Surround suppression and facilitation in the fovea: Very long-range spatial interactions in contrast perception

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Surround modulation of perceived contrast has been almost exclusively studied in short-range conditions, i.e., in situations where a tiny gap, at most, separates center from surround. Existing long-range studies suggest that suppression extends to 12-cycle distance, whereas facilitation of perceived contrast is suggested to arise from visual field regions enclosing the center. In V1 neurons, however, long-range surround modulation involves both suppression and facilitation. Thus, we investigated short- and long-range surround modulation by measuring the perceived contrast of a center in the presence of a surround either near (0.3 cycles, 0.1 degree) or far (19.8 cycles, 6.6 degrees) from the center. This study demonstrates that in addition to the well-known suppression, surround modulation involves remarkably long-range facilitation of perceived contrast. At low center contrasts, the long-range facilitation was stronger than the long-range suppression, whereas at high center contrast we found mainly long-range suppression. Because the current models of perceived contrast could not account for our data, we considered our results in the context of models developed for surround modulation in V1 neurons. However, neither mechanistic nor phenomenological models proved satisfactory. Moreover, with the current knowledge, it seems that straightforward pooling of V1 neurons’ responses cannot account for surround modulation of perceived contrast.

Keywords: human vision, surround modulation, psychophysics, contrast matching


Introduction

Surround suppression of perceived contrast refers to a phenomenon in which the contrast of a central stimulus appears reduced when it is displayed together with a high-contrast surround (Cai, Zhou, & Chen, 2008; Cannon & Fullenkamp, 1991; Chubb, Sperling, & Solomon, 1989; Ejima & Takahashi, 1985; Kilpela¨inen, Donner, & Laurinen, 2007; Meese & Hess, 2004; Snowden & Hammett, 1998; Solomon, Sperling, & Chubb, 1993; Takeuchi & De Valois, 2000; Xing & Heeger, 2000, 2001). Surround suppression is also found in the visual cortex. A grating in neuron’s classical receptive field elicits less spikes when it is accompanied with a co-oriented surround grating (Angelucci et al., 2002; Bair, Cavanaugh, & Movshon, 2003; Blakemore & Tobin, 1972; Cavanaugh, Bair, & Movshon, 2002a, 2002b; Levitt & Lund, 1997; Maffei & Fiorentini, 1976; Sceniak, Hawken, & Shapley, 2001; Shushruth, Ichida, Levitt, & Angelucci, 2009). Surround also suppresses blood oxygenation level-dependent signal in the human visual cortex (Nurminen, Kilpeläinen, Laurinen, & Vanni, 2009; Zenger-Landolt & Heeger, 2003).

Surround usually suppresses the perceived contrast, but under some stimulus conditions, it may also increase (facilitate) the perceived contrast—particularly, when the center contrast is higher than the surround contrast (Ejima & Takahashi, 1985; Snowden & Hammett, 1998; Takeuchi & De Valois, 2000; Xing & Heeger, 2001). Even the strongest facilitation is typically weaker than the strongest suppression (Snowden & Hammett, 1998; Xing & Heeger, 2001), although in some observers the facilitation strength may exceed the suppression strength (Cannon & Fullenkamp, 1993). Xing and Heeger (2001) found that the facilitation strength is the same with narrow and wide
surround (3 vs. 8 cycles), as opposed to the suppression strength that increases with surround width. Accordingly, it has been suggested that the facilitation of perceived contrast arises from regions of the surround in the vicinity of the center (Cannon & Fullenkamp, 1993; Xing & Heeger, 2001). In line with this suggestion, in all the studies showing surround facilitation of perceived contrast (Cannon & Fullenkamp, 1993; Ejima & Takahashi, 1985; Snowden & Hammett, 1998; Takeuchi & De Valois, 2000; Xing & Heeger, 2001), the surround has abutted or nearly abutted the center.

While facilitation of perceived contrast may arise merely from the surround regions closely enveloping the center (Cannon & Fullenkamp, 1993; Xing & Heeger, 2001), suppression arises from a spatially extensive region of the visual field (Cannon & Fullenkamp, 1991, 1996; Xing & Heeger, 2001). The strength of the suppression first steeply increases as the outer diameter of the surround increases and then levels off around 4.8- to 6.4-cycle surround width (Cannon & Fullenkamp, 1991). Interestingly, Cannon and Fullenkamp (1991) found that when an unmodulated gap was inserted between the center and the surround, suppression extended even farther. With 9.6-cycle gap (the widest one studied), there was still noticeable suppression. Similarly in V1 neurons, the surround suppression extends to approximately 1.5 times larger region with a gap than without a gap that separates the center and the surround (Angelucci et al., 2002). Thus, both in contrast perception and in single neurons, a gap between the center and the surround reveals long-range surround modulation that would otherwise stay hidden.

