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Measurement and modeling of center-surround suppression and enhancement

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Abstract

The apparent contrast of a central stimulus is affected by the presence of surrounding stimuli. For some stimulus conditions, the apparent contrast is suppressed and for other conditions the apparent contrast is enhanced. This report is intended to offer a coherent description of the stimulus factors that influence suppression and enhancement. Using a contrast-matching protocol, we measured the contrast dependence of center-surround interactions by systematically varying the suprathreshold contrasts of the central and surround gratings. Different spatial configurations of the surround stimuli were studied. Our results confirmed previous findings that (1) a surround stimulus could produce either contrast enhancement or contrast suppression depending on the balance of the central and surround contrasts; (2) suppression varied with the width of the surround stimulus and was strongly orientation-specific; and (3) enhancement was less sensitive to changes in surround configurations (in particular, enhancement did not depend on the colinearity of the central and surround gratings). Based on the experimental data, we developed a computational model to account for center-surround suppression and enhancement.

Keywords: Contrast; Matching; Suppression; Enhancement; Lateral interactions

1. Introduction

The apparent contrast of a visual stimulus is affected by neighboring stimuli. The presence of a surround stimulus can suppress or enhance the apparent contrast of a central patch of texture. When contrast is suppressed, for example, the bright points of the central texture patch appear dimmer and its dark points appear lighter (Chubb, Sperling, & Solomon, 1989; Cannon & Fullenkamp, 1991, 1993, 1996; Ejima & Takahashi, 1985; Snowden & Hammett, 1998).

The stimulus factors that influence contrast suppression and enhancement for suprathreshold stimuli have been studied primarily using contrast-matching tasks. The relative contrasts of the central and surround stimuli are critical, such that suppression occurs when the surround contrast is higher than the central contrast, and enhancement occurs when the surround contrast is lower than the central contrast (Ejima & Takahashi, 1985; Cannon & Fullenkamp, 1993). The effect of the surround can also be varied from suppression to enhancement by changing the size of the surround (Cannon & Fullenkamp, 1993). Takeuchi and DeValois (2000) recently reported that contrast enhancement occurred when the surround moved at a higher speed than the center. Some have reported that enhancement depends on the relative phase of central and surround gratings (Ejima & Takahashi, 1985), although others have reported that not to be the case (Solomon, Sperling, & Chubb, 1993). There are notable individual differences in the strength of the enhancement (Cannon & Fullenkamp, 1993). Contrast suppression depends on the relative orientations and spatial frequencies of the central and surround stimuli (Chubb et al., 1989; Solomon et al., 1993).

The detectability and discriminability of a central stimulus patch can also be affected by neighboring stimuli (Sagi & Hochstein, 1985; Polat & Sagi, 1993, 1994; Zenger & Sagi, 1996; Snowden & Hammett, 1998; Bonneh & Sagi, 1998; Polat, 1999; Solomon & Morgan,

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2000). A surround can cause suppression (i.e., increased thresholds) or facilitation (i.e., decreased thresholds). Facilitation at target threshold depends on the precise collinear alignment of the center and surround (Polat & Sagi, 1993; Polat, 1999; Solomon, Waston, & Morgan, 1999).

Analogous effects have been observed in electrophysiological recordings from neurons in visual cortex. For example, Levitt and Lund (1997) demonstrated that the responses to a stimulus placed within a V1 neuron's receptive field can be either increased or decreased by adding a stimulus in the region surrounding the receptive field. Critically, as in some of the perceptual studies cited above, they reported suppression when the surround contrast was higher than the central contrast. Several studies have reported, in agreement with the other perceptual studies cited above, that enhancement depends on the precise spatial configuration (i.e., collinearity) of the surround (Kapadia, Ito, Gilbert, & Westheimer, 1995; Toth et al., 1996; Polat & Norcia, 1996, 1998; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998).

Several computational models have been proposed to account for the center-surround effects observed both physiologically and psychophysically. Heeger (1992) proposed a normalization model to describe the suppression of neural responses in primary visual cortex. According to the model, a neuron's response is divided by a quantity proportional to the pooled activity of a large number of other neurons from the nearby cortical neighborhood. Foley (1994) adapted this model to fit psychophysical measurements of contrast discrimination. Cannon and Fullenkamp (1996) and Snowden and Hammett (1998) proposed related models for characterizing the perception of a central stimulus in the presence of a surround. None of these models, however, predict that contrast enhancement could occur in the presence of a surround stimulus. Zenger and Sagi (1996) used an accelerating transducer function to account for the observed facilitation in their threshold detection measurements. Polat (1999) and Solomon and Morgan (2000) proposed models based on collinear lateral excitation and non-selective lateral inhibition to explain facilitation at contrast threshold. These models do not, however, purport to explain contrast enhancement at suprathreshold contrasts.

The factors that appear to influence center-surround interactions (relative center and surround contrasts, relative phase/collinearity, width of surround, relative orientations, spatial frequencies, and speeds, threshold vs. suprathreshold, individual differences) are not mutually exclusive. It is possible that they all contribute to contrast enhancement and suppression. The goals of this study were (1) to gain a coherent description of some of the stimulus factors that influence suppression and enhancement, by replicating some of the previous findings, and (2) to develop a model to account for these interactions. We used a contrast-matching task that allowed us to study center-surround interactions at suprathreshold contrasts.

2. Methods

2.1. Subjects

One of the authors and one additional subject were tested. The latter was naive about the purpose of the experiment. Both subjects had normal or corrected-to-normal vision.

2.2. Visual stimuli

Subjects compared the contrast of an isolated, contrast-reversing (8 Hz) sine-grating patch (Fig. 1a) with the contrast of the same patch embedded in surround gratings (Fig. 1b). Beyond the gratings, the screen was a uniform gray field of equal mean luminance (36.2 cpd/m^2). A small (0.3°), high contrast square at the center of the stimulus served as a fixation mark. Grat-

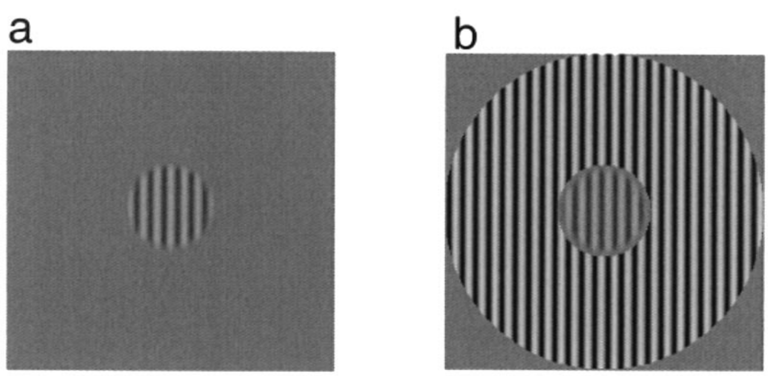

Fig. 1. Visual stimuli. (a) Isolated central patch and (b) Center-surround stimulus. A narrow gap separates the central and the surround patches. The embedded central patch is physically the same as the isolated patch, but it is perceived to have a lower contrast.

