

Cross- and Iso- oriented surrounds modulate the contrast response function: The effect of surround contrast

Cong Yu

School of Optometry, University of California at Berkeley,
Berkeley, CA, USA



Stanley A. Klein

School of Optometry, University of California at Berkeley,
Berkeley, CA, USA



Dennis M. Levi

School of Optometry, University of California at Berkeley,
Berkeley, CA, USA



The detectability and appearance of visual targets can be modulated by surround stimuli. In this study we asked how cross- and iso-oriented surrounds modulate contrast detection and discrimination in foveal vision. We systematically measured the Threshold-versus-Contrast (TvC) functions over a wide range of pedestal and surround contrasts. Our results show that cross-oriented surrounds lower the contrast threshold over the entire range of pedestal and surround contrasts, but iso-surround modulation of the TvC function is dependant on the relative contrast, being facilitative when the surround/pedestal contrast ratio $C_{sur}/C_{ped} < 1$ and suppressive when $C_{sur}/C_{ped} > 1$. Data fitting indicates that cross-surround modulation (facilitation) is mainly due to improved gain, except at very low and high surround contrasts. Iso-surround modulation on the other hand is more complicated, probably reflecting more than one surround process as determined by the relative contrast.

Keywords: surround modulation, cross-orientation, iso-orientation, Stromeyer-Foley d' function, TvC function, classical receptive fields

Introduction

The responses of V1 neurons can be modulated by stimulation outside the neurons' classical receptive fields (e.g., Hubel & Wiesel, 1965; Nelson & Frost, 1985; Knierim & Van Essen, 1992; Kapadia, Westheimer, & Gilbert, 2000; etc). This surround or contextual modulation indicates that V1 neurons are not simply isolated bar and edge detectors. Instead they interact with each other with a potential for serving more complex visual functions. Among various issues of surround modulation studied by researchers in both neurophysiology and psychophysics are the roles of relative surround orientation, ranging from collinear (iso) to orthogonal (cross). In neurophysiological studies, surround facilitation and suppression have been reported at both iso and cross surround orientations (Hubel & Wiesel, 1965; Nelson & Frost, 1985; Knierim & Van Essen, 1992; DeAngelis, Freeman, & Ohzawa, 1994; Kapadia, Ito, Gilbert, & Westheimer, 1995; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995; Toth, Rao, Kim, Somers, & Sur, 1996; Das & Gilbert, 1999; Hupe, James, Girard, & Bullier, 2001; Jones, Wang, & Sillito, 2002). The results are not always consistent, but the relative stimulus contrast has been cited as one important factor to account for some of the controversies about whether

surrounds produce facilitation or suppression (Kapadia et al., 2000).

At the psychophysical (visual system) level, the influences of surround stimuli on contrast detection and discrimination may also provide insights into the surround modulation issue (e.g., Dresch, 1993; Polat & Sagi, 1993; Zenger & Sagi, 1996; Snowden & Hammett, 1998; Solomon, Watson, & Morgan, 1999; Yu & Levi, 2000). Collinear or iso-surround modulation has been studied most often (e.g., Polat & Sagi, 1993; Zenger & Sagi, 1996; Yu & Levi, 1997; Snowden & Hammett, 1998; Solomon et al., 1999), but only a small number of studies have investigated psychophysical surround modulation by cross-surround stimuli (Raasch, 1988; Polat & Sagi, 1993; Yu & Levi, 1998, 2000; Chen & Tyler, 2002; Yu, Klein, & Levi, 2002).

Strong cross-surround facilitation of contrast detection was demonstrated by Yu, Klein and Levi (2002), both with annular surround stimuli (replotted in this paper, Figure 3, top left panel) and with Gabor flankers similar to those used by Polat and Sagi (1993). Similar effects were first reported in a thesis by Raasch (1988). Yu, et al. (2002) found that cross-surround facilitation of contrast detection is surround-contrast dependent. It mainly manifests at low surround contrasts but not at high surround contrasts, which explains why no cross

facilitation was evident in Polat and Sagi (1993). Control measurements by Yu, et al. (2002) showed that cross-surrounds facilitate contrast detection mainly by improving the internal signal/noise ratio rather than by reducing stimulus uncertainty.

For contrast discrimination, Yu and Levi (2000) reported two distinct types of surround effects, one narrowly tuned to iso-orientation, and the other broadly tuned to cross-orientation. Surround modulation of contrast discrimination at cross- and iso-orientations for a fixed pedestal contrast (0.40) is generally facilitative, but with distinct contrast dependencies. Cross-surrounds at contrasts higher than the pedestal contrast produce stronger facilitation that could completely eliminate masking. In contrast, iso-surround facilitation is diminished when the surround contrast is higher than the pedestal contrast.

In the current study we expanded our investigation to systematically study cross- and iso-surround modulation over a broad range of pedestal and surround contrasts by measuring complete threshold versus contrast (TvC) functions at multiple surround contrasts. We also fit the data quantitatively using a variant of the standard contrast-response function (which we call the Stromeyer-Foley function) to examine how the underlying contrast response function is modulated by cross- and iso-surrounds. Our experiments and data fitting enable us to test conclusions of previous researchers based on data collected from limited stimulus conditions, and to obtain a better understanding of psychophysical cross- and iso-surround modulation.

Methods

Observers and Apparatus

Three adult observers with normal or corrected-to-normal vision served in the study. BJ and ND were new to psychophysical observation and received several sessions of training. YC, one of the authors, was highly experienced.

The stimuli (Figure 1) were generated by a VisionWorks computer graphics system (Vision Research

Graphics, Inc., Duham, NH) and presented on a U.S. Pixel Pxl9 monochrome monitor (1024 x 512 resolution, 0.28 mm (H) x 0.41 mm (V) pixel size, 117 Hz frame rate, 62 cd/m² mean luminance, and 3.8° x 3.0° screen size at the 5.64-meter viewing distance). Luminance of the monitor was made linear by means of a 15-bit look-up table. Experiments were run in a dimly lit room.

