal two-alternative forced-choice (2AFC) paradigm was used to measure contrast threshold. In each trial, the pedestals were presented in both intervals and the target was randomly presented in one of the two intervals, separated by a 600 ms inter-stimulus interval. The duration of the target and the pedestal was 96 ms. The cue was presented 80 ms before the onset of the pedestal and/or target with a duration of 16 ms. An audio tone indicated the beginning of each interval. The observers’ task was to judge which stimulus interval contained the target. Audio feedback for a correct response was provided. The \( \Psi \) threshold-seeking algorithm (Kontsevich & Tyler, 1999a) was used to measure the threshold at 75% correct level. There were 40 trials for each threshold.
measurement. Each datum point reported was an average of 4 to 6 repeated measurements. The order of the four conditions was randomized.

Five observers participated in this study, including the two authors of this paper and three paid observers who were naive as to the purpose of the study. All observers had corrected to normal (20/20) visual acuity.

Results

Figure 2 shows the averaged target threshold vs. pedestal contrast (TvC) functions for four conditions. The different symbols represent the data in each condition. The blue solid circle, green circle, red solid square, and pink square represent the baseline, cue alone, flankers alone, and cue plus flankers conditions respectively. The smooth curves are the fits of Model 4, discussed below.

When there was no flanker, the TvC functions showed, in both cued and non-cued conditions, a classic dipper shape, as had previously been well-established (Chen & Foley, 2004; Chen & Tyler, 2008; Foley, 1994; Kontsevich & Tyler, 1999b; Legge & Foley, 1980; Nachmias & Sansbury, 1974; Ross & Speed, 1991). As the pedestal contrast increased, the threshold first decreased and then increased, with the greatest threshold reduction being when the pedestal contrast was at about its own detection threshold. The cue shifted the whole Tvc function downward about $-2$ dB on log-log coordinates, suggesting a general facilitating effect of cueing on target detection (Cohn & Lasley, 1974; Foley & Schwarz, 1998; Lu & Dosher, 1998; Pestilli & Carrasco, 2005; Zenger, Braun, & Koch, 2000). When the collinear flankers were presented, the contrast discrimination threshold decreased at low pedestal contrasts, and increased at high pedestal contrasts, regardless of whether the cue was presented. This cross-over phenomenon has repeatedly been reported (Chen & Tyler, 2001, 2002, 2008; Morgan & Dresp, 1995). If the flanker effect is mostly caused by uncertainty reduction, we would expect the cues and the flankers to have a similar effect on TvC functions. However, we found that the effect of the cues, a general reduction of target threshold at all pedestal contrasts, and the effect of the flankers, a cross-over of TvC functions, are very different.

Figure 3 shows the change of threshold in the cue alone, flankers alone, and cue plus flanker conditions from that of the no cue or flanker condition. The positive values denote suppression while negative values denote facilitation. In the no pedestal condition ($-\infty$ dB or 0% contrast), the results were similar to that reported by Petrov et al. (2006) in similar conditions. The presence of the cue, flankers, and cue plus flankers all had a facilitating effect. The effect of the cue plus flankers was largest, about $-4$ dB, equivalent to 36.9% reduction of threshold. In addition, the facilitating effects produced by the cue presented alone and the collinear flankers presented alone were 2.67 dB (26.5% reduction of threshold) and 2.32 dB (23.5% reduction of threshold) respectively. The facilitation of cueing reported by Petrov et al. (2006) was close to 28% reduction. Notice that the facilitation effects were similar in both cue alone and flanker alone conditions. The sum of the threshold reductions produced by cue alone and flankers alone (50%) was much larger than the threshold reduction produced by cue plus flankers (36.9%). Hence, the additivity assumption does not hold up.

When pedestals were presented, the effect of the flankers became suppressive when pedestal contrast is
larger than \(-26\) dB while the effect of cues remained facilitative at all pedestal contrasts. Again, the effects from the flankers and the cues were qualitatively different. As a result, while the cue itself facilitated the contrast discrimination threshold, the cue plus flankers, instead of producing more facilitation, actually had a suppressing effect, when it had any, on contrast discrimination.

**Discussion**

In our results, we showed that, on average, the flankers produced a cross-over effect on TvC functions. That is, the flankers facilitated contrast discrimination at low pedestal contrasts but had an opposite effect at high pedestal contrasts. On the other hand, the cues generally provided a facilitative effect on contrast discrimination regardless of the level of pedestal contrast. Here, we further analyze the effects of cueing and flankers with different models of the mechanism of spatial vision.