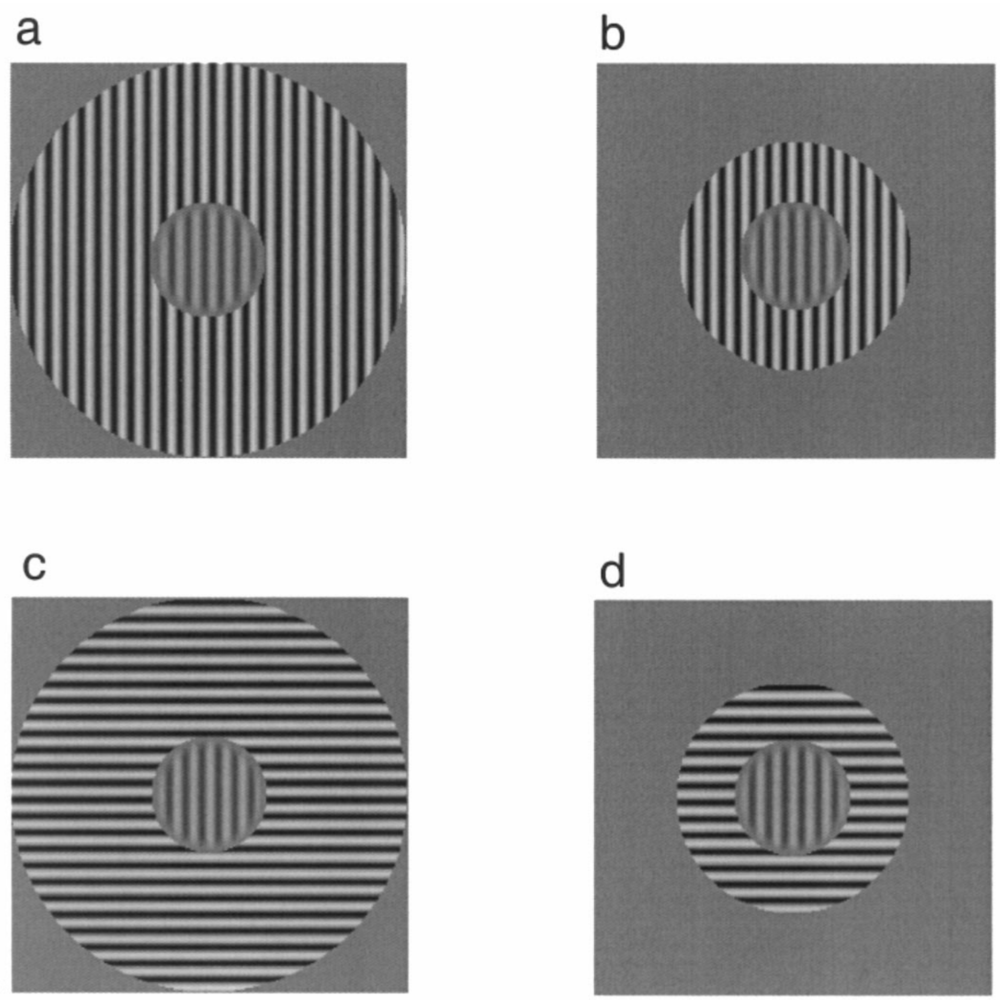

Fig. 2. The four tested configurations of center-surround stimuli. (a,b) The central and surround gratings are parallel. (a) Wide-Surround and (b) Narrow-Surround. (c,d) The central and surround gratings are orthogonal. (c) Wide-Surround and (d) Narrow-Surround.

ing contrast was defined in the usual way, $C = (L_{\max} - L_{\min})/(L_{\max} + L_{\min})$, where $L_{\max}$ and $L_{\min}$ were the maximal and minimal luminances, respectively. Unless specified otherwise, the spatial phases of the central and surround gratings differed by 180°. A small gap was introduced between the central patch and the surround to help the subjects to focus their contrast judgments only on the central patch. To avoid an edge artifact, the gratings were windowed by half a cycle of a raised cosine function so that the contrasts near the gap smoothly decreased to zero.

The spatial configuration of the central patch was fixed in all experiments while that of the surround patch varied. The spatial frequency of the gratings was 2 cpd. The diameter of the central patch was 3.5°; thus, the central patch had ~ 7 cycles of gratings. The central gratings were oriented vertically. Four different surround patterns were used with different sizes and orientations (Fig. 2). (1) In the Wide-Surround configuration (Fig. 2a), the surround gratings were vertical, i.e., parallel to the central gratings. The surround patch had a diameter of 12°, i.e., ~ 8 additional cycles of gratings on each side of the central patch. From previous psychophysical studies, we know that this covers nearly the entire zone of suppressive interactions (Cannon & Fullenkamp, 1996). (2) In the Narrow-Surround configuration (Fig. 2b), the surround gratings were again vertical, but had a diameter of 7°. Thus, it had ~ 3 cycles of gratings on each side. (3) The Orthog-Wide-Surround configuration (Fig. 2c) was the same as the Wide-Surround configuration except that the surround gratings were horizontal, orthogonal to the central ones. (4) The Orthog-Narrow-Surround configuration (Fig. 2d) was the same as the Narrow-Surround configuration except that the surround gratings were orthogonal to the central ones.

2.3. Experimental procedures

Each trial of the two-interval-forced choice task consisted of two 500 ms stimulus intervals that were separated by a 300 ms blank interval. The isolated grating patch was displayed in one stimulus interval and the center-surround stimulus was displayed in the other interval (in fully randomized order). Subjects pressed one of two buttons to indicate the interval that appeared to have higher central contrast. The screen was a uniform gray field, except for the fixation point, during both the blank and response intervals. No feedback was provided. Subjects were instructed to pay attention only to the central grating patches in making their judgments.