Long-range surround modulation in V1 neurons does not limit to suppression, but in 61% of the neurons, a surround that is separated from the center by a large gap can either suppress or facilitate the neural responses (Ichida, Schwabe, Bressloff, & Angelucci, 2007). A surround facilitates the neural responses to a low-contrast center, whereas suppression is typically observed with high-contrast center (Ichida et al., 2007). In human vision, long-range facilitation has often been demonstrated by measuring the effect of spatially displaced Gabor stimuli on the detection threshold of a centrally viewed Gabor (Chen & Tyler, 2001, 2002, 2008; Kurki, Hyvärinen, & Laurinen, 2006; Levi, Klein, & Hariharan, 2002; Polat & Sagi, 1993, 1994; Solomon, Watson, & Morgan, 1999; Williams & Hess, 1998). These studies have found facilitation of detection up to 12-cycle distance (Polat & Sagi, 1993) and suppression that extends to approximately 8-cycle distance (Petrov & McKee, 2006; Saarela & Herzog, 2008, 2009). However, the contrast dependency of long-range surround modulation of perceived contrast has been nearly set aside in previous studies. Cannon and Fullenkamp (1991) used one center contrast (25%) and two surround contrasts (12.5% and 50%) and they observed merely suppression. Given the surprising findings of contrast-dependent long-range suppression and facilitation in V1 neurons (Ichida et al., 2007) and the almost non-existent psychophysical studies on long-range surround modulation of perceived contrast, the current picture of surround modulation in human vision may be incomplete.

Our study investigated both short- and long-range surround modulation by measuring the perceived contrast of a center grating in the presence of an annular surround grating. The annulus width was constant and its inner radius was either small (1.5 cycles) or very large (21 cycles). It was crucial to provide a comparison baseline for the long-range effects by first running the short-range experiment, because surround modulation of perceived contrast exhibits large individual differences (Cannon & Fullenkamp, 1993). As long-range surround modulation of perceived contrast has previously been investigated with a remarkably limited set of contrasts, this study complemented the previous studies by using several center and surround contrasts.

**Methods**

**Subjects**

Four subjects (two females) participated in the study. All subjects had normal or corrected-to-normal vision. Subjects LN and TP were authors of the study and also subject MK knew the main purpose of the experiments. Subject SS was an inexperienced observer and naive to the purpose of the study. SS participated only in the experiment in which the size of the gap between the center and the surround was varied. Written informed consent was obtained from the subjects.

**Apparatus**

The stimuli were created with Matlab (Mathworks, Natick, MA, USA) and displayed on a 22" Mitsubishi Diamond Pro 2070 CRT monitor (NEC-Mitsubishi Electronics Display-Europe, Munich, Germany) via Visage stimulus generator providing 14-bit gray-scale resolution (Cambridge Research Systems, Kent, UK). The monitor had 800 × 600 pixel (39.0 × 29.2 cm) resolution and 100-Hz refresh rate. Luminance output of the display was gamma corrected. Chin rest was used to stabilize the viewing distance to 85 cm. Viewing was binocular.

**Stimuli**

Test stimuli consisted of sinusoidally modulated sharpedged circular center and annular surround luminance gratings (Figure 1). The spatial frequency of the sinusoid was 3 cpd, both in the center and in the surround. Unless otherwise stated, the center and surround were centered on
The comparison stimulus was always presented without a test stimulus in order to span the psychometric function. The stimuli used in the short- and long-range experiments on the surface of V1. The stimuli were projected to the cortex using Schwarz’s (1994) formula, \( w = k \cdot \log(z + a) \) in which \( z \) is a complex number representing a point in visual field, \( w \) is a complex number representing a point on the cortex, \( a \) controls the area devoted to fovea, and \( k \) is a scaling factor. We used \( a = 1 \) and \( k = 17 \), which correspond to the average magnification factor in human V1 (Duncan & Boynton, 2003). The estimated cortical gap widths were 1.2 mm and 29.6 mm in the short- and long-range conditions, respectively. In the gap size experiment, the gap width was 19.8 cycles (6.6 degrees). We estimated the gap widths in the short- and long-range experiments on the surface of V1. The stimuli were projected to the cortex using Schwarz’s (1994) formula, \( w = k \cdot \log(z + a) \) in which \( z \) is a complex number representing a point in visual field, \( w \) is a complex number representing a point on the cortex, \( a \) controls the area devoted to fovea, and \( k \) is a scaling factor. We used \( a = 1 \) and \( k = 17 \), which correspond to the average magnification factor in human V1 (Duncan & Boynton, 2003). The estimated cortical gap widths were 1.2 mm and 29.6 mm in the short- and long-range conditions, respectively. In the gap size experiment, the gap width was 19.8 cycles (6.6 degrees). We estimated the gap widths in the short- and long-range experiments on the surface of V1. The stimuli were projected to the cortex using Schwarz’s (1994) formula, \( w = k \cdot \log(z + a) \) in which \( z \) is a complex number representing a point in visual field, \( w \) is a complex number representing a point on the cortex, \( a \) controls the area devoted to fovea, and \( k \) is a scaling factor. We used \( a = 1 \) and \( k = 17 \), which correspond to the average magnification factor in human V1 (Duncan & Boynton, 2003). The estimated cortical gap widths were 1.2 mm and 29.6 mm in the short- and long-range conditions, respectively. In the gap size experiment, the gap width was 19.8 cycles (6.6 degrees). We estimated the gap widths in the short-

