Facilitation of contrast detection by cross-oriented surround stimuli and its psychophysical mechanisms

Cong Yu School of Optometry, University of California, Berkeley, CA, USA

Stanley A. Klein School of Optometry, University of California, Berkeley, CA, USA

Dennis M. Levi School of Optometry, University of California, Berkeley, CA, USA

Neurophysiological and psychophysical evidence indicates that neuronal surround modulation at cross-orientation (orthogonal to the preferred orientation of the classical receptive field) plays a key role in intermediate-level visual tasks, such as textural segregation and perceptual pop-out. What is missing is a psychophysical description of cross surround modulation at the spatial filter level in low-level vision. Moreover, neurophysiological evidence for how cross surround modulation is expressed at the neuronal level has been inconsistent. Here we report evidence for psychophysical facilitation of contrast detection by cross surround stimuli (orthogonal to the target orientation) that may provide insights into both the neurophysiology and psychophysics of cross surround modulation. We found that cross surround facilitation is a surround-contrast dependent effect mainly evident at low surround contrasts, and is narrowly tuned to spatial frequency and broadly tuned to orientation. To understand whether cross surround facilitation results from low-level processing of signal-to-noise enhancement or is due to uncertainty reduction at a higher-level decision stage, we (1) studied cross surround facilitation with an equivalent noise protocol, (2) estimated the changes in the slope of the psychometric function and the uncertainty parameter, M, and (3) measured cross surround effects at the dipper of the TvC function. The converging evidence suggests that cross surround facilitation of contrast detection is mainly a result of low-level signal-to-noise enhancement, and is little affected by uncertainty change.

Keywords: surround modulation, cross orientation, contrast detection, classical receptive field, uncertainty

Introduction

Many researchers suggest that cross surround modulation of response properties of the classical receptive fields in the primary visual cortex plays a fundamental role in intermediate-level visual tasks, such as textural segregation and perceptual pop-out (Knierim & Van Essen, 1992; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995; Levitt & Lund, 1997; Sengpiel, Sen, & Blakemore, 1997; Das & Gilbert, 1999; Nothdurft, Gallant, & Van Essen, 1999; Walker, Ohzawa, & Freeman, 1999; Hupé, James, Girard, & Bullier,, 2001). Psychophysical studies indeed link perceptual pop-out to excitatory connections between orthogonal spatial filters mimicking V1 simple neurons (Wolfson & Landy, 1999). However, there have been contradictory reports on how neuronal responses are influenced by cross surround stimuli (orthogonal to the preferred orientation) placed outside the classical receptive fields. Some studies reported cross surround facilitation in a significant portion of V1 neurons (Sillito et al., 1995; Levitt & Lund, 1997; Nothdurft et al., 1999; Hupé et al., 2001), while others reported mostly cross surround suppression (Knierim & Van Essen, 1992; Sengpiel et al., 1997; Das & Gilbert, 1999; Walker et al., 1999). Psychophysical investigation of surround modulation of low-level visual tasks such as contrast detection using comparable stimuli would be expected to provide some insights into the inconsistent neurophysiological data. These investigations could also reveal detailed properties of interactions between orthogonal psychophysical spatial filters and build the links between neurophysiology and higher-level vision. However, in an influential paper (Polat & Sagi, 1993), contrast detection for a Gabor (Gaussian windowed sinusoidal grating) target was reported unaffected by laterally placed Gabor flankers orthogonal to the target orientation, though significant facilitation was evident when the same flankers were collinear with the target. Lack of cross surround effects on contrast detection at the visual psychophysical level has been cited by other researchers (Chen & Tyler, 2001), but is inconsistent with neurophysiological data, and if true would in some measure cast doubt on the meaningfulness of cross surround effects at the neuronal level.

Recently we reported significant cross surround modulation of suprathreshold contrast discrimination (Yu & Levi, 2000) and perceived contrast (Yu, Klein. & Levi, 2001). We found that contrast discrimination is generally facilitated by cross surround stimuli. At high surround contrasts, masking can be completely eliminated by the cross surrounds. Cross surrounds also enhance the

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perceived contrast of the center stimuli, particularly when the surround has high contrast. These findings prompted us to reconsider the previous experimental evidence for cross surround modulation of contrast detection.

In the first half of the work, which includes Experiments I, II, and III, we describe cross surround modulation of contrast detection and its spatial properties. In these experiments, we measured cross surround modulation with a wide range of surround contrast conditions and demonstrated significant cross surround facilitation at low surround contrasts. We also studied the spatial frequency and orientation tuning properties of cross surround facilitation, as well as the roles of end and side portions of the surround stimuli. The second half of this work (Experiments IV) deals with the psychophysical mechanisms of cross surround facilitation: specifically, whether cross surround facilitation is a result of low-level signal-to-noise enhancement, or is due to uncertainty reduction at a higher-level decision stage. We conducted three experiments: cross surround facilitation with the target in noise (IVa), estimation of uncertainty from the slope of the psychometric function (IVb), and cross surround facilitation at the dipper of the TvC function (IVc). Our data indicate a major contribution of low-level visual mechanisms to cross surround facilitation and little evidence for uncertainty reduction. The findings of this study may help clarify some controversies surrounding the issue of neurophysiological cross surround modulation and link relevant neurophysiology to psychophysics and higher-level visual tasks.

Methods

Observers & Apparatus

Adult human observers with normal or corrected-to-normal vision served in this study. Some earlier experiments were carried out at the University of Houston and the later ones at the University of California, Berkeley, so we were not able to use the same observers throughout the study. All observers except S.T. and Y.C. were new to psychophysical observations and received training prior to data collection. Only Y.C. was aware of the purpose of the experiments.

The stimuli were generated by a VisionWorks computer graphics system (Vision Research Graphics, Inc., Duham, NH) and presented on a U.S. Pixel Px19 monochrome monitor (U.S. Pixel Corporation, Framingham, MA). The monitor had a 1024 x 512 resolution, 117 Hz frame rate, 50 cd/m^2 mean luminance, and 3.8° x 3.0° usable screen size at the viewing distance of 5.64 meters. The luminance of the monitor was made linear by a 15-bit look-up table.

Stimuli & Procedure

In most cases, the target (Figure 1a) was a spatially localized D6 grating (a sixth derivative of a Gaussian) blurred along its long axis by a Gaussian window (σ= 4.8 arcmin) and truncated at the target length (10 arcmin). The surround was a sinusoidal grating annulus at cross-orientation. The inner and outer diameters of the surround annulus were 18 and 45 arcmin, respectively. The peak spatial frequency of the target and the spatial frequency of the surround stimuli were the same at 8 cycles per degree (cpd). Some variations of the cross surrounds were also used, which will be detailed in related experiments. In one occasion, we also used Gabor stimuli (Figure 1b) to replicate experiments conducted previously (Polat & Sagi, 1993). Here the target was a vertical Gabor grating flanked on the top and bottom by two orthogonal Gabor gratings. These Gabor gratings had the same spatial frequency (8 cpd) and circular Gaussian window (σ = 4.8 arcmin). The Gabor flankers were separated from the central Gabor target by a center-to-center distance of 3 λ (λ= 7.5 arcmin).