The matching contrast of the embedded central patch was determined using a double random staircase procedure. The physical contrast of the embedded patch, called the test contrast C_t, was constant. The contrast of the isolated central patch, called the matching contrast C_m, varied across trials. Each staircase block consisted of 40 trials. When the subject reported that the isolated patch had a higher contrast than the embedded patch, the matching contrast was decreased by one step in the next trial. If the subject reported a lower contrast for the isolated patch, the matching contrast was increased by one step. After the first few trials, the matching contrast typically alternated between the step values at which the isolated central patch appeared to have about the same contrast as the embedded patch. At the end of the block, the resulting psychometric function was fit with a log cumulative normal function using a maximum likelihood fitting procedure (Watson, 1979). The final measured matching contrast was the contrast that yielded 50% probability in the fitted psychometric function, that is the performance level to which the one-down, one-up staircase converges. We report the mean of five repeats of each condition. We quantified the variability in the psychophysical data as the standard error of the mean of the five repeats.

2.4. Model equations

Contrast response functions for grating stimuli, measured electrophysiologically and inferred from psychophysics, have been fitted using equations of the following form

$$R_m = \frac{kC_m^p}{(1 + aC_m^q)}, \tag{1}$$

where R_m is the response (firing rate), C_m is the contrast of an isolated grating patch, a, p and q are free parameters and k is a constant. At low contrasts, Eq. (1) can be approximated by: $R \propto C_m^p$. At higher contrasts, it can be approximated by: $R \propto C_m^{(p-q)}$.

We extended Eq. (1) to include surround suppression. According to Heeger's normalization model, a visual response is normalized by the pooled activity from neighboring neurons. Thus, we have the following equation to describe surround suppression

$$R_t = \frac{kC_t^p}{(1 + aC_t^q + W_i C_s^{qi})}, \tag{2}$$

where R_t is the response to a central stimulus, C_t is the central contrast, C_s is the surround contrast, W_i is the suppression weight, and q_i is the exponent of the surround suppression.

Next, we extended the model to include surround enhancement. Initially, we included both multiplicative and additive enhancement

$$R_t = \frac{k((1 + W_e C_s^{pe})C_t^p + W_{e2} C_s^{pe2})}{(1 + aC_t^q + W_i C_s^{qi})}, \tag{3}$$

where $(1 + W_e C_s^{pe})$ is the multiplicative excitation and $W_{e2} C_s^{pe2}$ is the additive excitation. Later, we found that additive excitation was not needed; the best fit values for the parameter W_{e2} were very close to zero for each of the eight sets of data (four surround configurations for each of two subjects). Therefore, we dropped additive excitation from the model. The final version of the model is

$$R_t = \frac{k(1 + W_e C_s^{pe})C_t^p}{(1 + aC_t^q + W_i C_s^{qi})}. \tag{4}$$

Note that Eq. (4) simplifies to Eq. (1) when the surround contrast (C_s) is zero. Additive excitation, although not needed to fit our suprathreshold contrast-matching data, might be needed to explain threshold facilitation for superimposed masking (Zenger & Sagi, 1996).

2.5. Model fitting procedure

In order to fit the model to the contrast-matching data, we assumed that the matching stimulus and test stimulus had the same contrast appearance when the contrast responses evoked by the two stimuli were equal. Thus, with C_m in Eq. (1) representing the matching contrast and C_t in Eq. (4) representing the test contrast, we have the following equation for an ideal contrast-match

$$R_m = R_t. \tag{5}$$

We used an iterative optimization algorithm (the simplex method) to search for parameter values that minimized

$$\Sigma \frac{(\hat{C}_m - C_m)^2}{SE^2}, \tag{6}$$

where SE is the standard error of the mean matching contrast, C_m is the measured matching contrast, and $\hat{C}_m$ is the predicted matching contrast given the model parameter values. There were seven parameters to be estimated: p, q, a, W_e, W_i, pe, qi. Due to the lack of measurements at very low central contrasts, this full set of parameters was not well-constrained by the data. In particular, we observed a trade-off between the a and p

parameters that resulted in approximately the same fitting accuracy. To simplify matters, we fixed $a = 0.01$, a value that is similar to what has been reported both by fitting psychophysical measurements of contrast discrimination (Foley, 1994; Boynton, Demb, Glover, & Heeger, 1999) and by fitting V1 contrast response measurements (Albrecht & Hamilton, 1982; Heeger, 1992; Carandini, Heeger, & Movshon, 1997).

Even with $a = 0.01$ fixed, the optimization algorithm was slow to converge. Hence, we fixed the values of p and q (along with a, these parameters determine the contrast responses when there is no surround stimulus) and searched for the best fitting values of W_e, W_i, p_e and q_i. This process was repeated for each of the eight data sets (four surround configurations for each of two subjects) in Figs. 3 and 4. Then the entire procedure was repeated for several different values of p and q, systematically varied over the range of values reported in previous studies (Foley, 1994; Boynton et al., 1999):

p: 1.7, 1.9, 2.1, 2.3, 2.5, 2.7, 2.9;

p–q: 0.3, 0.4, 0.5.

We observed that the best fitting values for p_e and q_i varied little across the eight data sets (two subjects, four stimulus configurations): p_e varied between 0.07–0.11, and q_i varied between 0.85–1.1. The fitting error was quite insensitive to the p_e and q_i parameter values within these ranges. Therefore, we fixed $p_e = 0.1$ and $q_i = 1$, so that, we could directly compare W_e and W_i, the weights of enhancement and suppression, respectively, across the four stimulus configurations.

In summary, the final model fits were computed with $a = 0.01$, $p_e = 0.1$ and $q_i = 1$ fixed across all eight data sets (four stimulus configurations, two subjects) and with p and q fixed for each subject (subject JX, $p = 2.3$, $q = 2$; subject ZP, $p = 2.4$, $q = 2.1$). Only W_e and W_i varied across the four stimulus configurations.

3. Results

3.1. Center-surround interactions with parallel surround gratings

This experiment examined the contrast-dependence of center-surround interactions when the surround gratings were parallel to the central gratings. We first examined the Wide-Surround configuration (Fig. 2a). We measured matching contrasts at four test contrasts ($C_t = 0.1$, 0.2, 0.4 and 0.8) and four surround contrasts ($C_s = 0.1$, 0.2, 0.4 and 0.8).