Stimuli and Procedure

The target (Figure 1) was a 10 arcmin long spatially localized D6 grating (the sixth derivative of a Gaussian, T in Figure 1b) centered in-phase on a circularly windowed sinusoidal grating pedestal (P in Figure 1b) of the same spatial frequency (8.0 cpd) and orientation (vertical) with contrast varying from 0 to 0.40. The D6 target (similar to a Gabor function with $\sigma = 4.1$ arcmin) was multiplied by a Gaussian window along its long axis ($\sigma = 4.2$ arcmin) and truncated at the target length. The size of the circular pedestal was larger than the target ($d = 18$ arcmin), which would maximize masking at high pedestal contrasts (Yu & Levi, 1997, 2000) because of a desensitization effect (Westheimer, 1967), but would change masking very little at low pedestal contrasts because desensitization at low pedestal contrasts is nearly negligible (Westheimer, 1967). The surround (S in Figure 1b) was a sinusoidal grating annulus abutting the pedestal with contrast varying from 0 to 0.80. The outer and inner diameters of the surround were 45 and 18 arcmin, respectively. Contrast thresholds were measured with a successive two-alternative forced-choice staircase procedure. The pedestal was presented in each of the two stimulus intervals (300 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 pedestal. 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 contrast change in preliminary reversals was 7.5% of the previous contrast

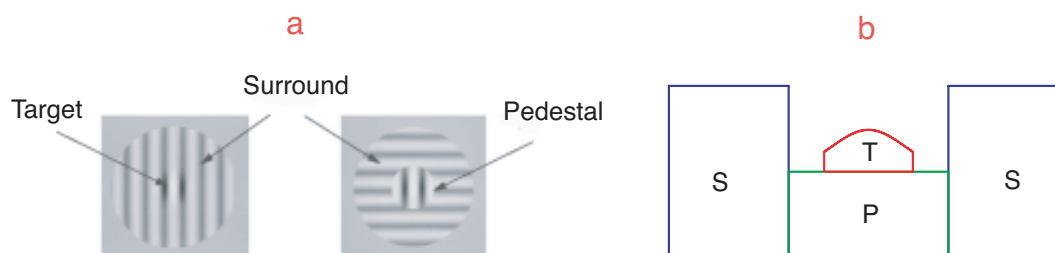


Figure 1. Stimuli. The stimuli consisted of a D6 grating target centered on a circularly windowed sinusoidal grating pedestal. The pedestal was abutted by an annular sinusoidal grating surround. (a) Iso-surround (left) and cross-surround (right) conditions. (b) The stimulus profile at the x -axis. T is the D6 target, P is the pedestal, and S is the surround grating.

and in experimental reversals it was 2.5%. Each correct response lowered the target contrast by one step and each incorrect response raised the target contrast by three steps, which resulted in a 75% convergence level of the staircase. The mean of the eight experimental reversals was taken as the contrast threshold. Each datum represents the mean of 5-6 replications, and the error bars represent ± 1 standard error of the mean.

Each experimental session typically consisted of three segments lasting for approximately two hours. Each segment measured one TvC function (six staircases for six pedestal contrasts at $C_{ped} = 0$ to 0.40 in a random order). TvC functions at different surround orientations (cross and iso) and contrasts ($C_{sur} = 0$ to 0.80) were measured in a balanced order.

Results

Our results show that cross-oriented surrounds lower the contrast threshold over the entire range of pedestal and surround contrasts, but iso-surround modulation of the TvC function is dependant on the surround/pedestal contrast ratio (C_{sur}/C_{ped}), being facilitative when $C_{sur}/C_{ped} \leq 1$ and suppressive when $C_{sur}/C_{ped} > 1$. These effects are evident in [Figures 2-4](#).

[Figure 2](#) shows the TvC functions of the mean data from three observers and data fitting outputs (see later Data Fitting section) (cross-surround data in the left column and iso-surround data in the right column). The error bar for each datum represents either the average of the three corresponding individual error bars, or the standard errors of individual thresholds, whichever is larger. Each row shows cross- and iso-surround TvC functions at one surround contrast (in ascending order from 0.025 to 0.80), as well as the baseline TvC function ($C_{sur} = 0$). Individual data and data fitting outputs can be retrieved by clicking [here](#).

Baseline TvC Function

The mean and individual baseline functions (i.e., the TvC function with no surround shown by black asterisks and dashed lines replicated in each panel) resemble a typical TvC function (e.g., [Legge & Foley, 1980](#)). As the pedestal contrast increases, the contrast threshold first decreases and then increases, forming a dipper near the detection threshold.

Cross-surround Modulation

Cross-surrounds facilitate the entire TvC function at all surround contrasts (red circles). At low and moderate surround contrasts ($C_{sur} = 0.05$ to 0.40), especially at $C_{sur} = 0.10$ & 0.40, facilitation is mainly due to a downshift of the TvC function. At the lowest surround contrast ($C_{sur} = 0.025$), facilitation is minimal at

detection ($C_{ped} = 0$), most evident at the dipper ($C_{ped} = 0.025 \sim 0.10$), and weakens as the pedestal contrast increases (which results in a steeper slope of the TvC function at high pedestal contrasts). At the highest surround contrast ($C_{sur} = 0.80$), facilitation is mainly evident at high pedestal contrast with little effect at low pedestal contrasts, and the TvC function is flatter at high pedestal contrasts.

Iso-surround Modulation

Iso-surrounds facilitate the entire TvC function at the lowest surround contrast ($C_{sur} = 0.025$) except for detection ($C_{ped} = 0$) (blue circles). As the surround contrast increases, facilitation is limited to higher pedestal contrasts, and iso-surround modulation at lower pedestal contrast becomes suppressive, raising thresholds above the baseline when $C_{sur} = 0.80$. The transition from suppression to facilitation appears to be determined by the relative contrast of the surround and pedestal (considered below). At $C_{sur} = 0.40$, suppression changes to facilitation dramatically, producing a kink in the TvC function at high pedestal contrasts. At the highest surround contrast ($C_{sur} = 0.80$), suppression is evident at low pedestal contrasts ($C_{ped} \leq 0.1$) with thresholds equal to the baseline at $C_{ped} = 0.20$ and 0.40.

Cross- vs. Iso-surround Modulation Compared at Various Pedestal Contrasts

Several interesting properties emerge when the mean cross and iso data are plotted together (replotted from [Figure 2](#)) at each pedestal contrast as a function of the surround contrast ([Figure 3](#) - lower abscissa). First, at higher pedestal contrasts ($C_{ped} = 0.10 \sim 0.40$), cross- and iso-surrounds produce nearly identical facilitation when $C_{ped} > C_{sur}$ (values less than 1 on the top abscissa, which shows the ratio of surround to pedestal contrast). Similar data reported previously at $C_{ped} = 0.40$ ([Yu & Levi, 2000](#)) are also included ([Figure 3](#), bottom right). However, iso facilitation diminishes when $C_{ped} < C_{sur}$, suggesting the influence of the relative contrast of pedestal and surround stimuli (see below).

Second, at lower pedestal contrasts, although cross facilitation tends to be strong, iso surrounds do not have much effect on contrast thresholds, except for slight facilitation at the lowest contrasts ($C_{sur} = 0.025$) and some suppression when the surround contrast is much higher than the pedestal contrast ($C_{sur} = 0.80$). Lack of surround modulation at lower pedestal contrast, especially at detection, is specific to the annular iso-surround stimuli we used, as significant iso-facilitation is evident when collinear flankers restricted to near the ends of a target stimuli are used (e.g., [Polat & Sagi, 1993](#)).