For most experiments, contrast thresholds were measured with a successive 2-alternative forced-choice (2AFC) staircase procedure. The cross surround or Gabor flankers were presented in each of the two stimulus intervals (400 msec each) separated by a 400 msec inter-stimulus interval. Each stimulus interval was accompanied with an audio tone of the same duration. The target was randomly presented in one of the two stimulus intervals with the same onset and offset as the surround stimuli. The observers' task was to judge which stimulus interval contained the target. Each trial was preceded by a 6.3' x 6.3' fixation cross which disappeared 100 msec before the beginning of the trial. Audio feedback was given on incorrect responses. Each staircase consisted of four preliminary reversals and eight experimental reversals. The step size of the staircase was 0.05 log units. A classical 3-down-1-up staircase rule was followed, which resulted in a 79.4% convergence level of the staircase. The mean of the eight experimental reversals was taken as the contrast threshold. Each datum represents the mean of 4 to 6 replications, and the error bars represent ±1 standard error of the mean.

In one measurement of Experiment IV, a rating scale method with constant stimuli (Levi, Klein, & Aitsebaomo, 1984) was used to obtain the psychometric function. In each block of 125 trials, the target stimulus was presented at five near threshold contrasts, including one at 0 contrast (e.g., 0, 0.01, 0.02, 0.03, and 0.04). The observer responded with numbers from 0 to 4 to indicate which contrast the target belonged to (0 referred to the zero contrast target, and 4 referred to the highest target contrast). Feedback on the correct target contrast was given after each response. One observer (J.E.) completed 19 blocks of trials, 11 blocks with two sets of target contrasts for no surround and cross surround conditions and 8 blocks with another two sets of target contrasts. The other observer (M.L.) completed 11 blocks with the same two sets of target contrasts. Further details of the experiments and data analysis will be provided in Experiment IV.

A brief report of our data was presented at the Vision Science Society conference in Sarasota, Florida, in May 2001).

Results

Experiment I. Cross Surround Modulation of Contrast Detection and the Effects of Surround Contrast

We first measured detection thresholds for the D6 target (Figure 1a) under the influence of the annular cross surround at various contrasts ranging from 0.025 to 0.80. Contrast thresholds for the D6 target only (with no surround) were also measured as baselines. In contrast to previous reports, our data (Figure 1a) show significant facilitation of contrast detection by cross surrounds. However, unlike iso (collinear) surround facilitation of contrast detection, which reportedly is unaffected by surround contrast (Polat & Sagi, 1993), cross surround facilitation is a surround-contrast dependent effect. At lower surround contrasts (0.05 and 0.10), the cross surrounds reduce contrast detection thresholds by as much as 40%. However, at higher surround contrasts (0.40 and 0.80), the cross surrounds have very little or no effect on contrast detection. The surround at the lowest contrast (0.025) also has little effect on contrast detection, which may represent a threshold for cross surround facilitation.

This contrast dependency of cross surround modulation of contrast detection points to some potential limitations in previous psychophysical (and probably neurophysiological) studies that used surrounds of fixed high contrasts. To address this concern, we replicated the earlier psychophysical experiment (Polat & Sagi, 1993) that used Gabor stimuli (Figure 1b) and found ineffective orthogonal flankers in contrast detection, except that we used a range of flanker contrasts instead of a fixed one. Our data (Figure 1b) do show consistent and significant facilitation at lower flanker contrasts (0.10 and 0.20) with an average 33% reduction of the contrast threshold, but little effect at 0.40, the flanker contrast used previously (Polat & Sagi, 1993).

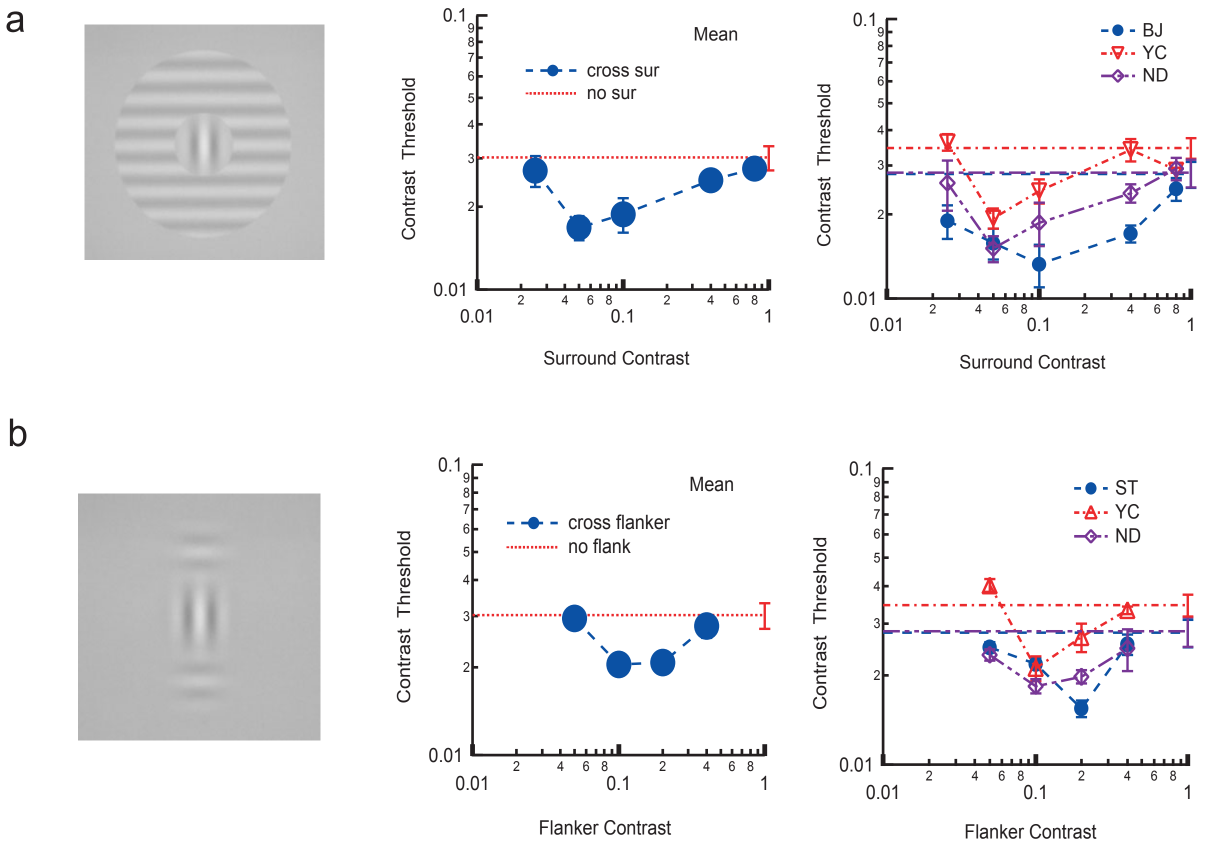

Figure 1. Cross surround modulation of contrast detection. a. The stimulus image shows a D6 center target surrounded by an annular sinusoidal grating at cross orientation. The mean and individual data show cross surround effects on contrast thresholds as a function of the surround contrast. A lower-than-baseline contrast threshold indicates cross surround facilitation. b. The stimulus image shows a Gabor target and two identical Gabor flankers at cross orientation. The mean and individual data show flanker effects on Gabor detection as a function of the flanker contrast.