We computed a suppression ratio to quantify the strength of the center-surround interactions. The suppression ratio was defined as the matching contrast divided by the test contrast (C_m/C_t). A value of 1 for the suppression ratio means that the surround patch had no effect on the matching contrast of the central patch. Values less than 1 mean that the surround was

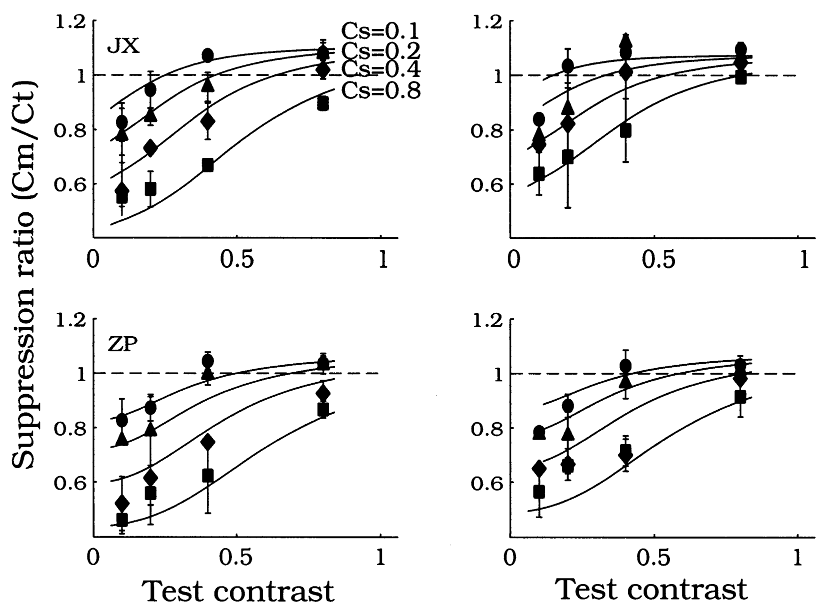

Fig. 3. Center-surround interactions with parallel surround gratings. In each panel, the horizontal axis indicates the test contrast and the vertical axis indicates the suppression ratio. The dashed horizontal line indicates a suppression ratio of 1, i.e., when the physical test and match contrasts are equal. Top row, subject JX. Bottom row, subject ZP. Left, Wide-Surround configuration. Right, Narrow-Surround configuration. Different plot symbols correspond to different surround contrasts (circles, $C_s = 0.1$; triangles, $C_s = 0.2$; diamonds, $C_s = 0.4$; squares, $C_s = 0.8$). The four curves represent the fitted suppression ratios from the model. Error bars represent ± 2 SEM. In some cases, the error bars are smaller than the plot symbols.

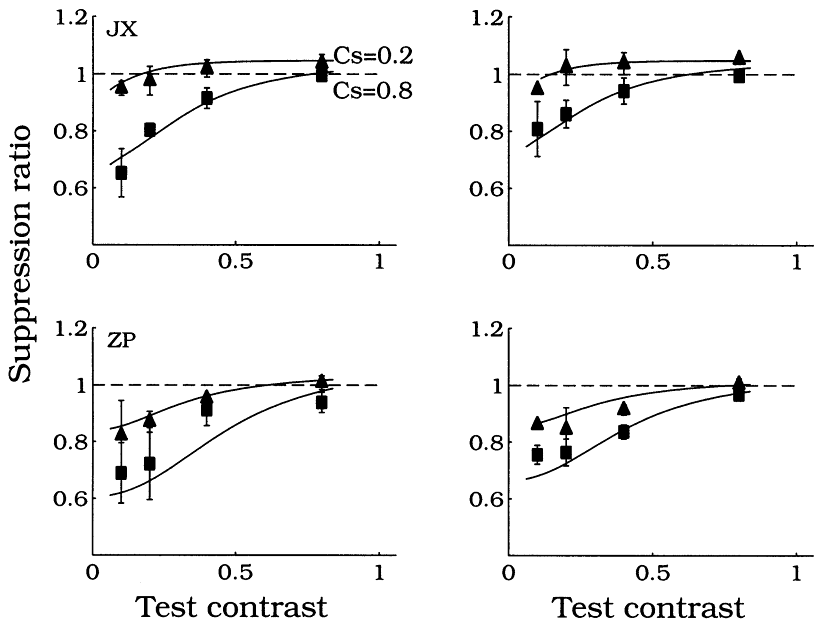

Fig. 4. Center-surround interactions with orthogonal surround gratings (same format as in Fig. 3). Left, Orthog-Wide-Surround configuration. Right, Orthog-Narrow-Surround configuration. Different plot symbols represent different surround contrasts (triangles, $C_s = 0.2$; squares, $C_s = 0.8$).

suppressive. A value of zero means that the matching contrast was completely suppressed by the presence of the surround. Values greater than 1 mean that the matching contrast was enhanced, i.e., higher than the test contrast.

The suppression ratios measured with the Wide-Surround pattern are shown in the left panels of Fig. 3. The upper-left panel of Fig. 3 is for subject JX and the lower-left panel is for subject ZP. The horizontal axis of each graph indicates the test contrast and the vertical axis indicates the suppression ratio. The dashed line indicates a suppression ratio of 1, i.e., where the physical contrasts of the test and match stimuli are equal. The different plot symbols correspond to the four-tested surround contrasts. The four curves represent the fitted suppression ratios from the model (see below).

The data indicate that the overall effect of the surround was suppressive because most plot symbols fell below the dashed line. The suppression increased with surround contrast; the highest tested surround contrast ($C_s = 0.8$, squares in Fig. 3) produced suppression ratios as low as ~ 0.4. The suppression decreased with increases in test contrast yielding enhancement when the test contrast was greater than the surround contrast. The enhancement was weak compared to the suppression. The largest enhancement gave a suppression ratio of 1.14. The enhancement, although weak compared to the suppression, was statistically significant ($P < 0.05$). These results suggest that the center-surround interactions depend on the central and surround contrasts and that the effect can be reversed simply by changing the balance of the two contrasts.

Next, we tested the contrast-dependence of center-surround interactions when the surround gratings were restricted to be close to the central patch (Narrow-Surround configuration, Fig. 2b). The results (right panels of Fig. 3) were similar in some ways to those obtained with the Wide-Surround configuration. The suppression increased with the surround contrast and decreased with the central contrast. The enhancement increased with the central contrast and decreased with the surround contrast.

The suppression, but not the enhancement, depended on surround width. Compared to the Wide-Surround configuration, the Narrow-Surround configuration produced less suppression, consistent with previous reports (Cannon & Fullenkamp, 1993). This reduction in suppression was more evident for subject JX than for subject ZP. The amount of enhancement, on the other hand, was about the same for both the Wide- and Narrow-Surround configurations. For subject JX, for example, the maximal suppression ratios were 1.15 and 1.12 for the Narrow- and Wide-Surround, respectively. The model fits (see below) supported the conclusion that enhancement was relatively insensitive to surround width.