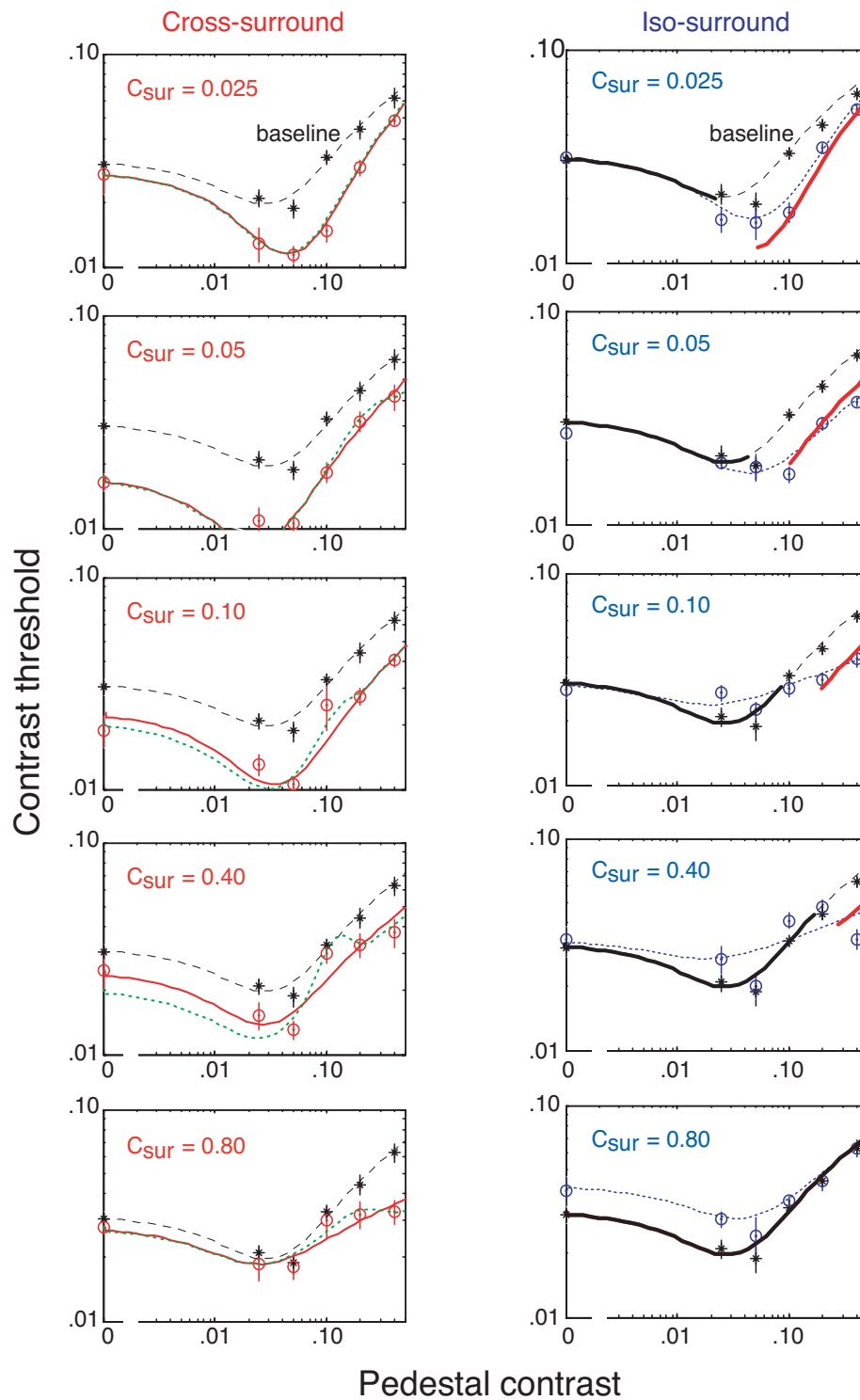


Figure 2. TvC functions modulated by cross and iso surrounds at various surround contrasts. A. Averaged data from three observers. Baseline, cross and iso data are indicated by **black** asterisks, **red** circles in the left column, and **blue** circles in the right column, respectively. The baseline data are repeated in each panel for ease of comparison. The dashed **black**, solid **red** and dotted **blue** curves show baseline, cross and iso data fitting outputs based on Equation 1 (see the Data Fitting section below). The dotted **green** lines in the left column show improved cross data fits. The thick solid **black** and **red** lines in the right column represent a combination of baseline fit and cross fit that approaches iso data. For individual data and data fitting outputs click [here](#).