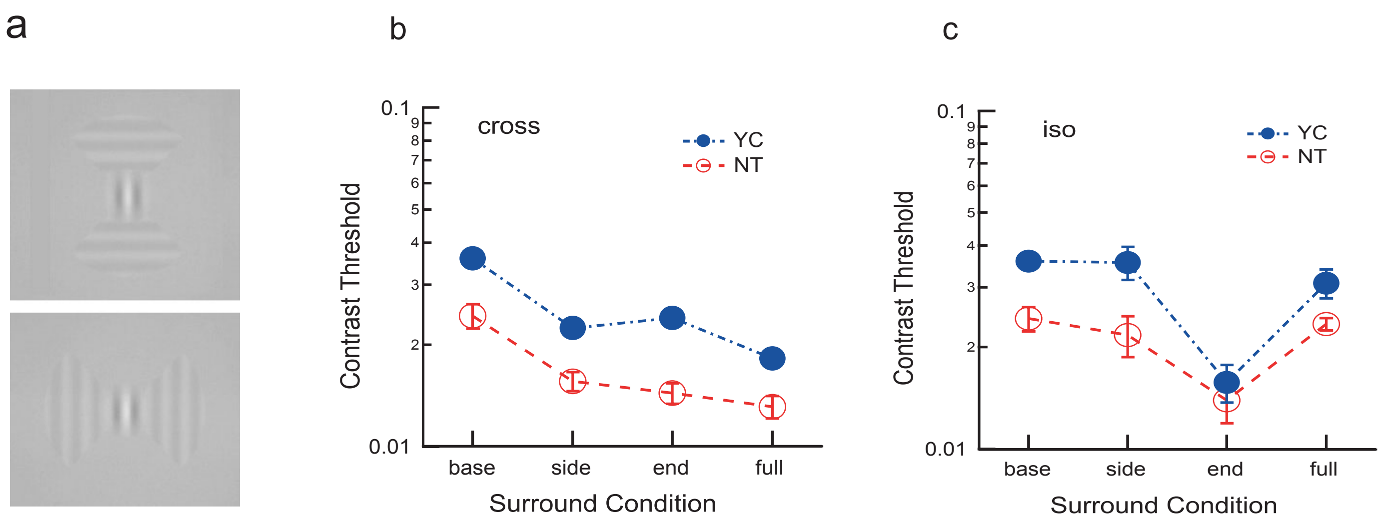

Figure 2. The contributions of different parts of the surround to the modulation of contrast detection. a. Butterfly-shaped end and side surround flankers. Either the top and bottom quadrants or the left and right quadrants of a full surround grating (Figure 1a) were removed to form butterfly-shaped end flankers (top, showing cross-orientation) and side flankers (bottom, showing iso-orientation). The contrast of the surround stimuli was 0.10, a contrast associated with maximal cross-orientation facilitation in Figure 1a. b. The effects of cross-oriented side and end flankers and full surrounds on contrast detection. c. The effects of iso-oriented side and end flankers and full surrounds on contrast detection as a control measurement.

Experiment II. Contributions of the End and Side Components of the Surround Stimuli to Cross Surround Facilitation of Contrast Detection

There exists neurophysiological evidence that surround modulation outside the classic receptive fields is not uniform (Walker et al., 1999), and that stimulating different parts of the surround area could produce either excitatory or inhibitory modulation (Kapadia, Westheimer, & Gilbert, 2000). In psychophysics, for iso surround stimuli, only those placed near the ends of a target (e.g., collinear flankers) reportedly facilitate detection, while those placed on the sides or on both ends and sides (thus forming a full surround) are ineffective (Snowden & Hammett, 1998; Solomon & Morgan, 2000). A two-stage model was proposed (Solomon & Morgan, 2000), in which a second-stage spatial filter consists of excitatory lobes near the ends and inhibitory lobes near the sides of the spatial filter center. Inhibition from the side lobes thus would cancel excitation from the end lobes when a full surround stimulus is used.

By using butterfly-shaped flankers at an optimal contrast (0.10) covering only the end or side portions of the surround (Figure 2a), we found that at cross-orientation, both side and end flankers facilitate detection, though facilitation by the full surround is the strongest (Figure 2b). Therefore, the two-stage spatial filter model (Solomon & Morgan, 2000) may need to be revised to accommodate cross surround modulation. For example, the side lobes of the second-stage filter become excitatory when excited by cross surround stimuli. On the other hand, our iso-orientation data (Figure 2c) from a control measurement show that only end-flankers facilitate detection while full- and side-flankers do not, consistent with Solomon and Morgan (2000). However, neither previous data nor our current data show evidence for inhibition by iso side-flankers that would directly support the existence of inhibitory side lobes in second-stage spatial filters. An alternative and probably better explanation might be drawn from a surround modulation model (Li, 2000) that proposes that smooth contours (collinear flankers in this case) may result in higher neural responses.

Experiment III. Spatial Frequency and Orientation Tuning of Cross Surround Facilitation of Contrast Detection

We used the full-surround stimulus configuration (Figure 1a) again to study the spatial frequency and orientation tuning properties of cross surround facilitation. For studying spatial frequency tuning, the surround contrast was set to the optimal (0.10) and the surround spatial frequency was varied from 4 to 16 cpd in half octave steps. It is clear that cross surround facilitation of contrast detection is sharply tuned to the target spatial frequency. For the D6 target at a peak spatial frequency of 8 cpd, cross-orientation surround facilitation peaks at the same spatial frequency and quickly diminishes when surround spatial frequency is about half an octave away from the target spatial frequency (Figure 3a). The sharp spatial frequency tuning is also seen in cross surround modulation of suprathreshold contrast discrimination (Yu & Levi, 2000) and in iso (collinear) surround modulation of contrast detection (Polat & Sagi, 1993) and suprathreshold contrast discrimination (Yu & Levi, 2000).

While surround facilitation is narrowly tuned to spatial frequency, it is very broadly tuned to orientation. Surround facilitation of contrast detection was nearly unaffected by orientation differences ranging from 90 degrees (cross orientation to the target) to as low as 40 degrees (Figure 3b) for the same stimulus configuration, except that it was the surround orientation, rather than the spatial frequency, which was varied. Surround facilitation is reduced at smaller orientation differences and is completely eliminated at iso-orientation (0 deg). These tuning properties suggest that neurons responding to the target could receive surround inputs from a group of neurons narrowly tuned to target spatial frequency but loosely tuned to cross-orientation, perhaps reflecting a signal pooling over a large range of orientations.

Experiment IV. Psychophysical Mechanisms of Cross Surround Facilitation: Uncertainty Reduction Versus Signal-to-Noise Enhancement

Psychophysical cross facilitation of contrast detection could be potentially interpreted in terms of two general visual processes: low-level internal noise reduction and/or target signal enhancement, as well as higher-level uncertainty reduction at a decision stage. It has been proposed that contrast detection is limited by the visual system’s internal noise and efficiency (Burgess, Wagner, Jennings, & Barlow, 1981; Pelli, 1981). Internal noise such as sampling errors of visual receptors and spontaneous neural activities, etc., reduce the signal-to-noise ratio of neural responses. At a higher-level decision stage, the visual system’s uncertainty about what constitutes the perfect stimulus template, and, therefore, what spatial channels to monitor, impairs efficiency and hinders contrast detection (Burgess et al., 1981; Pelli, 1981). Cross surrounds could improve efficiency and facilitate detection by reducing stimulus uncertainty. They could also facilitate detection by reducing the internal noise and/or enhancing the stimulus signals. Meanwhile, Lu and Dosher (1998) suggested that the reduction of additive internal noise is quantitatively the same as signal enhancement. Thus we will use “ signal-to-noise enhancement” in this experiment to refer to low-level visual processing affecting contrast detection, in contrast to higher-level uncertainty reduction.