**The basic divisive inhibition model**

The divisive inhibition or contrast normalization model (Chen & Foley, 2004; Foley, 1994; Meese, Summers, Holmes, & Wallis, 2007; Ross & Speed, 1991; Snowden & Hammett, 1998; Teo & Heeger, 1994; Watson & Solomon, 1997; Wilson & Humanski, 1993) is a widely accepted model of contrast discrimination. Figure 4a shows a diagram of this model. This model contains several stages. The first stage of a target channel \(j\) is a linear operator with a spatial sensitivity profile \(f_j(x, y)\) defined by a Gabor function. The excitation of this linear operator to an image \(g(x, y)\) is given as

\[
E'_j = \Sigma_x \Sigma_y f_j(x, y) \cdot g(x, y),
\]

(2)

where \(\cdot\) denotes the dot product of the image and the sensitivity profile. If the image \(g(x, y)\) is a periodic pattern with a contrast \(c\), as we used in our experiment, Equation 2 can be simplified to

\[
E'_j = S_{ej} \cdot c,
\]

(2')

where \(S_{ej}\) is a constant called the excitatory sensitivity of the \(j\)-th channel. Detailed derivation from Equations 2 to 2' has been discussed elsewhere (Chen, Foley, & Brainard, 2000).

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

\[
E_j = \max(E'_j, 0),
\]

(3)

where \(\max\) denotes the operation of choosing the greater number of the two.

If there is no flanker or cue presented, the response of the \(j\)-th channel is its rectified excitation raised to the power \(p\) and then divided by a divisive inhibition term \(I_j\) plus an additive constant \(z\). That is,

\[
R_j = \frac{E_j^p}{I_j + z},
\]

(4)

where \(I_j\) is the summation of a non-linear combination of the rectified excitations of all relevant channels within the
same hypercolumn feeds back to channel $j$. This divisive inhibition term $I_j$ is

$$ I_j = (S_{ij} \cdot c)^q, $$

where $S_{ij}$ is a positive value serving as an inhibitory sensitivity. If the uncertainty level throughout the whole experiment is the same, in a 2AFC experiment as ours, the observer’s performance can be determined by one channel.

Figure 4. A diagram of the divisive inhibition model (a), with sensitivity modulation (b) and uncertainty (c) extensions. See text for details.
that gives the greatest response difference between the two intervals (Tyler & Chen, 2000). The difference in response is given as

$$D = R_{j,b+1} - R_{j,b},$$

where j is the channel 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.

### Sensitivity modulation model

We consider two extensions of this model to account for the effects of flankers and cues: sensitivity modulation and uncertainty. The sensitivity modulation model was first 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 shown to explain the psychophysical data as well (Chen & Tyler, 2001). In particular, this model can account for the paradoxical result that the lateral effects increase with target contrast even though the flanker contrast remains constant (Polat et al., 1998) while conventional contrast normalization models (e.g., Hegger, 1992) cannot. A similar form of this model has been proposed to account for lateral interaction effects (Cavanaugh, Bair, & Movshon, 2002; Freeman, Ohzawa, & Walker, 2001; Meese et al., 2007; Xing & Heeger, 2001; Yu, Klein, & Levi, 2003).

In sensitivity modulation, the presence of flankers affects both the excitatory and the inhibitory sensitivities. Let the sensitivity modulation factors of the excitatory and the inhibitory sensitivities. Let the sensitivity modulation factors of the excitatory and the inhibitory sensitivities. Let the sensitivity modulation factors of the excitatory and the inhibitory sensitivities. Let the sensitivity modulation factors of the excitatory and the inhibitory sensitivities. Let the sensitivity modulation factors of the excitatory and the inhibitory sensitivities. Let the sensitivity modulation factors of the excitatory and the inhibitory sensitivities. Let the sensitivity modulation factors of the excitatory and the inhibitory sensitivities. Let the sensitivity modulation factors of the excitatory and the inhibitory sensitivities.