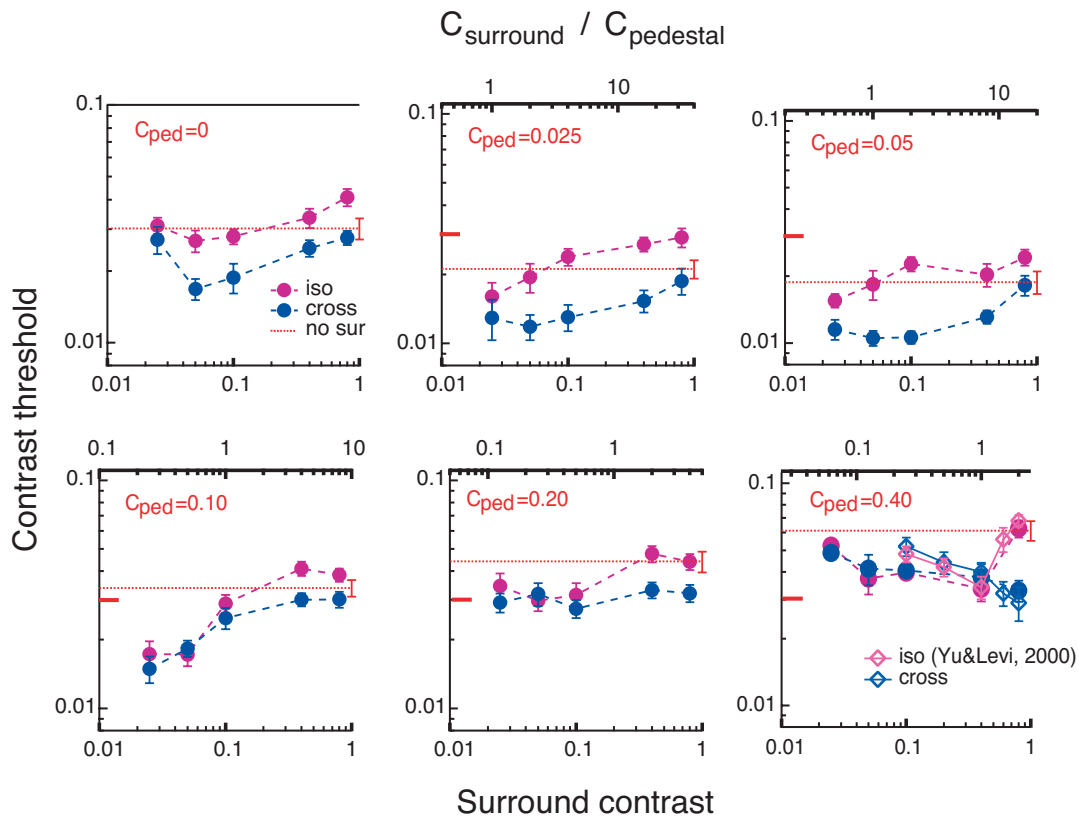


Figure 3. The mean contrast thresholds of Figure 2 are replotted here as a function of the surround contrast (bottom axes) and the surround/ pedestal contrast ratio $C_{surround}/C_{pedestal}$ (top axes except the $C_{ped} = 0$ panel) for each of six pedestal contrasts. The baseline threshold for each pedestal contrast is shown as the horizontal red line in each panel. The red horizontal bars intercepting the y axes indicate the detection threshold at $C_{ped} = 0$ and $C_{sur} = 0$.

Solomon & Morgan (2000) and Yu, et al. (2002) showed that collinear iso facilitation can be suppressed by non-collinear stimulus components in annular iso surround stimuli.

We hypothesize that cross and iso surround effects may share some common mechanisms. When $C_{ped} > C_{sur}$, these common mechanisms produce similar iso and cross surround facilitation. However, when $C_{ped} < C_{sur}$, iso surround facilitation is diminished and thresholds

approach the baseline. In later data fitting, we will show that a combination of baseline fitting and cross data fitting nicely describes many of the iso-surround effects; however, it fails to account for the iso-surround inhibition when the ratio $C_{sur}/C_{ped} > 1$ (top abscissa values greater than 1 in Figure 3, lower abscissa values > 1 in Figure 4, and easily seen in the lower right panel of Figure 2).

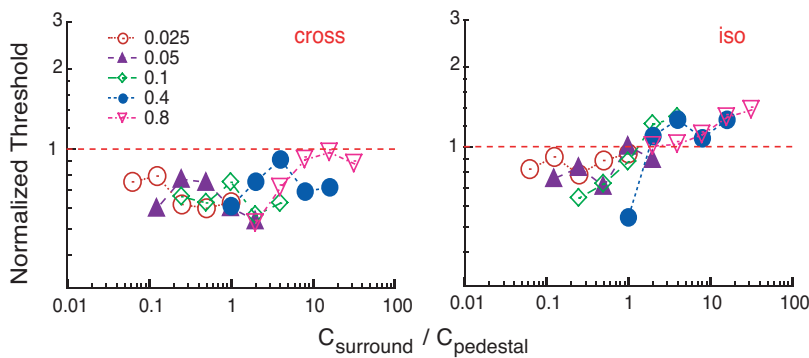


Figure 4. Cross and iso surround modulation as a function of surround/pedestal contrast ratio (C_{sur}/C_{ped}). Data are grouped in cross and iso panels. Each panel contains functions at five surround contrasts. Mean contrast thresholds are normalized by mean baseline values, so that data points above 1 indicate suppression and below 1 indicate facilitation.

Cross- and Iso-surround Modulation versus Surround/Pedestal Contrast Ratio

Cross and iso surround modulation can be summarized by plotting normalized mean contrast thresholds (i.e. threshold-with-surround/threshold-with-no-surround) against the surround/pedestal contrast ratio (C_{sur}/C_{ped}) (Figure 4). Clearly, cross-surrounds facilitate regardless of C_{sur}/C_{ped} , though facilitation tends to be stronger at a lower C_{sur}/C_{ped} . On the other hand, iso-surround modulation is dependent on C_{sur}/C_{ped} . As C_{sur}/C_{ped} increases, iso-surround modulation changes from facilitation to suppression. Iso-surrounds mainly produce facilitation when $C_{sur}/C_{ped} \leq 1$ and suppression when $C_{sur}/C_{ped} > 1$.

Data Fitting

In order to fit the TvC data we used a contrast response function (the d' function, Stromeier & Klein, 1974; Legge & Foley, 1980; Foley, 1994; Boynton, Demb, Glover, & Heeger, 1999; Chen & Tyler, 2001) to fit TvC data. This function can be written as:

$$d'(C) = \frac{KC^p}{(C_k^{p-w} + C^{p-w})} \quad (1)$$

We call this d' contrast response function the Stromeier-Foley function, in which C is the stimulus contrast, p is the log-log slope at low contrast, w is the log-log slope at high contrast, C_k is the contrast at the kink point where lines drawn through the high and low asymptotes intersect as seen in Figure 6a, and K controls the height of the function. A deeper exploration of the role each of the parameters plays in controlling the shape of the d' function and the TvC function is taken up in the Appendix.

The parameters of the d' function can be determined from contrast discrimination data such as shown in Figure 2. The connection between the d' function and the TvC function is given by:

$$d'(C_{ped} + C_{test}) - d'(C_{ped}) = 1 \quad (2)$$

where C_{ped} is the pedestal contrast and C_{test} is the test threshold in a contrast discrimination task.

When C_k is small compared to C as for the present data, Equation 1 becomes:

$$d'(C) \cong KC^w \quad (3)$$

Thus, K is approximately the d' value at 100% contrast. The connection of K to the high contrast Weber fraction is derived by keeping the leading terms of the Taylor's

expansion of Equations 2 and 3, based on the assumption that $\ll C_{ped}$.

$$1 = K((C_{ped} + C_{test})^w - C_{ped}^w) \approx Kw C_{ped}^{w-1} C_{test} \quad (4)$$

So the Weber fraction is given by:

$$C_{test}/C_{ped} = 1/(Kw C_{ped}^w) \quad (5)$$

At $C_{ped} = 1$ the Weber fraction is simply $1/Kw$. Equations 4 and 5 also illustrate that the log-log slope of the TvC function (C_{test} as a function of C_{ped}) is $1-w$. Thus the high contrast portion of the TvC function pins down the parameters K and w . A full understanding of the connection between C_{test} and C_{ped} in the TvC function depends on many factors including the nature of the underlying transducer function, the amount of uncertainty, early and late gain control, and the amount of additive and multiplicative noise. We present a simplified model of visual processing which includes each of these factors in the Appendix (Figure 7); for the present, we fit the data with the four parameter Stromeier-Foley function and look for systematic changes in the parameters produced by the iso and cross surrounds. In particular, we are interested in whether the Stromeier-Foley function can account for the surround effects on the basis of parameter changes, or whether additional factors need to be included.