3.2. Center-surround interactions with orthogonal surround gratings

In this experiment, we examined the contrast-dependence of center-surround interactions when the surround gratings were orthogonal to the central ones. We measured matching contrasts at four test contrasts ($C_t = 0.1, 0.2, 0.4, 0.8$) and two surround contrasts ($C_s = 0.2, 0.8$), using both wide surrounds (Orthog-Wide-Surround configuration, Fig. 2c) and narrow surrounds (Orthog-Narrow-Surround configuration, Fig. 2d).

The suppression produced by the Orthog-Wide-Surround configuration was markedly reduced compared to that produced by the parallel orientation Wide-Surround configuration, especially at low test contrasts (compare left panels of Fig. 4 with left panels of Fig. 3). For example, at $C_t = 0.2$ and $C_s = 0.8$ in subject JX, the suppression ratio produced by the parallel surround was 0.58, whereas, the suppression ratio produced by the orthogonal surround at the same test and surround contrasts was 0.8.

The enhancement, on the other hand, appeared to be less sensitive to changes in the surround orientation. At $C_t = 0.8$ and $C_s = 0.2$ in subject JX, for instance, the ratios produced with the parallel and orthogonal surrounds were 1.10 and 1.06, respectively. The model fits (see below) supported the conclusion that enhancement was relatively insensitive to surround orientation.

The suppression was further reduced in the Orthog-Narrow-Surround configuration (right panels of Fig. 4), especially at high-test contrasts. The amount of enhancement caused by wide and narrow surrounds were roughly equal. These results provide further evidence that enhancement is relatively insensitive to changes in the surround stimuli.

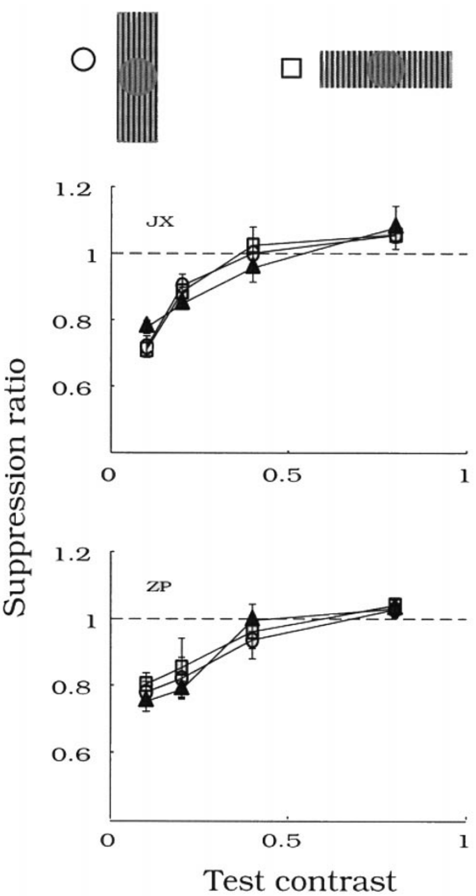

Fig. 5. Center-surround interactions are not specific to side- or end-surrounding. The horizontal axis indicates the test contrast and the vertical axis indicates the suppression ratio. The dashed horizontal line indicates when the physical test and match contrasts are equal. The surround contrast was 0.2. Upper panel, subject JX. Lower panel, subject ZP. Different plot symbols correspond to different surround configurations (triangles, full-surround; open circles, end-surround; open squares, side-surround). Error bars represent ±2 SEM.

3.3. Center-surround interactions with side- and end-surround configurations

So far, we have examined center-surround interactions with full annular surrounds. To examine how the geometry of the surround patch affects the interactions, we measured the matching contrasts when the surround patch was rectangular rather than circular. In this experiment, the surround patch was limited to a rectangular region either on both sides (side-surround) or on both ends (end-surround) of the central gratings (Fig. 5). The length of the rectangle equaled the diameter of the Wide-Surround configuration and the width of the rectangle equaled the diameter of the central patch. The surround contrast was 0.2.

Side-surrounds and end-surrounds were roughly equally effective in producing both enhancement and suppression (Fig. 5, open symbols). The effects caused by a full-surround (triangles in Fig. 5, copied from Fig. 3) were only slightly different from those caused by the side- or end-surrounds (Fig. 5, open symbols). In other words, the end- or side-surrounds on their own were approximately as effective as the full annular surrounds. We did not have sufficient data to infer the precise relationship between the partial- and full-surrounds. Nevertheless, the data indicate that the effects are not based on a linear spatial summation throughout the surround. Beyond a certain area, they do not seem to sum at all.

We also varied the relative spatial phase of the central and (side- and end-) surround gratings, we examined side- and end-interactions when the length of the surround rectangle equaled the diameter of the Narrow-Surround configuration, and we examined the interactions when the surround gratings were orthogonal to the central ones (data not shown). For all the cases tested, the effects of the end-surrounds were the same as those of the side-surrounds.

3.4. The phase dependence of center-surround interactions

With the wide-surround pattern, we varied the relative spatial phase between the central and surround

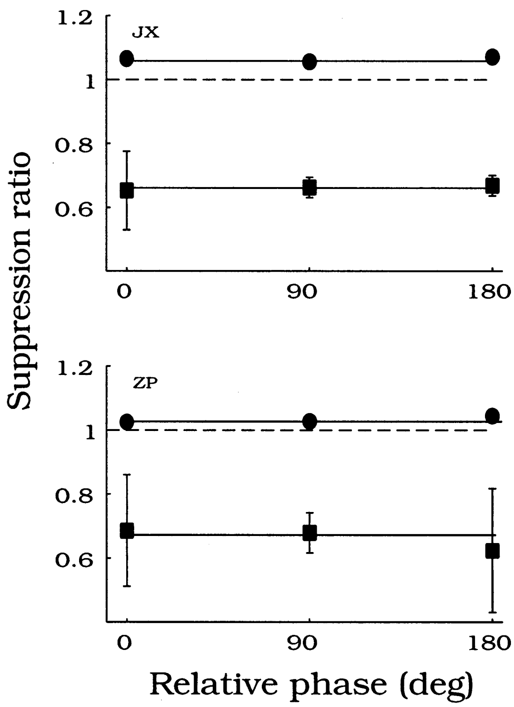

Fig. 6. Center-surround interactions are insensitive to the relative phase. The horizontal axis indicates the relative spatial phase between the central and the surround gratings. The phase of zero means that the central and the surround gratings were aligned. The vertical axis indicates the suppression ratio. The dashed horizontal line indicates when the physical test and match contrasts are equal. Test contrast was 0.4. Top panel, subject JX. Bottom panel, subject ZP. Different plot symbols represent different surround contrasts (circles, $C_s = 0.1$; squares, $C_s = 0.8$). Error bars represent ± 2 SEM.