Therefore, the response function in the presence of flankers becomes

$$R'_j = Ke \cdot E_j^b / (Ki \cdot I_j + z).$$  

Both Ke and Ki are functions of flanker contrast. When there is no flanker presented (e.g., 0% flanker contrast), Ke and Ki are set to 1 so that the response function can be reduced to Equation 4. When there are flankers presented (e.g., 50% flanker contrast), Ke and Ki are free parameters to be estimated. Both Ke and Ki are required in order to account for different aspects of the flanker effect (Chen & Tyler, 2001). Further, it is also proposed in the literature that the cueing effect modulates the sensitivities to the central stimuli as well (Lu & Dosher, 1998). Thus Equation 7 can be further expanded to

$$R'_j = Ke \cdot Ka \cdot E_j^b / (Ki \cdot Kb \cdot I_j + z),$$

where Ka and Kb are the sensitivity modulation caused by the cues.

### Uncertainty model

We need another extension to deal with uncertainty. Uncertainty occurs when the visual system needs to monitor more channels than those which are relevant to the demanded visual task (Pelli, 1985). Hence, the performance of the system is limited not only by noise in the relevant channels but also by the irrelevant channels. In a 2AFC paradigm such as the one we used, the task of the observer is to determine which of the two intervals contains the target. To achieve this, the observer picks the interval in which the maximum response of all monitored channels is greater than the other (Tyler & Chen, 2000). That is, in the context of the signal detection theory, the observer compares the distribution of the maximum responses from the two intervals. For the purpose of estimating threshold, the mean maximum response can be approximated by a fourth-power summation of the mean of all monitored channels (Quick, 1974). Suppose that the observer monitors m channels in a trial in which n channels are responsive to the target. At the decision stage, the observer is to compare two distributions with means

$$R'_b = \left( \sum_{j=1}^{m} R^4_{j,b} \right)^{1/4},$$

for the interval that does not contain a target, and

$$R'_{b+1} = \left( \sum_{j=1}^{n} R^4_{j,b+1} + \sum_{j=n+1}^{m} R^4_{j,b} \right)^{1/4},$$

for the interval that contains a target. The target is at the threshold when the response difference

$$D' = R'_{j,b+1} - R'_{j,b},$$

reaches unity. If cues or flankers are presented, they may provide information about the target (e.g., location). Hence, an observer does not need to monitor as many channels. This leads to the reduction of the number of monitored channels m and in turn the uncertainty level. If the observer’s performance can be considered to be determined by the one channel that gives the greatest response difference between the two intervals and the observer knows exactly which channel it is, both the number m and n in Equations 8 and 8' reduce to 1 and the decision factor (Equation 9) is reduced to Equation 6.
Models fit

Here we examine five models, listed below. To reduce the number of free parameters, some parameter values were constrained in the models: (1) All response function parameters, $S_e$, $S_i$, $z$, $p$ and $q$, were the same for all conditions; (2) the sensitivity parameter $S_e$ to the target was set at 100; (3) parameter $n$ was set to 1; (4) the lateral effect parameters $K_e$ and $K_i$ were set to 1 in the no-flanker conditions; and (5) the cueing effect parameter $K_a$ and $K_b$ were set to 1 in the no cue conditions. For the $T_vC$ function predicted by each model and their parameters, see Figure 5 and Table 1 respectively.

**Model 1: Both flankers and cues affect the level of uncertainty**

Petrov et al. (2006) proposed that the collinear lateral masking effect is mostly uncertainty reduction. That is, the presence of the flankers provides information as to the exact location of the target and thus allows the observer to monitor fewer channels. Hence, in this model, the
presence of either flankers or cues should reduce the number of monitored channels. This is implemented, in practice, by allowing parameter m to change with conditions in model fitting while keeping the sensitivity modulation factors at 1 (i.e., no sensitivity modulation). The parameter m in the cue plus flankers condition, where the uncertainty was minimum, was set to 1 to create further constraint. Notice that the detectability, $d'$, and in turn the threshold changes with the ratio of the monitored channel, m, and the relevant channel, n (Tyler & Chen, 2000) but not the number of the monitored channel itself. Hence, any change of m will be balanced out by the proportional change in n. Hence, set n = 1 would not reduce the goodness-of-fit of the model as long as m is a free parameter.

This uncertainty model did not fit the data as well as other models discussed below. The model cannot separate the effects of the cue and flanker at zero pedestal contrast and greatly overestimates the threshold of the cue alone at medium pedestal contrasts. The sum of squared error (SSE) and the root mean squared error (RMSE) were 64.49 and 1.42 dB respectively for the averaged data. The estimated number of total monitored channels for the condition containing neither cue nor flanker was 1.03, almost equal to that for the cue plus flankers condition. If this model were right, this would suggest that adding both cue and flankers does not reduce uncertainty at all. As a result, the TVC functions for these two conditions would be the same, which is inconsistent with the data. In addition, the cue alone can reduce the uncertainty by about 32% (m = 0.68) while the flankers alone increased uncertainty by a factor of 2.40. If this model were right, this would suggest that the flankers produce a uncertainty increment rather than uncertainty reduction effect. However, since the fit was not ideal, we should not infer too much from these parameters.