Fitting Cross-surround Effects

We first used Equation 1 to fit cross-surround effects. The cross TvC functions at all six surround contrasts were fitted simultaneously via a nonlinear least square method (the Matlab lsqnonlin function). To reduce the number of parameters, we experimented by letting one parameter be a single value (the same for all surround contrast conditions) and the other three parameters be vectors (different values for different surround contrast conditions). The total number of parameters was $3*6+1 = 19$. The number of data points being fit was 36. The goodness of the fit, chi square (χ^2), was the lowest ($\chi^2 = 28.4$, $df = 17$) when p was a single value. The χ^2 was reduced when all four parameters were allowed to float ($\chi^2 = 23.2$), but the values of parameters became unstable due to the high correlation between p and other parameters. In addition, the reduction of chi square from 28.4 to 23.2 was insufficient to justify the five extra parameters.

The fitted values of K , C_k , and w are plotted against the surround contrast in Figure 5 (p has a single value across the six surround contrasts), as are values of $1/wK$ (approximately the Weber fraction at $C = 1.0$ as shown in Equation 5). The error bars on the parameters estimates are based on the variance output by the lsqnonlin program (without making the reduced chi square

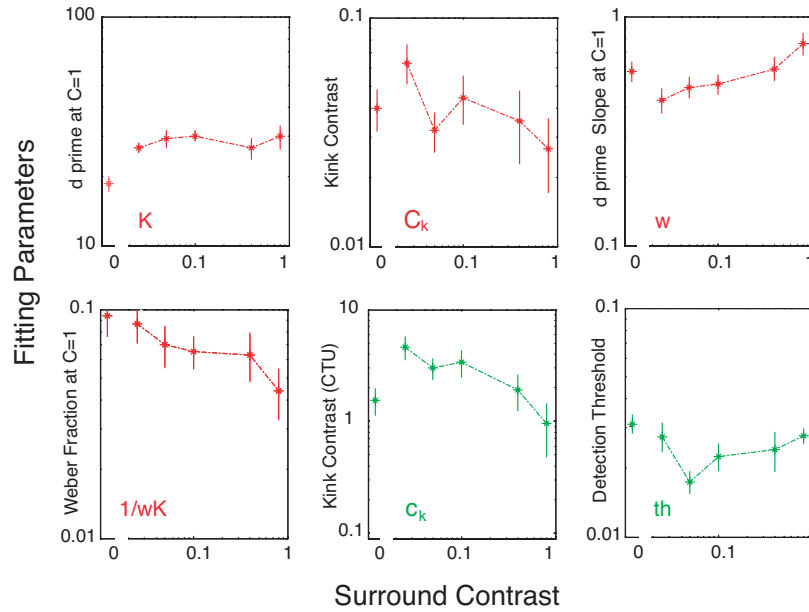


Figure 5. Fitting results for cross modulation data using Equation 1. The three parameters K , w , C_k and the combination $1/wK$ are shown as functions of the surround contrast. The fourth parameter p in the data fitting was constrained to be the same value at all cross surround contrasts ($p=2.27$). See Appendix for explanations of the additional panels (c_k & th). CTU: Contrast threshold unit

heterogeneity correction), except for error bars of $1/wK$ that were calculated with a Monte Carlo simulation based on the standard errors of w and K . The d' functions associated with these parameter values are also shown (Figure 6).

The Stromeyer-Foley function generally captures the properties of cross surround modulation (Figure 2, left column, solid red lines) quite well. As shown in Figure 5, K is nearly equally raised at all surround contrasts,

indicating that a cross surround at any (visible) contrast improves the gain. A more detailed analysis in the Appendix will show that a raised K vertically lifts the Stromeyer-Foley function. However, such a gain change could occur at different stages of visual processing (Node 3 or 7 of Figure 7), so the exact mechanism underlying gain change cannot be unequivocally determined. The gain improvement is clearly a dominant effect of cross surround modulation at $C_{sur} = 0.1 \sim 0.4$. At very low and

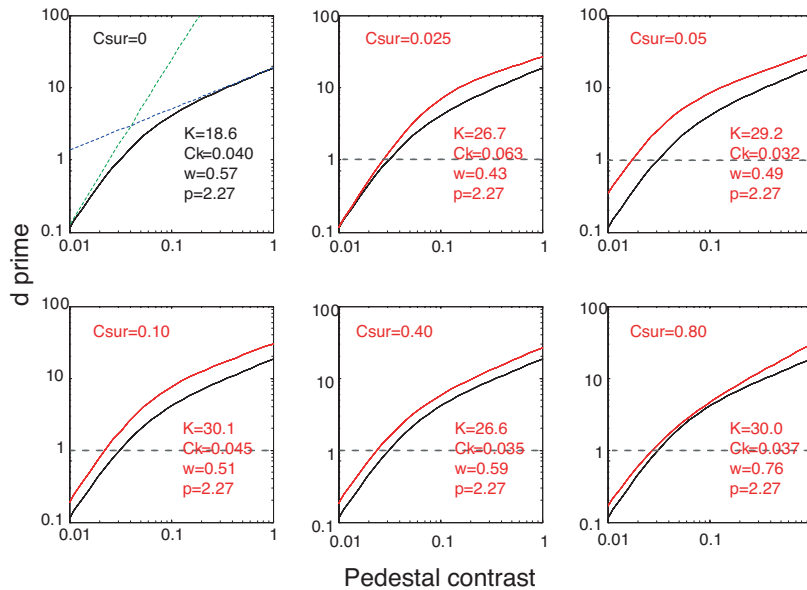


Figure 6. The d' functions at six cross surround contrasts constructed with fitted parameter values. In the upper left panel the two straight intersect at $C_k = 0.040$. The straight lines are asymptotes to the curved d' function.

seen at the highest surround contrast ($C_{sur} = 0.80$), probably as a result of multiplicative noise induced by high-contrast surround stimuli (discussed below).

Discussion

In this study we systematically measured cross- and iso-surround modulation of the TvC function over a wide range of surround contrasts. Cross-surround facilitation is evident across the entire TvC function. Iso-surround modulation of the TvC function is dependent on the relative contrast (C_{sur}/C_{ped}), being facilitative when $C_{sur}/C_{ped} \leq 1$ and suppressive when $C_{sur}/C_{ped} > 1$. Data fitting indicates that cross-surround modulation (facilitation) can be reasonably accounted for by changes in the Stromeier-Foley d' function, mainly a raised gain, except at very low and high surround contrasts. Iso-surround modulation on the other hand is more complicated, probably reflecting more than one process and is affected by the relative contrast.