We conducted three independent measurements to separate the contributions of uncertainty reduction and signal-to-noise enhancement to cross surround facilitation of contrast detection.

a. Measuring cross surround facilitation in external visual noise

First we adapted an equivalent noise protocol (Pelli, 1981; Pelli & Farell, 1999) and measured cross surround effects with the target in external visual noise. In this protocol, contrast detection is measured with the target presented in different amounts of external noise. At high external noise, any effect of internal noise would be masked, so that changes of efficiency and associated uncertainty due to cross surround facilitation can be isolated.

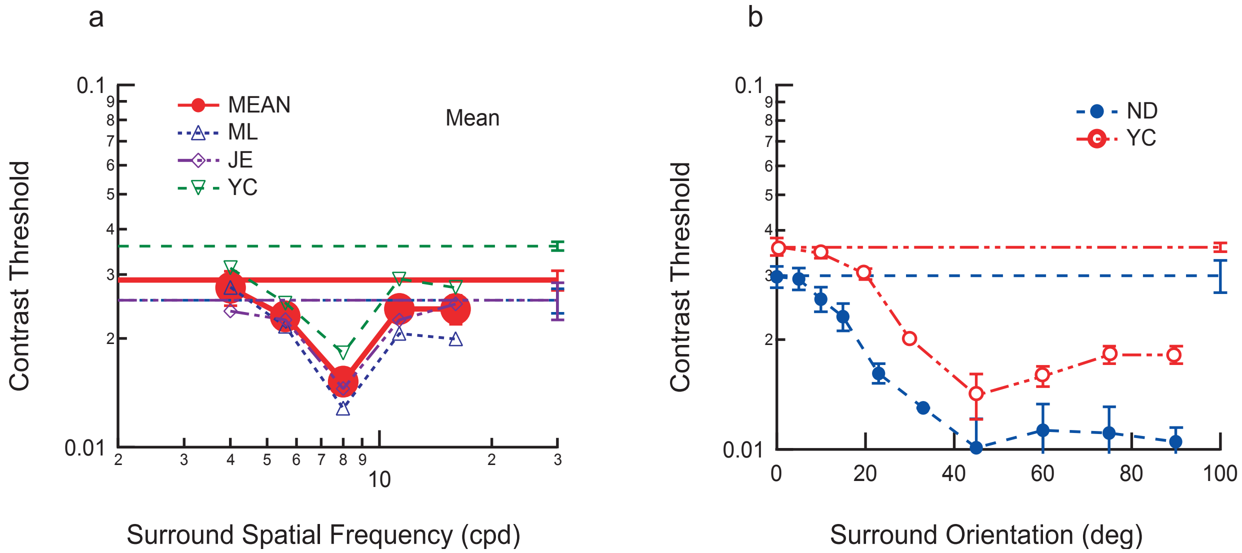

Figure 3. The spatial frequency and orientation tuning of cross surround facilitation of contrast detection. a. Spatial frequency tuning. The peak spatial frequency of the D6 target was constant at 8 cpd. b. Orientation tuning. The D6 target was at 0 deg orientation. In both experiments, the surround contrast was constant at a contrast of 0.10.

In the study, we added external Gaussian noise of various intensities to the target (Figure 4a, see figure legend for details of noise properties) and measured TvN (thresholds vs. noise) functions (Figure 4b) with and without the presence of cross surrounds. Results (Figure 4b) indicate contrast facilitation at all levels of external noise, though the effects are smaller when noise is intense. To characterize internal noise and efficiency changes, we fit the data with the function $Th = k(N_i^2 + N_e^2)^{1/2}$, where Th is the contrast threshold, N_e is external noise in noise threshold units, and k and N_i are free parameters. Noise threshold is 0.12 for Y.C. and 0.09 for the other two observers. For the TvN functions measured with no surround (simple detection), k is the high noise slope on linear axes and k^2 is inversely proportional to efficiency (large k^2 indicates poorer efficiency), and N_i is the equivalent internal noise (in noise threshold units). Data fitting indicates that the cross surround reduced both N_i and k (Figure 4b, Table 1). The reduction of k represents a downward shift (facilitation) of the entire TvN curve, and the reduction of N_i accounts for the remaining facilitation at zero and low external noise. For observers S.T. and Y.C., the cross surround/no surround ratio of N_i (R_{Ni}) is 0.80 ± 0.13 and 0.64 ± 0.07, and the cross surround/no surround ratio of k is 0.72 ± 0.05 and 0.74 ± 0.06, respectively. Because S.T.'s R_{Ni} reduction is relatively small, most of this observer's facilitation comes from the change of k, while R_{Ni} and k have similar contribution to Y.C.'s facilitation.

The cross surrounds might have reduced k (which is determined by the facilitation at high noise) by two means. First, the cross surrounds could reduce stimulus uncertainty by providing the visual system with better stimulus information, such as the location and spatial frequency cues, so that the visual system could place heavier weights on the relevant channels and exclude irrelevant ones. Second, the cross surrounds at high external noise could enhance the signal-to-noise ratio of the relevant channel. This could be done by suppressing multiplicative noise (whose amplitude is proportional to stimulus energy), a factor not included in the Pelli uncertainty model, but is considered in Lu and Dosher's Perceptual Template Model (Lu & Dosher, 1999), or by enhancing stimulus signals through low-level neural interactions even at high noise. The two stages that we consider are depicted in Figure 7 of the "Discussion." The following control experiment measured iso surround modulation of contrast detection in external noise and the results helped rule out the uncertainty reduction explanation.

With other stimulus parameters identical to the cross stimuli (Figure 4a), the surround (Figure 4c) is now in iso (collinear) orientation and butterfly shaped (a full iso surround would have no effect; see Figure 2c). Results (Figure 4d) indicate that iso surrounds only facilitate contrast detection at low noise and have no effect at external noise 2 to 3 times the noise detection threshold, which results in a significant change of N_i but no change of k (Table 1). The iso surrounds here provide not only the same temporal and spatial cues of the target (when, where, and what spatial frequency) as do the cross surrounds (Figure 4a), but also additional orientation and phase cues (it is also easier to compare spatial frequencies of collinear gratings). However, these target cues appear not useful to, or not used by, the visual system to reduce stimulus uncertainty and form a better stimulus template. It is unlikely that a threshold reduction at high noise due to these target cues is offset by iso surround suppression, because the butterfly-shaped iso surrounds at the current contrast (0.10) produce strong facilitation at low noise. On the basis of these iso surround data, we suspect that cross surrounds would have no effect on stimulus uncertainty. Therefore, facilitation at high noise and associated k reduction are mainly contributed by lower-level visual mechanisms, either multiplicative noise reduction or signal enhancement or their combination.