**Model 2: Both flankers and cues affect the excitatory and inhibitory sensitivities**

It is still possible that the same mechanism underlies flanker and cue effects even if it is not uncertainty reduction. The best candidate is sensitivity modulation, as it has been demonstrated that this model provides a good explanation for the collinear flanker effect. In implementation, we set the sensitivity parameters Ke and Ki to be non-unity free parameters for the flanker conditions, and Ka and Kb for the cue conditions. The uncertainty level was set to 1 by fixing m = n = 1.

This model fits quite well (SSE = 26.88, RMSE = 0.92). Both the flankers and the cue increase the excitatory and inhibitory sensitivities. The effect of the cue is greater on the excitatory sensitivity (Ka = 2.02) than on the inhibitory sensitivity (Kb = 1.59). This suggests that in the cue condition, the increment of excitation is greater than that of inhibition at all pedestal contrasts and thus...
leads to an overall downward shift of the TvC functions. The presence of flankers, in contrast, has more effect on the inhibitory (Ki = 2.85) than on the excitatory (Ke = 1.33) sensitivities. These parameter values reflect the cross-over effect on TvC functions produced by the flankers. At low pedestal contrasts, the inhibitory term is negligible when compared with the additive constant z. The response is dominated by the excitatory terms scaled by the additive constant. Hence, an increase in excitation produces a facilitation effect on the threshold. Both the flankers and the cue increase excitatory sensitivity and hence both show facilitation effects at low pedestal contrasts. However, at high pedestal contrasts, the inhibitory term is much greater than the additive constant. Hence, the response is dominated by the ratio between excitation and inhibition terms. Here, the inhibitory sensitivity for the flankers is greater than the excitatory sensitivity. Thus, the response in the flanker conditions is smaller than that in the no flanker condition, which in turn leads to an increment in threshold. On the other hand, the inhibitory sensitivity for the cues is smaller than the excitatory sensitivity. Hence, the response in the cue conditions is still greater than that in the no cue conditions, and as a result, the TvC functions show facilitation at all pedestal contrasts.

**Model 3: The flankers affect excitation and inhibition sensitivities while the cues affect the level of uncertainty**

This model combines the elements of the sensitivity modulation model for flanker effect (Chen & Tyler, 2001, 2002) and the uncertainty reduction model for cueing effect (Foley & Schwarz, 1998; Hubner, 1996; Palmer, 1994; Palmer, Ames, & Lindsey, 1993; Solomon, Lavie, & Morgan, 1997). In practice, Ka and Kb were always set to 1 and the Ke and Ki were non-unity free parameters for flanker conditions. In addition, m was set to 1 for the cue conditions and to a free parameter for the non-cue conditions.

This model fits slightly better than Model 1 (SSE = 58.12, RMSE = 1.35). However, it fails to catch the cue effect at low pedestal contrasts. The cross-over TvC function in the presence of the flankers is reached by more weights on inhibitory term (Ki = 2.87) than excitatory term (Ke = 1.34). The uncertainty in the cue conditions (m = 1) is about 52% of that in the no cue condition (m = 1.92), in line with our experimental design.

**Model 4: The flankers affect both the excitatory and inhibitory sensitivities while the cues affect only the excitatory sensitivity**

Lu and Dosher (1998) proposed that one of the possible mechanisms of the cueing effect is signal enhancement. In implementation, this is equivalent to an increase of Ka in our sensitivity modulation model. In this model we used this hypothesis for cueing effect, and combined it with the sensitivity modulation model for flanker effect. This was implemented by allowing Ke and Ki to be nonunity free parameters in the flanker conditions and Ka to be nonunity free parameters in the cue conditions. Kb was fixed to 1 for all conditions.

The model fits (SSE = 33.40, RMSE = 1.02) as well as Model 2 even with one less free parameter (F(1,24) = 4.69, p = .04). In this model, the effect of the flankers is similar to Model 2. The cue increases the excitatory term by 31% (Ka = 1.31) and thus shifts TvC functions downward relative to the no-cue condition.