Constraining the explanations for surround modulation. Our experimental results and data fitting suggest that surround modulation of contrast response is a complex process and is influenced by the surround contrast (cross) or relative contrast (iso). The contrast response function is varied differently by surrounds at different contrasts. This complexity is not captured by many previous (including our own) studies in which limited surround contrasts (often a single surround contrast) are used (e.g., Snowden & Hammett, 1998; Chen & Tyler, 2001). In these studies, results are often simpler and can be more smoothly fit to support authors' models. The trade-off is that these models may not be properly constrained and have limited application.

The original motive of the current study, as well as many other studies, is to pin down the underlying (psychophysical) mechanisms of surround modulation. However, this worthwhile goal is compromised by the complex nature of visual processing. As the Appendix details, multiple mechanisms at different stages of visual processing could be responsible for the change of a single parameter in the d' function. For example, a raised gain due to cross surround modulation could equally possibly occur at different stages of visual processing, even within the frame of our simple model. Similarly, a reduced high-contrast slope of the TvC function ($1-w$) could indicate either a change of saturation or gain control of the transducer, or increased stimulus dependent multiplicative noise. These multiple possibilities suggest that data fitting does not provide sufficient power to fully constrain the psychophysical mechanisms of surround modulation.

On the other hand, data fitting does help discount some possible mechanisms and constrain the explanation. Specific to our cross data, we can eliminate two possible explanations. First, nice fits are obtained with a single p

(the low-contrast slope) across surround contrasts. A change of p would indicate a change of uncertainty due to cross surround modulation. Indeed, the effects of cross-surrounds seen in Figure 2 do not resemble the pattern seen in Figure 8b which simulates the TvC function changes that would occur if p varies. Thus it is unlikely that the surround produces facilitation through an uncertainty reduction mechanism. Elsewhere, we (Yu, Klein & Levi, 2002) provided experimental evidence that the cross facilitation of detection cannot be fully explained by uncertainty reduction. One of these arguments is that the bottom of the dipper of the unflanked TvC curve can be strongly facilitated by the cross-oriented surrounds (see Figure 2). Uncertainty reduction is unlikely to account for the surround's facilitation of the dipper regime since the presence of the

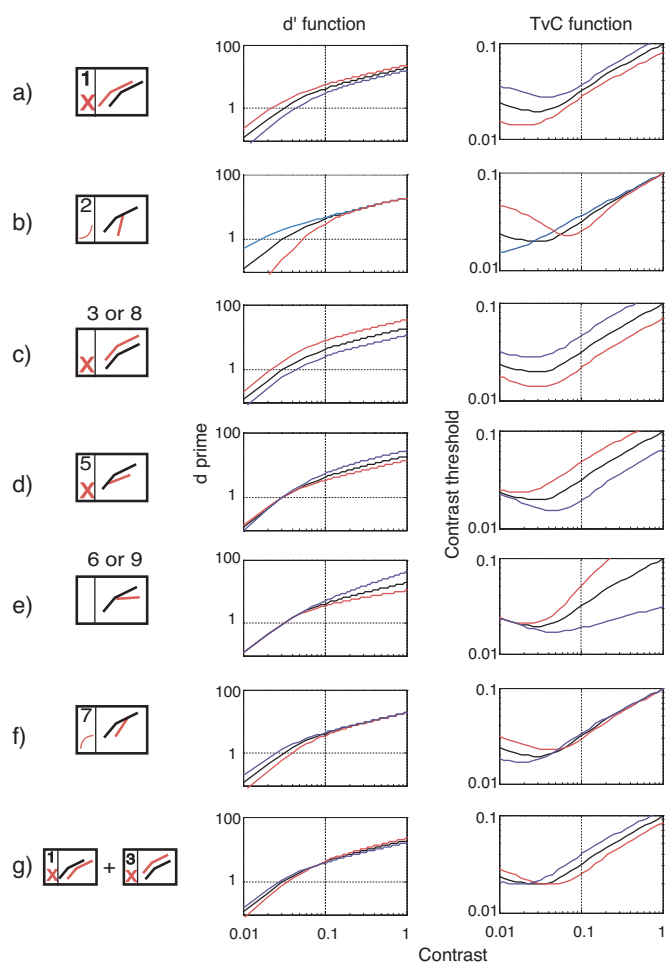


Figure 8. Nodes in Figure 7 are presented individually (left column) along with their associated d' functions (middle column) and TvC functions (right column). The d' and TvC functions in black color are identical across all rows. Other d' and TvC functions in red and blue colors simulate the effects of parameter changes.

pedestal should have minimized the uncertainty so there wouldn't be any uncertainty for the surround to minimize.

Secondly, contrast masking is often attributed to pooled divisive inhibition (Malik & Perona, 1990; Heeger, 1992; Albrecht & Geisler, 1991; Foley, 1994). This divisive pooling varies the saturation point C_k in Equation 1 and shifts the log-log d' curve diagonally approximately in the direction of the high contrast slope (see Figure 8f). If cross surrounds modulate contrast responses by solely manipulating the gain control pool, it would effectively change the value of C_k in the denominator of Equation 1. However, our data fitting indicates that a significant change of the value of C_k only occurs at very low and high surround contrasts, discounting the single gain control pool idea as a full explanation for cross-surround modulation.

Surround Modulation & the Westheimer Function

Our pedestals are slightly larger than the D6 target to approximately cover the full extent of the underlying receptive field center (or “perceptive field center” in a psychophysical sense) and to maximize masking (Westheimer, 1967; Yu & Essock, 1996; Yu & Levi, 1997). Thus, at high pedestal contrasts both cross- and iso- surround facilitation can be at least partially understood as variations of the Westheimer sensitization effect (Yu & Levi, 1997, 1998, 2000). That is, stimulation by a surround outside the perceptive field center could elicit antagonistic inputs that discount masking or desensitization. Similar iso-facilitation outside a central area larger than the stimulus is also reported by Adini and Sagi (2001). Adini and Sagi (2001) hypothesized that this facilitation effect reflects part of the dynamics of excitatory-inhibitory recurrent networks. This is consistent with our observations that iso- and cross facilitation takes around 70-100 msec to develop and therefore may reflect some intra-cortical feedback process (Yu & Levi, 1999; unpublished data).

The advantage of using an optimized pedestal (larger than the test) is that one obtains strong masking and surround effects. The disadvantage is that these effects may not be general. Snowden & Hammett (1998) measured iso TvC function with a pedestal matched to the test plus an annular grating surround at $C_{sur} = 0.48$. They reported that this high contrast iso-surround suppresses low contrast ($C_{ped} \leq 0.10$) discrimination but does not affect detection ($C_{ped} = 0$) or high contrast discrimination ($C_{ped} > 0.10$). These data are similar to ours at $C_{sur} = 0.40$ (Figure 2, row d), except that significant facilitation is shown in our data at high pedestal contrasts. A key difference is that Snowden and Hammett's target and pedestal were matched in size, while we used a larger pedestal that approaches the limits of the underlying perceptive field. Under their stimulus

conditions, the abutting iso-surround actually covers part of the perceptive field center as well as the antagonistic surround. The resulting mutual cancellation would diminish facilitation. Snowden and Hammett (1998) made the assumption that (iso) surround modulation is a variation of regular masking, and high contrast surrounds would act as low contrast pedestals because of the separation. This assumption would not predict the iso-surround facilitation shown in our experiments, since the presence of iso-surrounds would be equivalent to a small increase of the supra-threshold pedestal contrast, which would lead to slightly elevated contrast thresholds, rather than significant facilitation.