According to Pelli's equivalent noise model (Pelli, 1981; Pelli & Farell, 1999), if uncertainty is not reduced at high noise levels, it is also not reduced at low (or zero) noise levels, assuming a strong correlation between efficiency and uncertainty. Therefore, we would conclude that cross facilitation at zero or low external noise is only contributed by signal-to-noise enhancement. However, other models might allow independent mechanisms at low and high noise (e.g., Lu & Dosher, 1999). Thus, in order to make our conclusions less model dependent, we examined whether cross surrounds could affect uncertainty at zero and low noise, even though these surrounds are not effective in reducing uncertainty at high noise levels. The following two experiments served this purpose.

	cross surround			**iso surround**	
	N_i	**k**		**N_i**	**k**
ST			**AJ**		
w/o sur	1.38 ± 0.13	0.022 ± 0.001	w/o sur	1.16 ± 0.10	0.026 ± 0.001
w/ sur	1.11 ± 0.14	0.016 ± 0.001	w/ sur	0.62 ± 0.04	0.026 ± 0.000
ratio	***0.80 ± 0.13***	***0.72 ± 0.04***	***ratio***	***0.53 ± 0.06***	***0.99 ± 0.04***
YC			**YC**		
w/o sur	1.81 ± 0.15	0.020 ± 0.001	w/o sur	1.73 ± 0.36	0.018 ± 0.003
w/ sur	1.16 ± 0.09	0.015 ± 0.001	w/ sur	0.96 ± 0.22	0.018 ± 0.002
ratio	***0.64 ± 0.07***	***0.74 ± 0.05***	***ratio***	***0.55 ± 0.17***	***0.98 ± 0.20***

Table 1. Summary of fitting parameters (N_i and k) and their ratios

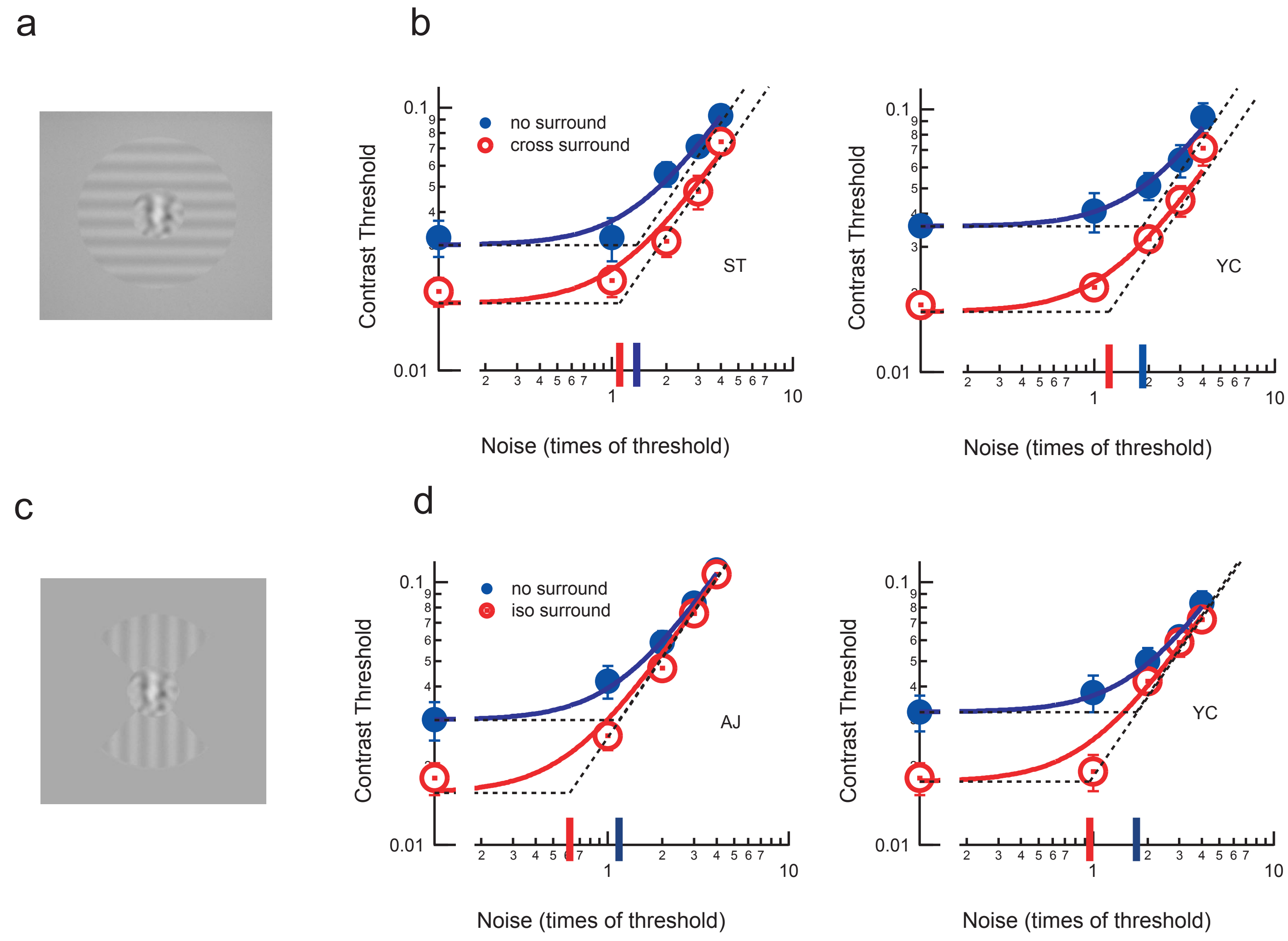

Figure 4. Cross surround facilitation of contrast detection in noise. a. Stimuli with full cross surrounds. The stimuli consisted of the same D6 target and cross-oriented surround as in Figure 1a except that a static two-dimensional Gaussian noise abutting the inner edge of the surround was added to the target. The surround contrast was 0.10. The random Gaussian had a central spatial frequency of 8 cpd and a bandwidth of 3 octaves. Noise with contrasts equal to 1 to 4 times the noise detection threshold was added to the target. The Gaussian noise was randomized for each trial. b. Threshold versus noise (TvN) functions and data fitting under baseline and cross surround conditions. Fitting parameters are summarized in Table 1. The sloping dashed lines indicate kN_e and the horizontal dashed lines indicate kN_i. The reduction of N_i is indicated by the horizontal difference of two bars on the x axis, and the reduction of k is indicated by the vertical shift of the two sloping dashed lines. c. Stimuli with butterfly-shaped iso surrounds. The target and noise conditions, as well as the surround contrast, are identical to those of the cross stimuli in “a.” d. Iso TvN functions and data fitting curves. The noise detection threshold was 0.09 for A.J. and 0.12 for Y.C. Fitting parameters are summarized in Table 1.

b. Estimating cross surroundinduced changes of the slope (β) of the psychometric function and the uncertainty parameter (M)

The uncertainty model (Cohn & Lasley, 1974; Pelli, 1985) assumes that for contrast detection, the observer needs to monitor a number of independent spatial channels to make a decision about the stimulus. Because of uncertainty about the relevant channel, some of the monitored channels are irrelevant. The number of the spatial channels the observer is monitoring, and therefore the uncertainty, is indicated by the parameter M. M is equal to 1 at zero uncertainty, and larger M indicates larger uncertainty. Higher uncertainty results in higher threshold and steeper slope of the psychometric function because of a maximum-of-channels rule that we assume for the decision stage (see “Discussion”). The Weibull β, a common index of the slope, is approximately 1.4 when M = 1 (Pelli, 1985). This experiment measured the slope change of the psychometric function under the influence of cross surround and the concurrent change of the uncertainty parameter (M).

Because our earlier data were collected with a 2AFC staircase method that did not allow a precise estimation of the slope (β) and the uncertainty parameter (M), we collected new data using a 5-level rating-scale method of constant stimuli (see "Methods"). The d' values (Figure 5a) for different target contrasts in an individual trial block were first determined using a maximum likelihood fit to the rating scale data. In order to carry out a standard uncertainty analysis, we converted these d' values to percentage correct in a 2AFC method. The standard errors of the percent correct data were calculated by a Monte Carlo simulation based on the standard errors of d'.