**Model 5: The flankers affect the excitatory and inhibitory sensitivities while the cues affect the inhibitory sensitivity**

Another possible cueing effect, according to Lu and Dosher (1998), is internal noise reduction. That is, the presence of the cue reduces the multiplicative noise that is proportional to signal strength. This is implemented by allowing Kb to change with the cueing conditions while Ka remains fixed at 1.

In this model, the effect of the flankers is also similar to Models 2 and 4. In addition, the presence of the cue decreases the inhibition factor (Kb) from 1 to 0.78. This leads to a greater reduction in threshold at high pedestal contrasts than at low pedestal contrasts. It thus under-estimates the difference between the cue and no cue conditions at zero pedestal contrast. The fit of this model (SSE = 41.92, RMSE = 1.14) is worse than Model 4 even though the number of free parameters is the same. This model also fits worse than Model 2 when the number of free parameters is considered (F(1,24) = 8.61, p = .007).

Out of the five models discussed above, the two models implementing uncertainty to explain the cue or flanker effect fit the data least well. The SSE of Model 1 is more than double that of Model 2. Hence, we can conclude that uncertainty reduction cannot explain our data. On the other hand, the three variants of the sensitivity modulation model showed better fit to the data. Statistically, there is no difference between Model 2 and Model 4 when the number of the free parameters is considered (p > .01).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimated value</th>
<th>95% confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Si</td>
<td>129.42</td>
<td>127.22 ~ 131.54</td>
</tr>
<tr>
<td>Ke</td>
<td>1.32</td>
<td>1.11 ~ 1.57</td>
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<tr>
<td>Ki</td>
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<td>p</td>
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<td>2.28 ~ 4.13</td>
</tr>
<tr>
<td>q</td>
<td>2.44</td>
<td>1.93 ~ 3.13</td>
</tr>
</tbody>
</table>

Table 2. The confidence interval of each parameter in Model 4.
Hence, we do not favor Model 2, on the principle of parsimony. Similarly, Model 5 is not favored because it fits the data worse than Model 4 even though the number of the free parameters are the same. The RMSE of Model 4, 1.02 dB, is close to the mean standard error of the data (0.97 dB). The model accounts for 94.5% of the variance of the averaged data and gives an excellent description of the data ($X^2(31, N = 5) = 10.24, p = .9999$).

To examine the stability of each parameter, we estimated 95% confidence interval for each parameter with an algorithm proposed by Bevington and Robinson (1992). That is, we increased or decreased the parameter values from the best fit while optimizing other free parameters until the increase of $X^2$ measurement for goodness-of-fit reached unity. This parameter increment and decrement defined the 68% confidence interval. Under the Gaussian noise assumption, the range of this confidence interval was multiplied by 1.96 to get the 95% confidence interval. Table 2 shows the results. In general, the fit parameter values for this model were quite stable.

The 95% confidence interval of the value $K_a$ ranges from 1.19 to 1.50, which is always greater than 1. This means that the facilitative effect of the spatial cues is indeed statistically significant. The confidence intervals of $Ke$ and $Ki$ also show that the flankers effect on both the excitatory and the inhibitory sensitivities are also beyond random variations.

We can therefore conclude from the model fit that collinear flanker facilitation is not due to uncertainty reduction but to lateral interaction through sensitivity modulation. Increments in both the excitatory and inhibitory term of the response function are needed to explain the cross-over phenomenon produced by the presence of the collinear flankers. Even the cueing effect can be explained by sensitivity modulation: an increment of excitatory sensitivity can account for it. This increment of excitatory sensitivity is consistent with the evidence for signal enhancement of cueing effect (Carrasco, Penpeci-Talgar, & Eckstein 2000; Ling & Carrasco, 2006; Lu & Dosher, 1998).

### Forward masking effect

We demonstrated that the cue decreases the discrimination threshold by increasing the excitation of the response function. It might be argued that the cue, appearing before the onset of the target, acts like a forward masker, and that this causes the cueing effect we observed, since a forward masker can have a facilitative effect on target detection (Breitmeyer et al., 2006). To test this hypothesis, we conducted a control experiment in which all the stimuli, including the target, flankers and cue, were always presented to the right of the fixation point. The pedestal was not used. Other than the location of the stimulus, all the procedures were the same as in the main experiments. That is, we removed the role of the cue as an indicator of the target’s spatial interval. Hence, if the cueing effect was due to forward masking, we would expect the cueing effect to be similar regardless of the number of possible target locations. Figure 6 shows the result. When there was no flanker, the cue decreased the threshold, on average, by about 1.09 dB or 13%. While this effect was statistically slightly different from null (paired $t(4) = 3.14, p = 0.034$), it was only about 1/3 of the cueing effect measured in the main experiment. Therefore the cueing effect we measured in the main experiment can hardly be due to forward masking.