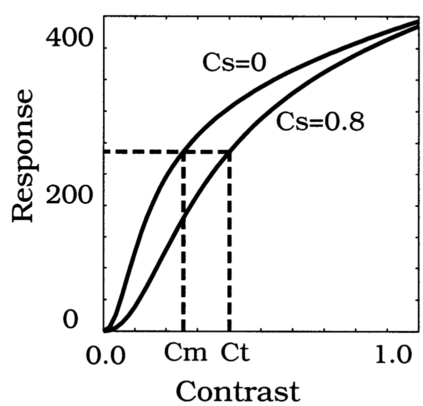

Fig. 7. An illustration of the model fitting process. The horizontal axis indicates the test contrast and the vertical axis indicates the iterative response. The two curves represent the contrast responses for two surround contrasts, $C_s = 0$ and $C_s = 0.8$. C_t is the test contrast and C_m is the matching contrast. An iterative optimization algorithm adjusted the model parameters so that the two responses were equal (as illustrated).

gratings and found that the spatial phase had no effect on the matching contrasts (Fig. 6). The test contrast was 0.4. The surround contrasts were 0.1 and 0.8. The surround caused suppression when the surround contrast was greater than the test contrast, and enhancement when the surround contrast was less than the test contrast. However, the matching contrasts remained the same for the three tested phases (0°, 90° and 180°), that is, the center-surround interactions were phase-independent. This phase-independence was also observed for the end-surround stimulus configuration (data not shown).

3.5. A model of center-surround interactions

We used an analytical formula to fit the data, thereby, quantifying the contrast dependence of center-surround interactions (Section 2.5). The formula we used, Eq. (4), is an extension of a model that has been previously proposed to fit psychophysical data on contrast discrimination (Foley, 1994; Boynton et al., 1999), which is closely related to models of the responses of V1 neurons (Albrecht & Hamilton, 1982; Heeger, 1992; Carandini et al., 1997).

The model implies that the response to a central patch is determined by four components: local excitation, local inhibition, surround excitation, and surround inhibition. These four components interact nonlinearly. Each of the components is characterized by an exponent parameter in the model: p for local excitation, q for local inhibition, pe for surround excitation, and qi for surround inhibition. There are also three weights, a, W_e, and W_i, that determine the relative contributions of the local excitation/inhibition, the surround excitation, and the surround inhibition, respectively.

In order to fit the model to the contrast-matching data, we assumed that the matching stimulus and test stimulus had the same contrast appearance when the contrast responses evoked by the two stimuli were equal, as illustrated in Fig. 7. The contrast response curves in Fig. 7 were computed from Eq. (4) using typical values for the various model parameters. The two curves represent the responses for $C_s = 0$ (no surround) and $C_s = 0.8$, as indicated. For a given measurement condition (C_t, test contrast; C_s, surround contrast; C_m, matching contrast), the fitting process adjusted the model parameters, which changed the shapes of the curves, so that the corresponding responses were (very nearly) equal. Using this method, we fitted the eight data sets (four surround configurations for each of two subjects), plotted in Figs. 3 and 4, each separately. Due to the lack of measurements at very low central contrasts, the full set of parameters was not well-constrained by the data. Hence, the parameters were constrained as described in Section 2.5. In particular, the model predictions were computed with a, p_e and q_i fixed across all eight data sets, and with p and q fixed for each subject, so that only W_e and W_i varied across the four stimulus configurations.

To examine the quality of the fits, we computed the matching contrasts from the model and compared them to the matching contrasts reported by the subjects (solid curves in Figs. 3 and 4). The model curves pass through the error bars of most of the plot symbols, and capture the main features of the data (1) the suppression increases with surround contrast and decreases with test contrast; and (2) the effect reverses and becomes enhancement when the central contrast is higher than the surround contrast.

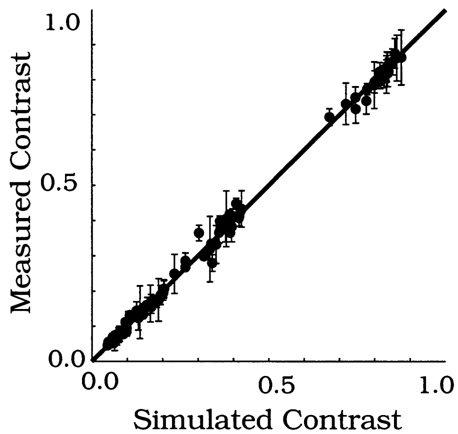

Fig. 8. Accuracy of the model fits. The vertical axis indicates the measured matching contrasts and the horizontal axis indicates the matching contrasts predicted from the model. There are 96 filled circles representing all the matching contrasts measured with the four stimulus configurations from the two subjects. The diagonal line indicates where the predicted matching contrasts equal the measured matching contrasts. The plot symbols clusters near the diagonal line. Error bars represent ± 2 SEM. The majority of the data ($\sim 89\%$) pass through the error bars.

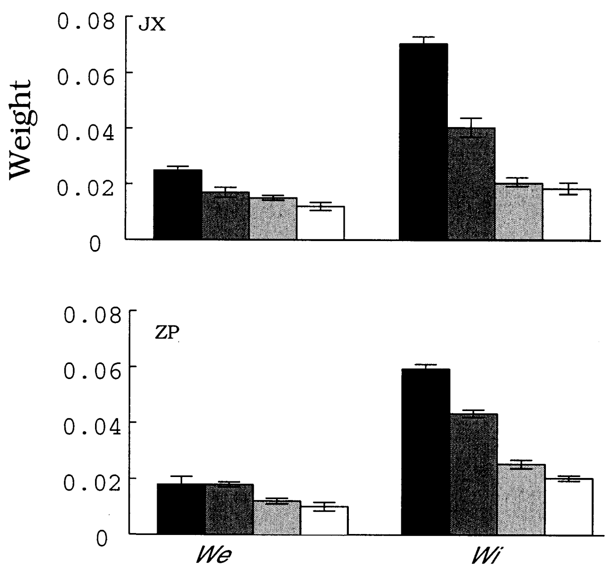

Fig. 9. Best fit values for the facilitation (W_e) and suppression (W_i) weights. Top, subject JX. Bottom, subject ZP. Left group of bars within each panel, facilitation weights. Right group, suppression weights. Within each group, the bars from left to right correspond to the Wide-, Narrow-, Orthog-Wide- and Orthog-Narrow-surround configurations respectively. Error bars represent ± 2 SEM, computed from the data by using a statistical bootstrapping procedure (Efron, Halloran, & Holmes, 1996).