We first fit these percentage correct data with a Weibull function:

$$P_{correct}(c) = 1 - 0.5 * 2^{-(c/th)^{\beta}} \qquad (1)$$

to estimate the threshold (*th*) at the 75% correct level and the slope of the psychometric functions (β). Here *c* in the equation is the target contrast. A nonlinear least square method (the Matlab lsqnonlin function) was used for optimization. Because of the large run-to-run differences of β within the same observer, we constrained β to be the same across runs, with threshold being variable from run to run. The left half of Table 2 gives each observer's mean thresholds (weighted mean across individual blocks) and β. Figure 5b shows each observer's mean percent correct data converted from d' and the simulated psychometric functions based on each observer's mean threshold and β under surround and no surround conditions. Table 2 shows cross surround facilitation (reduced contrast threshold) in both observers. For observer J.E., β is unchanged by the cross surround (1.53 ± 0.19 vs. 1.58 ± 0.18), implying no uncertainty change. However, for observer M.L., β is reduced but the change is not significant (1.83 ± 0.20 vs. 1.53 ± 0.16 with a change of 0.30 ± 0.26). The slope data therefore do not provide strong support for uncertainty reduction in cross surround facilitation.

In addition to the Weibull fit, we also fit the data with an uncertainty model where the observer attends to M channels in each of the two intervals (Pelli, 1985). Only one of the M channels carries a signal. The equation used to fit the data is written as:

$$P_{correct}(c) = \int_{-\infty}^{\infty} \begin{bmatrix} f(x-kc)F(x)^{2M-1} + \\ (M-1)f(x)F(x)^{2M-2}F(x-kc) \end{bmatrix} dx. \qquad (2)$$

Here *c* is the target contrast, *f(x)* is the Gaussian probability density function, *F(x)* is the cumulative Gaussian, *k* is the sensitivity or gain parameter, and M is the uncertainty parameter. We used a maximum rule whereby the observer is assumed to choose the interval that contains the maximum response. The first term gives the probability that the channel with the signal has the maximum output; the second term is the probability that a noise channel in the signal interval has maximum output. The data were fit by a method similar to that used for fitting the Weibull function. There were as many gain parameters (gain is the theoretical sensitivity when M=1) as there were repeated runs for a given surround condition. An additional parameter specified M, the number of attended channels on each stimulus presentation. The weighted mean of the gain parameters and uncertainty parameters for each observer are listed in the right half of Table 2. Figure 5c shows each observer's mean percent correct data and the simulated psychometric functions based on each observer's mean gain and M values. Results show unchanged M (2.0 ± 1.2 vs. 1.9 ± 1.1) for J.E. and insignificantly reduced M (6.0 ± 3.6 vs. 1.9 ± 1.0) for M.L. because of the large errors, again not supporting a significant uncertainty reduction in cross surround facilitation. Meanwhile, the gain is increased for observer J.E. (from 0.50 ± 0.03 to 0.65 ± 0.04) but unchanged for observer M.L. (0.64 ± 0.04 vs. 0.65 ± 0.03).

In summary, these two observers' data do not support uncertainty reduction in cross surround facilitation. As Table 2 suggests, the number of monitored channels with no surround is very small (2-6), very low when compared to M > 100 at high uncertainty situations (Pelli, 1985). There is really not much uncertainty even with no surround in our tasks for these two observers. This is especially seen in observer J.E. with M=2.0 ± 1.2. This low value of M suggests that the surround is not able to do much uncertainty reduction.

		Weibull fit		M fit	
		threshold	beta	gain	M
JE	baseline	2.33 ± 0.11	1.53 ± 0.19	0.50 ± 0.03	2.0 ± 1.2
	cross	1.75 ± 0.08	1.58 ± 0.18	0.65 ± 0.04	1.9 ± 1.1
ML	baseline	2.37 ± 0.10	1.83 ± 0.20	0.64 ± 0.04	6.0 ± 3.6
	cross	1.84 ± 0.07	1.53 ± 0.16	0.65 ± 0.03	1.9 ± 1.0

Table 2. Summary of parameters from Weibull fit (Figure 5b) and M fit (Figure 5c). Thresholds and gains are averaged from fitting of individual data sets (see text).