In addition, the stimulus configuration of our control experiment was very similar to that of Petrov et al. (2006) except that our target and cue were placed at three degrees in the periphery while theirs were placed in the fovea. We observed less cueing effect in the no flanker conditions (13%) than they did (28%). One possibility is that the visual system may be less sensitive to a peripheral cue than to a foveal one. Hence, our cue, presented in the periphery, may produce a lesser effect on the visual system than a cue presented in the fovea.

### Alternative interpretations

As discussed above, it is suggested that the presence of flankers serves as a spatial cueing function to the target location, which reduces spatial uncertainty, thus facilitating target detection (Petrov et al., 2006). In our experiment, there were two possible locations for the target. When the cue was not available, the observers had to attend to both locations regardless of whether the flankers were presented. Hence, the flanker provided no indication as to the target location. Thus, the uncertainty was always there regardless of whether the flankers were presented. Hence, if the collinear effect were due to the reduction of uncertainty, we would expect that there would be little, if any, facilitation produced by the flankers. However, our

![Figure 6: Cueing effect in no flanker and flankers conditions in the control experiment.](http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/933044/ on 06/18/2017)
results showed that the flankers did have a pronounced effect on both the facilitation effect at the low contrast pedestal conditions and the masking effect at the high pedestal contrast conditions. Hence, our flanker effect cannot be explained by uncertainty reduction.

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 of the flankers decreases. As a result, the effect of a high-contrast flanker away from the target could mimic that 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 and Dresp (1995) and Snowden and Hammett (1998) also offered an explanation of the long-range interaction that shared many assumptions and a similar conclusion with Solomon et al. (1999).

In our experiment, the flanker contrast was the same for all test conditions. Since, in the overlapped receptive field model, the effect of a flanker is to mimic that of a low contrast pedestal, the flanker effect on the mechanism response is equivalent to add a constant to the excitatory (Equation 2) and the divisive inhibitory terms (Equation 5). 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 overlapped receptive field model predicts that the TvC function in flanker conditions will converge to the TvC function in the no-flanker conditions as pedestal contrast increases. Snowden and Hammett (1998) derived the same prediction for contrast discrimination in the presence of a patterned surround. This prediction is inconsistent with our result that the TvC functions for the flanker and no-flanker conditions are parallel at high pedestal contrasts and show no sign of convergence. Chen and Tyler (2001, 2002, 2008) and Zenger et al. (2000) also reported similar results.

We fit the model proposed by Solomon et al. (1999) to our data. Since Solomon et al. (1999) did not specify cueing effects, we fit the cue and the no-cue conditions with different sets of parameters. Notice that the model of Solomon et al. (1999) contains an array of linear filters. The decision variable is based on a nonlinear summation of the responses of all filters tuned to different locations in the image and thus allows an off-peak looking. Thus, it may predict a slower convergence than a single receptive field model would do. Nevertheless, for both the cue and no-cue conditions, their model still predicts a smaller threshold difference between the flanker and no-flanker conditions at high pedestal contrasts than that showed in our data. The SSE of the fit from their model was 44.07, or about 60% more than our best model. Hence, the flanker effect reported here cannot be explained by overlapped receptive fields.

Conclusion

In this study, we measured the contrast discrimination threshold in four \((2 \times 2)\) conditions: with or without collinear flankers, and with or without a spatial pre-cue that indicated the presence of the target. Our data showed that the presence of the flankers has a facilitating effect at low pedestal contrasts but a suppressing effect at high pedestal contrasts. However, the effect of the cue was always facilitation, across the range of pedestal contrasts. The TvC functions are well fitted by our extended sensitivity modulation model. The results showed that the presence of collinear flankers increases both the excitatory and inhibitory terms of a divisive inhibition response function, suggesting that the collinear flankers outside of the receptive field can modulate the response of the target mechanism. The mechanism of spatial cueing increases the excitatory term, indicating that signal enhancement plays a role in the perceptual stage. Thus we can conclude that the mechanisms of both cue and flankers took effect in the perceptual response stage rather than affecting uncertainty reduction in the decision stage.

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