To view the overall fitting performance, we plotted all the matching contrasts against the corresponding model predictions (Fig. 8). In the figure, the vertical axis represents the measured matching contrast and the horizontal axis represents the matching contrast predicted by the model. Each data point (and its associated error bar) corresponds to one of the data points in Fig. 3 or Fig. 4. The diagonal line indicates where the model predictions were perfect. The data are clustered near the diagonal line; 89% of the data points pass within ± 2 SEM of the model predictions, close to the 95% that would be expected according to the null hypothesis that the model is a completely accurate description of the data.

The four exponents in the model largely determine the shape of the contrast response function in Eq. (4): p, local excitation; q, local inhibition; p_e, surround excitation; q_i, surround inhibition. The values of these exponents were robust to changes in the stimulus configuration. Hence, they were held to the same values for all four stimulus configurations (Section 2).

A number of aspects of the results can be interpreted in terms of the best fit values of the model parameters:

- For both subjects, $(p - q)$ was 0.3, consistent with previous psychophysical studies of contrast discrimination and contrast appearance (Legge, 1981; Foley, 1994; Boynton et al., 1999).
- The local suppression exponent ($q = 2$) was greater than the surround suppression exponent ($q_i = 1$). This explains why surround suppression was less effective at high central contrasts. Local suppression increased rapidly with central contrast, whereas, surround suppression increased more gradually with surround contrast. At high central contrasts, therefore, the suppressive contribution from the surround was small relative to the suppressive contribution from the center. Ultimately, due to this relative reduction in the contribution of surround suppression, the net effect of the surround was enhancement for high central contrasts.
- The best fitting value for the surround enhancement exponent was relatively small, $p_e = 0.1$. The small value for this exponent means that surround enhancement changed slowly with surround contrast. The amount of enhancement depended mainly on the central contrast, although the enhancement was caused by the presence of the surround.

Fig. 9 plots the final fitted values for the weights of surround enhancement (W_e) and surround suppression (W_i), across the four different spatial configurations. For both subjects, the enhancement was found to be relatively insensitive to the extent (wide vs. narrow) and orientation (parallel vs. orthogonal) of the surround (left group of bars in each panel of Fig. 9). The suppression, on the other hand, was quite sensitive to both the extent and orientation of the surround (right group of bars). As the surround varied from parallel to orthogonal, the suppression weight W_i was decreased by 300–500%, while the enhancement weight W_e was decreased by only 20–50%. The suppression weights were approximately the same for both subjects, although they were slightly greater for subject ZP than for subject JX. Surround enhancement exhibited a larger difference between the two subjects; the average W_e for ZP was 0.017 while that for JX was 0.04. Another way to look at this is to compare the balance of W_e and W_i of each subject; subject ZP was more suppression-dominant than subject JX.

4. Discussion

Using a contrast-matching task, we systematically examined the contrast-dependence of center-surround interactions. The main results are summarized as follows: (1) The presence of a surround stimulus could produce either contrast enhancement or contrast suppression; the net effect depended primarily on the balance of the central and surround contrasts. (2) The suppression was strongly orientation-specific, but the enhancement was less sensitive to changes in surround orientation. (3) The enhancement depended only on the immediately adjacent surround (i.e., increasing the surround width beyond this adjacent region had no effect on the enhancement), whereas the suppression depended on a much wider surround region. (4) Neither the suppression nor the enhancement depended on the relative phase of the central and surround gratings. (5) Neither the suppression nor the enhancement depended on whether the surround was restricted to the sides or the ends of the central grating. (6) We developed a computational model that was capable of fitting the data accurately.

The model provides an adequate explanation of the contrast-dependence of surround enhancement and suppression. Two model parameters (the weights of suppression and enhancement), however, varied with surround orientation and surround extent. In principle, the model could be extended to explicitly pool with different weights across a range of spatial positions and orientations. The detailed pooling rules will have to be determined with further experiments.

4.1. Related psychophysical studies of contrast appearance

Using a contrast-matching task, Cannon and Fullenkamp (1993) reported that the effect of the surround could be varied from suppression to enhancement by changing the size or the relative contrast of the surround. We observed very similar effects of surround size and the contrast. Cannon and Fullenkamp (1993) also reported that surround enhancement exhibited large individual differences among the eight tested subjects. Because we only tested two subjects, the data were not sufficient to fully explore individual differences. Even so, subject JX showed a stronger enhancement effect than did subject ZP. This was particularly evident with the Narrow-Surround pattern. Our results are similar to those reported by Snowden and Hammett (1998); one of their subjects showed a relatively strong enhancement like our subject JX, while their other subject showed weaker enhancement like our subject ZP.

The suppression that we observed in our experiments was roughly equal in magnitude to that reported by Cannon and Fullenkamp (1991, 1993). In both our results and their results, the maximal reduction of the matching contrast was $\sim$40–60%. However, the enhancement reported by Cannon and Fullenkamp was greater than what we observed. The contrast enhancement in their subjects was as large as 200% with a central contrast of 0.031 and 150% with a central contrast of 0.125. In our data, the maximal enhancement with a central contrast of 0.1 was 115% and 106% for subjects JX and ZP, respectively. This discrepancy could be simply due to individual differences (as suggested by Cannon & Fullenkamp, 1993). An important difference in the stimuli may also contribute to the discrepancy. The center and the surround patches in our experiments were separated with a narrow gap while no such gap existed in Cannon and Fullenkamp's stimuli. It is possible that the enhancement is reduced when there is a clear boundary between the center and the surround.

We found that the net effect of the interactions reversed by changing the relative contrasts of center and surround. The reversal point of the relative contrast varied with the spatial configuration of stimuli. With the Wide-Surround configuration, the reversal occurred when the central and surround contrasts were roughly equal; enhancement was produced if the central contrast was higher than the surround contrast and suppression was produced if it was the other way around. With the Narrow-Surround pattern, enhancement occurred even when the central contrast was slightly less than the surround contrast. These results agree with the findings by Cannon and Fullenkamp (1993) that increasing the width of the surround usually caused enhancement to be replaced by suppression.

Cannon and Fullenkamp (1993) measured contrast matches and plotted the suppression ratios as a function of the ratio of surround to central contrasts. When plotted this way, they found that most of the curves overlapped. Our data also exhibit a tendency to overlap when plotted in this way, but not perfectly so. This is consistent with our model fits, which revealed that the central and surround contrasts had different exponents in influencing the matching contrast. Thus, our contrast matches were not adequately predicted by the surround-center contrast ratio alone.