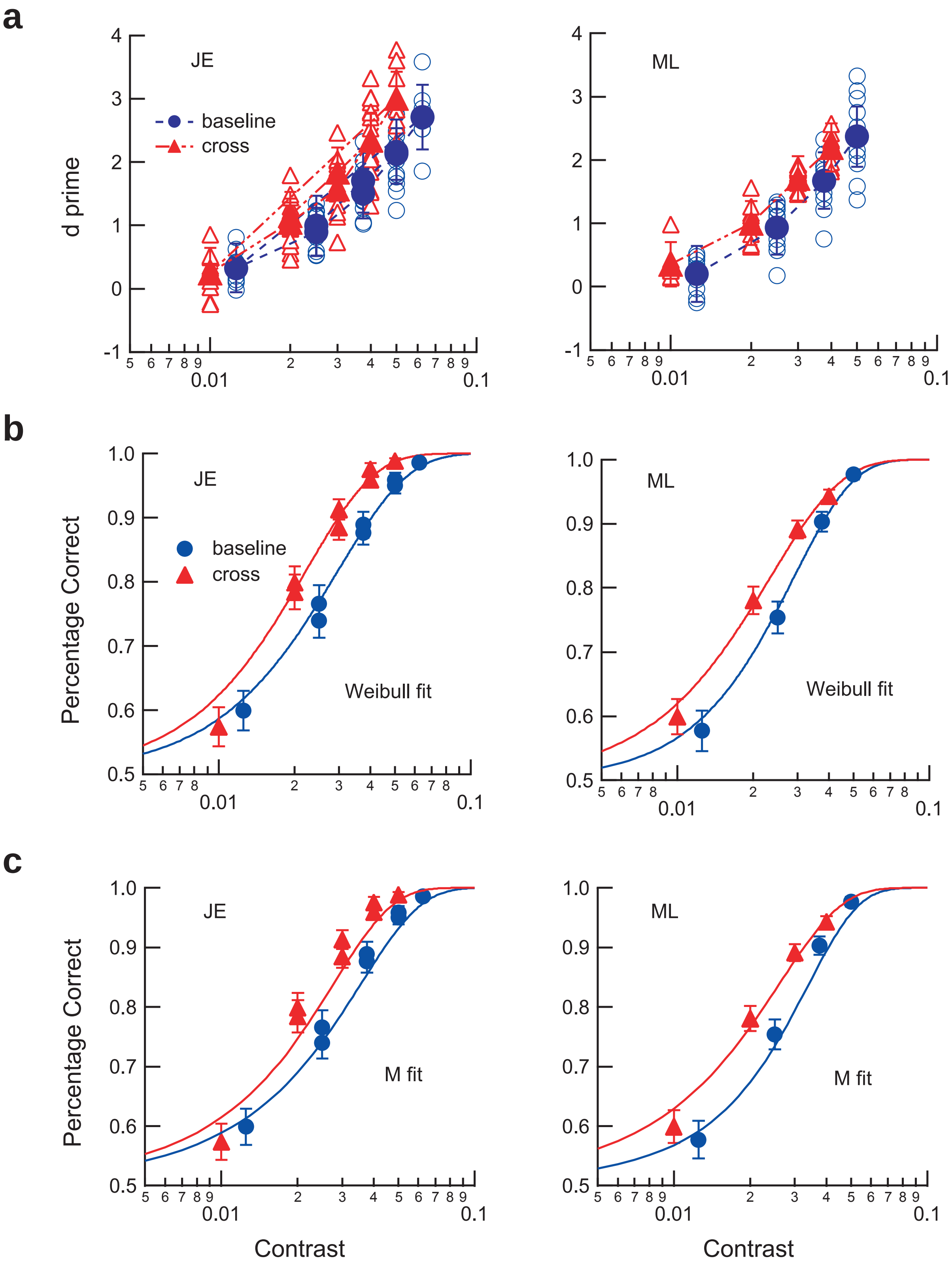

Figure 5. Estimating changes of the psychometric function slope and the uncertainty factor (M) under the influence of the cross surround. a. d' for each target contrast. The empty symbols indicate d' for individual blocks, and the filled symbols indicate the mean d'. J.E. had two sets of target contrasts for baseline and cross surround conditions. b. Mean percent correct data converted from d' (filled symbols) and Weibull fits (Table 2, left). c. Mean percent correct data (filled symbols) and M fits (Table 2, right). The curves in both b and c do not optimally match the mean d' data because the fitting was done on individual data sets rather than on the mean d's (see text).

c. Measuring cross surround facilitation at the dipper of the TvC function

We also studied the effect of cross surrounds on near-threshold contrast discrimination, which we believe provides a more robust means to examine the role of uncertainty in cross surround facilitation. It is well known that contrast threshold for a target presented on a near-threshold pedestal is lower than the detection threshold, which forms a dipper in the TvC function. Pelli's uncertainty model (Pelli, 1985) explains such contrast facilitation as the reduction of uncertainty. Legge, Kersten, and Burgess (1987) showed that the log-log d' slope of the psychometric function reduces from around 2 for detection to around 1.5 for near-threshold discrimination. According to the uncertainty model, a slope decrease would indicate diminished uncertainty (Weibull β is nearly 1.41 when M = 1). Moreover, as Table 2 indicates, uncertainty for detecting the target stimulus is not very high (β = 1.53 and 1.83 and M = 2.0 and 6.0 for two observers, respectively). If the sole function of the cross surround is to reduce uncertainty, it would not have much uncertainty to reduce when a near-threshold pedestal is already there. Therefore, it can be predicted that a cross surround would not be able to significantly reduce the contrast threshold at the dipper. On the other hand, if the cross surround improves the gain through signal-to-noise enhancement, it would reduce the already low threshold at the dipper and form a "super dipper." To test these predictions, we measured near-threshold discrimination with or without the cross surround presentation and compared it with cross surround facilitation of contrast detection.

The same three observers in Experiment 1 (Figure 1) participated in this experiment and contrast thresholds were again measured with a 2AFC staircase method. The stimulus configuration was the same as that in Figure 1, except that the surround contrast was constant at 0.10 and a circular-windowed sinusoidal grating pedestal was added. The pedestal abutted the surround grating from inside (pedestal diameter = surround inner diameter), had the same spatial frequency and orientation as the target (8 cpd, vertical), and had contrasts ranging from 0 to 0.10. Figure 6 shows that (1) baseline thresholds with no surround presentation were reduced from detection to near-threshold discrimination (mean thresholds from 0.03 at 0 pedestal contrast to 0.02 at 0.05 pedestal contrast), showing the dipper effect typically seen in a TvC function. (2) The cross surround greatly reduced contrast thresholds, not only for detection, but also for near-threshold discrimination at the dipper. Facilitation for near-threshold discrimination was consistent among all three observers and the average threshold at the dipper was reduced from 0.02 to as low as 0.01 at 0.05 pedestal contrast, indicating the formation of a "super dipper"! This evidence argues strongly against an uncertainty-reduction explanation of cross surround facilitation and favors a lower-level signal-to-noise enhancement theory.

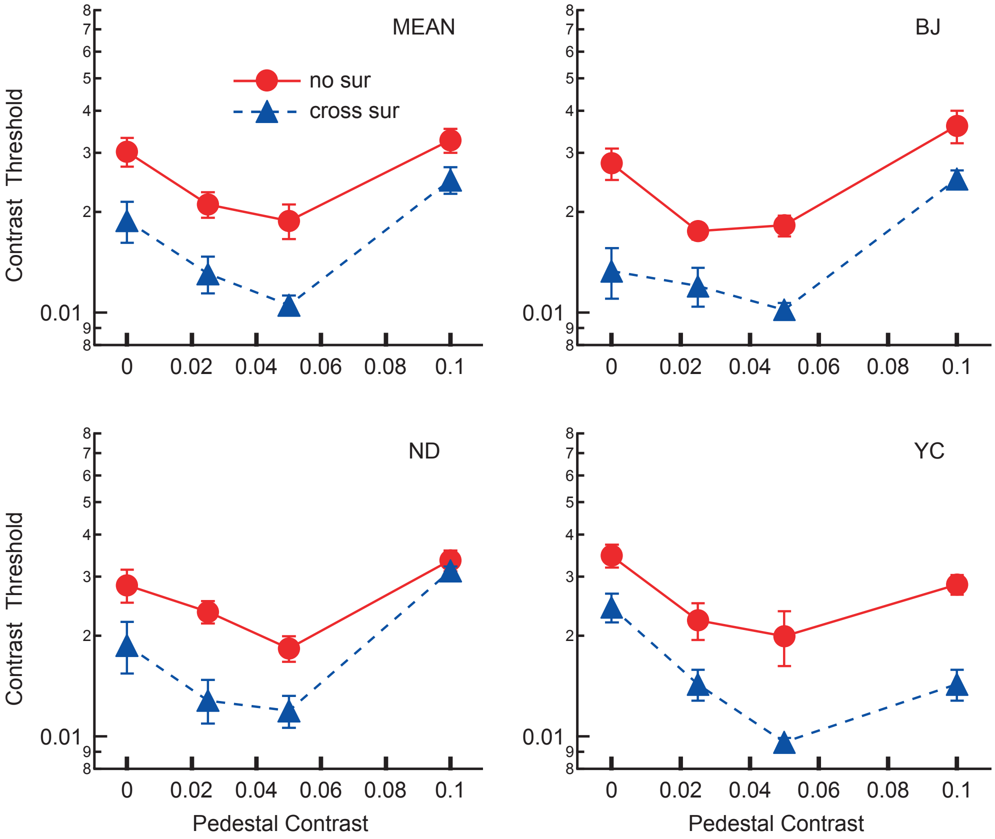

Figure 6. Cross surround effects on near-threshold contrast discrimination.

Discussion

Our experimental findings can be summarized as following: (1) The cross surround stimuli, whether they are full- or partial-annular gratings or Gabor patches, can facilitate contrast detection under appropriate contrasts (Figure 1-2). (2) Cross surround facilitation is sharply tuned to target spatial frequency (Figure 3a) but only loosely tuned to cross orientation (Figure 3b). (3) Low-level psychophysical mechanisms of signal-to-noise enhancement, rather than higher-level uncertainty reduction, make a major contribution to cross surround facilitation, as indicated by three separate measurements in Experiments 4a, 4b, and 4c.