Appendix

The Stromeyer-Foley (S-F) Function and the Underlying Visual Processing

The Stromeyer-Foley (S-F) function does a reasonably good job of fitting the cross-orientation data. Below we discuss two aspects of the S-F function: (a) how the four parameters of the S-F function are estimated by the TvC data, (b) how the parameters could be determined by different nonlinearities or noise sources in a model of visual processing.

How the data fixes the four parameters of the S-F function

We have shown earlier that the Stromeyer-Foley d' function can be written as:

$$d'(C) = \frac{KC^p}{(C_k^{p-w} + C^{p-w})}. \quad (1)$$

Besides Equation 1, the function can also be written in terms of the detection threshold:

$$d' = \frac{(1 + c_k^{p-w})c^p}{(c_k^{p-w} + c^{p-w})}. \quad (6)$$

Here c and c_k are the contrasts C and C_k from Equation 1 expressed in threshold units ($c = C/th$; $c_k = C_k/th$). c_k is the contrast at which the denominator doubles. The parameters p and w are the same as in Equation 1. The detection threshold, th , is defined to be the contrast giving $d'=1$, as can be seen by setting $c = 1$ ($C = th$) in Equation 6. The connection between K and th , obtained by equating Equation 1 and 6, is:

$$K = (1 + c_k^{p-w})/th^w \quad (7)$$

The S-F function is characterized by four parameters: p , w , K and C_k in Equation 1 or p , w , th and c_k in Equation 6. The parameters th and p are determined by the low pedestal contrast region of the TvC curve, with th being the threshold ($d' = 1$) for zero pedestal contrast and

p being the slope of the log-log d' function at low pedestal contrasts. The parameters K and w are determined by the large pedestal contrast region of the TvC curve with $1-w$ being the log-log slope of the TvC function (see Equation 5) and $1/Kw$ being the test contrast for $C_{ped} = 1.0$ (see Equation 5) under the assumption that $C_k \ll 1.0$, as is typical for spatial frequencies below about 15 c/deg. For the parameters of the unflanked condition (see Figure 6), the jnd at a 100% pedestal ($C = 1.0$) is $1/Kw = 1/(18.6 \cdot 0.57) = 0.094$. A test contrast of 9.5% at a 100% pedestal gives a Weber fraction of 0.094, a reasonable value at high pedestal contrasts. Another way of looking at these numbers is that a 9.4% test contrast together with the high contrast TvC slope of $w = 0.57$ gives $K = 1/(0.094 \cdot 0.57) = 18.6$. K is approximately the d' at $C = 1.0$. This means that there are approximately $K = 19$ jnds from zero contrast to 100% contrast.

The parameter C_k can be calculated from the parameters th , p , K and w using Equation 7. C_k can also be determined graphically by drawing two straight lines on the log-log d' function that match the high and low contrast asymptotic regions as shown in Figure 6a. C_k is the pedestal contrast where the two asymptotic lines intersect. It specifies the region where the d' slope changes from p to w .

How the four parameters of the S-F function are determined by the underlying visual processing

Figure 7 shows a simplified model of visual processing that consists of three stages: Early processing stage (Nodes 1 & 2), intermediate processing stage including an excitatory branch (Nodes 3 & 4) and a divisive inhibitory branch (Nodes 5, 6 & 7), and an output stage (Nodes 8 & 9). Each of the nine nodes indicates where a nonlinearity or gain control process could be influenced by the surround. A detailed discussion of each node will be presented in conjunction with Figure 8; here we present an overview of the nodes. Nodes 1, 3, 5 and 8 represent gain control mechanisms where the signal gets multiplied by a constant, i.e. output = constant * input. Node 1 is in the early stage and affects threshold, th . Nodes 3 (excitatory branch of intermediate processing) and 8 (output), control the output scale factor, K . Node 5, in the divisive inhibitory branch of intermediate processing will be seen to affect the high contrast region of the d' function. Nodes 2, 4 and 6 correspond to power law nonlinearities in their respective branches of the model, i.e. output = input^{power}. Node 7 corresponds to an additive gain control that affects the saturation point of the divisive inhibition branch of the model. This node corresponds to the pooled gain control found in many models of cortical processing, as will be discussed. Node 9 is multiplicative output noise.

In the lower left corner of each node in Figure 7 is one of four symbols representing the action performed at that node: (a) An X (nodes 1, 3, 5 and 8) represents a gain

control stage where the signal is multiplied by a constant. (b) An accelerating curve (nodes 2, 4 and 6) represents a nonlinearity where the output is a power function of the input ($y = x^a$). (c) A decelerating curve (node 7) represents a saturating stage. For example, the surround could contribute to a gain control pool that adds a constant to the denominator of the S-F function. Even without a surround there would be a semi-saturation constant contributing to the denominator. (d) A letter "N" (node 9) represents multiplicative noise at the output. The multiplicative nature of this noise will reduce the log-log slope of the d' function at high contrasts.

The right side of each node shows how the S-F function is altered at each node. The S-F function is represented by a broken line where the break is at C_k with the slopes of the two line segments given by p and w , and the height of the lines given by K or th . A pair of broken lines are shown in each node representing how the surround can alter the S-F function by modulating that node. The black lines are identical across all nodes and set the baseline, and red lines show how the S-F function is changed by surround influence. For a multiplicative node the surround would modify the gain at that stage. For a nonlinear node the surround would change the power exponent. For the additive gain control pooling node 7 the presence of the surround would give an additive contribution at that node. For the output noise node 9, the surround could suppress or enhance the noise. The division sign between nodes 4 and 8 represents the divisive inhibition typical of feed-forward gain control models.

We now discuss how a surround can modify specific parameters of the S-F function. To illustrate these effects Figure 8 shows separate nodes from Figure 7 (left panel) and associated plots of the S-F function (middle panels) and TvC function (right panels). The middle of the three curves in each S-F or TvC panel is the S-F or TvC function with parameters that best fit our unflanked averaged data: $p=2.27$, $w = 0.57$ (or $q = p-w = 1.70$), $K=18.4$, $C_k=0.040$ (corresponding to $th = 0.031$ and $c_k = 1.29$). The other two curves shown in red and blue correspond to the S-F and TvC functions with specific model parameters decreased and increased by a factor of $\sqrt{2}$ except as discussed below.