Ejima and Takahashi (1985) also reported a reversal from suppression to enhancement, but there is a discrepancy between their results and ours. They found (using stimuli like our end- and side-surround configurations) that the enhancement depended on the relative phase of the central and surround gratings, being strongest when the gratings were in-phase. We did not observe any phase-dependence of suppression or enhancement. The stimulus used by Ejima and Takahashi did not have a gap to separate the center and the surround. Once again, this might be a possible reason for the discrepancy in the results. However, our results are consistent with other reports that surround suppression is phase independent (Solomon et al., 1993).

Using a contrast-matching task, Solomon et al. (1993) found that contrast matches depended on the relative orientation of the center and surround. The maximal suppression ratio caused by parallel surrounds was about 0.4–0.5, while that caused by orthogonal surrounds was about 0.85. These numbers were well in accordance with our results. Chubb et al. (1989) found that the effect of surround suppression was maximal when the center and the surround patches had the same spatial frequency. We observed a similar spatial frequency specificity, reported elsewhere (Xing & Heeger, 2000).

4.2. *Related psychophysical studies of pattern detection and the role of collinearity in contour integration*

One of the most important aspects of our results concerns the hypothesis that collinear alignment is an important factor in center-surround interactions. Results from a number of studies have suggested that surround facilitation depends on the precise collinear alignment of the surround, and several models have been proposed along these lines (Polat & Sagi, 1994; Bonneh & Sagi, 1998; Solomon & Morgan, 2000; Polat, 1999). Most of these previous studies used contrast detection protocols, rather than the contrast-matching protocol that we adopted. However, one would expect that if collinearity was critical then it's effect would be evident in both types of measurements.

We, however, found no effect of collinearity. (1) Enhancement did not depend on orientation. Parallel (Fig. 3) and orthogonal (Fig. 4) surrounds produced roughly equal amounts of enhancement. (2) Enhancement did not depend on the shape of the surround. End- and side-surrounds produced roughly equal amounts of enhancement (Fig. 5).

Polat and Sagi (Polat & Sagi, 1994; Polat, 1999) and Gilbert (Gilbert, 1992; Gilbert, Das, Ito, Kapadia, & Westheimer, 1996) have proposed that surround facilitation might subserve grouping phenomena such as contour integration (Kovacs & Julesz, 1993; Field, Hayes, & Hess, 1993). This proposal is based on some apparent similarities between surround facilitation and contour integration.

Williams and Hess (1998) questioned this proposal based on several notable differences between surround facilitation and contour integration. Two of their results are particularly interesting in light of our findings. (1) Contour grouping can occur in the periphery, whereas, they found facilitation of detection thresholds only in the fovea. (2) Contour grouping occurs when the individual elements are all well above contrast threshold. Williams and Hess found (using a contrast-matching protocol) no contrast enhancement for stimuli at twice threshold contrasts, even though the same stimulus configuration did facilitate thresholds.

Our results tend to support Williams and Hess's viewpoint that the facilitation reported by Polat and coworkers is a purely threshold phenomenon that does not have consequences for suprathreshold grouping. (1) We report elsewhere (Xing & Heeger, 2000) that there is no surround enhancement of contrast appearance (measured using a contrast-matching task) in the periphery. (2) We observed no effect of collinearity on suprathreshold perception. End- and side-surrounds produced the same amount of enhancement under all of the tested configurations that included variations in surround width, center-surround separation and in the relative phase of center and surround. Furthermore, we found that enhancement only occurred when the center contrast was greater than the surround contrast. This seems more suited to the purpose of segmentation than contour integration.

Our model does not explain why detection thresholds are lower in the presence of collinear surrounds. It is not surprising that our model does not explain these detection threshold results, given that the model was designed to fit psychophysical data on contrast-matching for stimuli that were well above threshold. Hence, we leave open the possibility that there may be additional facilitative mechanisms operating near threshold, like the second-order filtering models of Polat (1999) or Solomon and Morgan (2000). But even though such mechanisms may contribute to detection threshold, they do not appear to contribute to suprathreshold pattern appearance.

4.3. Related physiological studies

It is attractive to interpret our results and our model in terms of the known physiological and anatomical properties of V1. There are a number of points on which there appears to be agreement.

First, Levitt, and Lund (1997) reported suppression when the surround contrast was higher than the central contrast and facilitation when the surround contrast was lower than the central contrast. Our model produces just this pattern of responses. A complementary result, reported by several studies, is that the responses to a near-threshold target were facilitated by a collinear surround, whereas, the responses were suppressed by the surround when target contrast was higher (Nelson & Frost, 1985; Kapadia et al., 1995; Toth et al., 1996; Polat & Norcia, 1996, 1998; Polat et al., 1998). Putting these together with the Levitt and Lund's result, we suggest that there are three contrast regimes: (1) facilitation when the target contrast is near threshold, but only for a collinear surround; (2) suppression when the target contrast is well above threshold but below the surround contrast; and (3) enhancement when the target contrast is greater than the surround contrast. Levitt and Lund focused on the latter two (higher contrast) regimes. The other studies focused on the first two (lower contrast) regimes. The results for near-threshold targets (regime 1) do not have any direct bearing on the interpretation of our suprathreshold data. Our psychophysical data and our model are entirely consistent with the results for the two higher contrast regimes.

Second, also consistent with our results, DeAngelis, Freeman, and Ohzawa (1994) found no phase-dependence for surround inhibition either from the sides or from the ends of the receptive fields of visual cortical cells.

Third, the surround suppression, as parameterized by W_i in our model, was very sensitive to surround orientation. This agrees with the physiological finding that long-range inhibition is strongest when the central and surround stimuli have the same orientation (Polat & Norcia, 1996; Knierim & van Essen, 1992; DeAngelis et al., 1994; Ts'o, Gilbert, & Wiesel, 1986). The local inhibition in our model, on the other hand, is pooled evenly across all orientations. This is consistent with reports by DeAngelis, Robson, Ohzawa, and Freeman (1992) that inhibition within the receptive field was generally independent of orientation.

Fourth, the local inhibition and the surround inhibition are different in our model. In particular, the best fit values for the exponents in our model were $q = 2$ (for local inhibition) and $q_i = 1$ (for surround inhibition). This difference might be explained by the different anatomical substrates that presumably subserve local and long-range inhibition in V1 (Gilbert & Wiesel, 1989; Lund, Yoshioka, & Levitt, 1993; see Callaway, 1998 for review). Local inhibition may arise from direct inhibitory connections from neurons in the same or adjacent hypercolumns, whereas, surround inhibition may arise via local inhibitory inter-neurons from longer range excitatory connections.

On the other hand, Sillito et al., (1995) and Gilbert et al. (1996) observed a variety of context-dependent interactions in V1 that appear to be considerably more complicated than our model would suggest.

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