The general class of models that we are considering is shown in Figure 7. This example has nine mechanisms feeding into three second-stage collator channels (Mussap & Levi, 1995). Only one of the nine mechanisms (R) is carrying relevant information. We assume that the second stage mechanisms linearly summate the first stage inputs with weights that can be modulated by the surround. Because the initial mechanisms are assumed to have independent noise, the ideal summation corresponds to d' summation with a Minkowski exponent of two (Quick, 1974). We further assume that the outputs of the second stage channels are combined by a maximum rule (Max), rather than by linear summation. The Max rule summation corresponds to d' summation with a Minkowski exponent of infinity. When the maximum rule summation take place at the decision stage, late in visual processing, it is commonly referred to as the uncertainty explanation (Pelli, 1985) because the presence of irrelevant channels at the decision stage is called "uncertainty." This two-stage model is able to handle a wide variety of data that include uncertainty manipulations (Cohn & Lasley, 1974; Pelli, 1985).

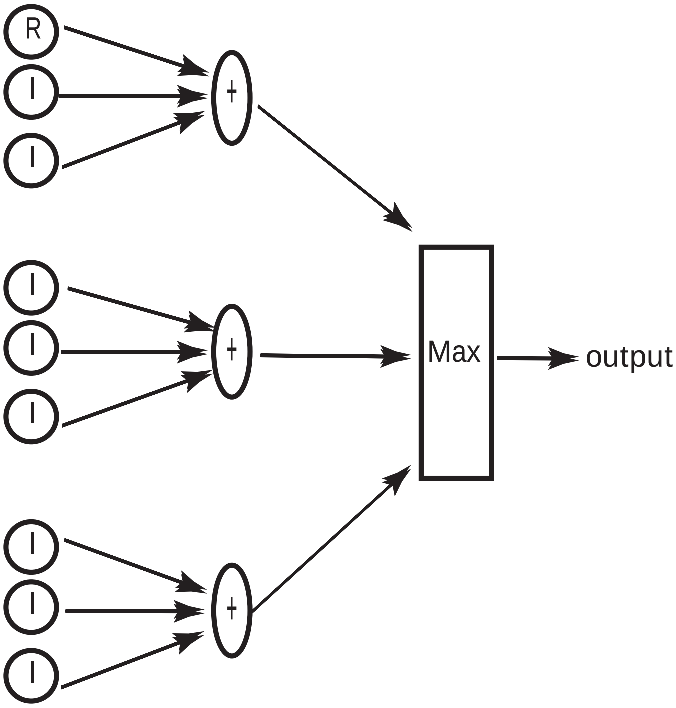

Figure 7. A general uncertainty model. The responses of the relevant mechanism (R) and irrelevant mechanisms (I) (circles) are first linearly summated by second-stage collator channels (ellipses). The outputs of collator channels are then combined following a maximal rule at the decision stage (rectangle). The presence of irrelevant channels at the decision stage produces uncertainty.

Experiment 4a used noise masking to show that the cross surround produced more facilitation than did the iso surround at high noise masking. We argued that if the facilitation were due to a reduction of uncertainty then the iso surround should have produced more facilitation because it provides more cues to the relevant mechanisms than does the cross surround. We further argued that the lack of uncertainty reduction at high noise levels should also apply to the zero noise level that is the primary interest of this work. However, because it is possible that uncertainty reduction could work differently at high and low noise (Lu & Dosher, 1998), we carried out two further experiments.

Experiment 4b examined the shape of the psychometric function with and without a cross surround with no noise present. The logic of these experiments was that if the cross surround reduced the number of irrelevant channels at the decision stage (uncertainty reduction), then both the psychometric function slope (the Weibull β parameter) and the uncertainty parameter, M (the total number of channels feeding into the stage where the maximum summation rule is applied), would be reduced. We used the method of constant stimuli to measure d' at four stimulus levels near threshold. The d's were fitted with a 2AFC Weibull function and with a 2AFC uncertainty function. In a 2AFC experiment, there are a total of 2M-1 irrelevant channels and one relevant channel at the max rule stage. The Weibull fit of both observers showed that the cross surround produces a 30% reduction of threshold, compatible with our other studies. Observer J.E. showed that the threshold reduction did not involve a change in psychometric function shape in that the Weibull β parameter and the uncertainty M parameter were unchanged by the surround. The threshold reduction was achieved by an increase in the gain of the signal channel. For observer M.L., on the other hand, the threshold reduction was achieved by a reduction of M rather than by a change in gain. However, the large standard errors in estimates of M make us cautious about claiming that the change of M is significant. The striking thing about the psychometric functions is that they have relatively shallow slopes (low values of β and M) with or without a surround. The largest value of M is 6.0 ± 3.6, which is quite low when compared to the uncertainty levels found in other studies (Pelli, 1985). Thus we believe that under the conditions of our experiments and with our trained observers, the uncertainty was always small.

Experiment 4c compared the amount of facilitation at the trough of the dipper function both with and without the surround. We found that the presence of the surround produced about the same amount of facilitation at the trough of the dipper as it did at the detection threshold. If the surround facilitation had been produced by uncertainty reduction, then we would expect that the presence of the pedestal would have removed most of the uncertainty and in the presence of the cross surround the dipper would have been shallower than the no surround case.

Neurophysiological surround modulation has been known to be contrast dependent (Toth, Rao, Kim, Somers, & Sur, 1996; Levitt & Lund, 1997; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Kapadia et al., 2000). The surround contrast dependence of cross surround facilitation resembles some recent neurophysiological data of surround modulation. Kapadia et al. (2000) reported that iso surround modulation of classical receptive fields in alert monkeys is facilitative at low surround contrasts and suppressive at high surround contrasts. They suggested that low-contrast surround stimuli produce direct excitatory inputs to visual neurons, but high-contrast surround stimuli also produce additional inhibitory inputs through inhibitory interneurons that cancel excitation. We speculate that the cross surround facilitation evident in our psychophysical experiments could reflect similar excitation-inhibition dynamics.

Our psychophysical evidence for cross surround facilitation in low-level vision at least partially supports Wolfson and Landy's model (Wolfson & Landy, 1999) regarding the roles of spatial filter interactions in texture segregation and visual search. Their model attributes superior performance of detecting or searching a textural element surrounded by orthogonal elements to excitatory interactions between orthogonal spatial filters and poorer performance with iso surround elements to inhibitory interactions between iso spatial filters. However, this performance asymmetry could also be explained as a result of stronger surround inhibition at iso orientation and reduced suppression at cross orientation as pointed out by Walker et al. (1999), who reported weak neuronal cross surround suppression but no facilitation. Our data taken together with recent physiological studies (Kapadia et al., 2000) suggest that excitatory interactions do exist between orthogonal spatial filters at low-level vision and can make a contribution.

On the other hand, poor visual search performance under iso surround textural conditions and inhibitory interactions between iso spatial filters proposed by Wolfson and Landy (1999) are inconsistent with iso surround facilitation of contrast detection (Polat & Sagi, 1993), but are supported by other low-level evidence like iso surround suppression of perceived contrast (Cannon & Fullenkamp, 1991). The usefulness of iso surround facilitation in intermediate-level visual tasks such as contour integration has been recently questioned (Hess & Field, 1999). Our psychophysical data indeed suggest that iso surround facilitation is a very delicate effect and is easily disturbed by either weak noise (2-3 times noise threshold, Figure 4b) or by a full iso surround (Figure 2c) In contrast, cross surround facilitation is more robust and less affected by external visual noise. It is plausible that weak iso surround facilitation may be masked in complex stimulus configurations, and plays very little role in intermediate-level vision.

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