Figure 8a shows the effect of a gain control modulation at node 1, producing a change in threshold, th , in Equation 6, while fixing p , w , and c_k . This manipulation of parameters shifts the d' curve horizontally. The TvC curve (right panel) shows a downward shift which is greater at low contrast than at high, similar to the effect of a low contrast cross surround as seen in the second and third panels of Figure 2 (also see Figure 6 for d' function change).

Figure 8b shows the effect of a modification in node 2. The main effect is to change p , the log-log slope at low contrast. The semi-saturation contrast, C_k is also altered. It is interesting that the high contrast portions of the S-F

curves including parameters K are unchanged. This is because the signal is altered in both the numerator and denominator of the S-F function. There has been a long-standing debate over whether the low contrast facilitation associated with $p > 1$ is caused by uncertainty reduction when a pedestal is present or by an accelerating transducer function (Legge, Kersten, & Burgess, 1987). An increase of stimulus uncertainty depresses the d' function at low contrast while leaving it unchanged at high contrast, precisely as is seen in Figure 8b. A similar effect is obtained by a change of exponent at node 2 in Figure 7 giving a d' function whose p dependence is:

$$d' = K C^p / (b + C^{p-w}) \quad (8)$$

This form of the d' function, in which a fixed b has replaced C_k^{p-w} of Equation 1, would have C_k change as p is varied. The effects of cross-surrounds seen in Figure 2 do not resemble the pattern seen in Figure 8b so it is unlikely that the surround produces facilitation through an uncertainty reduction mechanism or through a node 2 mechanism.

A comparison of the blue and black curves in Figure 8b provides a good example of the seemingly paradoxical finding that inhibition can produce facilitation. In the d' function the red curve is reduced compared to the baseline black curve, indicating higher uncertainty or suppression at low contrast. Indeed this suppression raises the detection threshold substantially, as seen at the leftmost portion of the TvC function (the right panel). However, there is a crossover whereby for pedestal contrasts above 6% the d' suppression results in contrast discrimination facilitation, such that the red curve is below the black curve. This result occurs because the suppression at low d' steepens the d' function at medium contrasts as occurs with iso surround inhibition. Another mechanism for crossover will be discussed in connection with Figure 8g.

Figure 8c shows the effect of a modification at either node 3 or 8 of Figure 7, producing a change in K in Equation 1 without changing p , w , and C_k . This manipulation of parameters simply shifts the log-log d' curve vertically. Figure 5 shows that one of the clearest effects of a cross surround of any contrast is to produce an increase in K , which is a dominant change in the middle region of cross surround contrasts (10%-40%). However, at very low and high surround contrasts K is not the only parameter that is affected by the surround.

Figure 8d shows the effect of altering the gain control at node 5. This manipulation shifts the log-log d' curve diagonally in the direction of the low contrast slope. Node 5 is on the branch of the model that affects the denominator of Equation 1 and Equation 6. Chen and Tyler (2001) use this as one of their sites of gain control. By attenuating the signal portion of that branch there is minimal effect at very small signal strength as shown in

Figure 8d. This is the type of shift that is seen in the iso surround data of Figure 2 at low surround contrasts.

Figure 8e shows the effect of a change in either node 6 or node 9. The effect here is on w , the log-log slope at high contrast while leaving unchanged th and p , the low contrast parameters of Equation 6, and also c_k , the log-log break point in threshold units. The TvC function, shown in the right panel of Figure 8e has a high contrast log-log slope of $1-w$ (as discussed following Equation 3), thus the slope of the right hand side of the TvC changes, similar to the effect of an 0.8 contrast cross surround (Figure 2 bottom panel, also see Figure 6). There are two general explanations of factors controlling w : transducer saturation (node 6) or stimulus dependent (multiplicative) noise (node 9). The approach taken in this paper is largely agnostic on this topic since one could argue that the denominator of the Stromeyer-Foley function could come either from saturation (or gain control) of the transducer function or it could come from multiplicative noise. Foley (1994) associates the threshold elevation of the TvC function at high contrasts with a divisive gain control of the contrast response function. Stromeyer and Klein (1974), on the other hand, fit the increasing contrast discrimination threshold at high pedestal contrasts using multiplicative noise. Kontsevich, Chen, & Tyler (2002) present data and arguments in favor of the multiplicative noise explanation. Based on unpublished data, we conclude that both factors (a saturating transducer function plus multiplicative noise) strongly contribute to the shape of the d' function at large pedestal contrasts. For simplicity, in the present article we do not introduce multiplicative noise (it would slightly modify the S-F function with a Pythagorean sum of the various noise sources in the S-F denominator), but it is important to keep in mind that such noise could well play an important role in suprathreshold discrimination. The connection of this discussion to the effect of the surround on the parameters shown in Figure 5 is that the presence of a low contrast surround could suppress the multiplicative noise, thereby reducing w .

Figure 8f shows the effect of varying the saturation point, C_k in Equation 1, by a modification at node 7. This manipulation shifts the log-log d' curve diagonally approximately in the direction of the high contrast slope. This is the model of pooled divisive inhibition proposed by Malik & Perona (1990), Heeger (1992), Albrecht & Geisler (1991) and Foley (1994). In this proposal the surround would add to the gain pool at node 7, effectively increasing the value of C_k in the denominator of Equation 1. Figure 8f shows that this manipulation has a sizeable effect on the low contrast region but minimal effect at high pedestals of both the d' and the TvC functions. Since this is not what is seen in our cross-surround data, we can discount the single gain control pool idea as a full explanation for the effect of cross-oriented surrounds. However, in the iso-surround case we do see strong examples of extra inhibition at low pedestal

contrasts when the surround contrast is high. This is precisely what is expected for the standard gain control (or noise intrusion) shown in [Figure 8f](#).

As our final example, [Figure 8g](#) shows that by combining a shift downward plus an equal shift leftward one can produce an approximately leftward shift of the TvC function. This type of shift has been reported by [Chen & Tyler \(2001\)](#), but it is not seen in our data. There is an ambiguity as to which nodes are involved in producing the shifts seen in [Figures 8g](#) as well as [8a, c and d](#), since there are four nodes (1, 3, 5 and 8) that produce translations in different directions, but a general translation can be represented by just two parameters.

A similar ambiguity is present for the slope parameters, p and w . Node 4 just affects the slope of the branch in the numerator, thereby altering both the low and the high contrast slopes (not shown in [Figure 8](#)). Since there are four nodes (2, 4, 6, 9) that affect the two slope parameters, the present experiments are unable to pin down the nodes where the surround modifies the slope. As was discussed earlier in connection with [Figure 5](#), the surround had minimal effect on p and only a small effect on w .

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