The orientation tuning of the long-range surround modulation was examined by running an experiment in which the orientation of the surround was orthogonal with respect to the center orientation. In this experiment, the center contrast was 15% and the surround contrasts were selected to produce reliable suppression (45% surround contrast) or facilitation (5% surround contrast).

**Procedure**

The perceived contrast of the center was measured with 2-interval method of constant stimuli. Each trial began with 300-ms presentation of the fixation point followed by 300 ms of blank screen. Next, either the comparison or test stimulus was displayed, in randomized order, for 500 ms. After a 500-ms inter-stimulus interval, the second stimulus was displayed for 500 ms. The subject indicated with a button press the interval in which the center contrast appeared higher. The response time was unlimited and subject’s response initiated a new trial. The subjects were instructed to pay attention only to the stimulus center and to ignore the surround.

For a single psychometric function, each comparison contrast was repeated 10–15 times. The proportion of trials in which the observer reported that the contrast of the comparison stimulus appeared higher was plotted against the comparison contrast. Experimental data were fitted with a cumulative Gaussian using a bootstrapping method implemented with Psignifit 2.5.41 (Wichmann & Hill, 2001) Matlab toolbox. The mean of the fitted Gaussian, i.e., the point of subjective equality (PSE), determines the perceived contrast. Figure 2 illustrates examples of fitted experimental data. For one center–surround configuration and center contrast (e.g., 0.3-cycle gap, 5% center contrast), all the surround contrast conditions were measured in succession and in counter-balanced order. Two such sessions were usually accomplished in a single day. The reported perceived contrasts are averages of two or, in one case (subject LN, long-range, 5% center contrast), three sessions in different days. The averaged perceived contrast was normalized with the corresponding center contrast. The normalized perceived contrast values \(<1\ indicate suppression and values \(>1\ indicate facilitation.

![Figure 1](http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/933482/)
The maximum suppression and facilitation strengths were computed using the following formula:

$$\max(\text{abs}(1 - C_{\text{norm}})),$$

where $C_{\text{norm}}$ is a vector containing the normalized perceived contrasts for a single gap width, center contrast, and all the surround contrasts, abs denotes the absolute value, and max selects the largest value of the vector. Suppression and facilitation were treated separately, i.e., the $C_{\text{norm}}$ contained either the normalized values that were larger than one (facilitation) or those that were smaller than one (suppression) but not both. When computed in this way, the strengths of suppression and facilitation were made directly comparable.

The surround-to-center contrast ratio at which the long-range facilitation changed to suppression was computed by linearly interpolating between the normalized perceived contrast values and determining the surround-to-center contrast ratio at which the interpolated normalized perceived contrast crossed 1 (i.e., no effect from the surround). This was done separately for each measurement session.

Results

Short-range surround modulation

In the short-range condition, surround reduced the perceived contrast of the center in all observers (Figure 3).
Increasing the contrast of the surround increased the suppression strength, which leveled off when the surround contrast was approximately twice the center contrast. At low surround-to-center contrast ratios, the modulation strength was largely independent of the absolute center contrast. Observer LN showed facilitation with the lowest surround-to-center contrast ratio.

The maximum short-range suppression was always stronger than the maximum short-range facilitation (Figure 4). For observers MK and TP, the strength of the maximum suppression increased when center contrast increased from 5% to 15% (Figure 4). Computed over the subjects (Equation 1), the mean ($\pm SE$ of the mean) of the maximum short-range suppression was 0.35 ($\pm 0.065$) for 5% center contrast and 0.42 ($\pm 0.043$) for 15% center contrast. The maximum short-range facilitation was 0.027 ($\pm 0.027$) for 5% center contrast and 0.042 ($\pm 0.029$) for 15% center contrast.

**Long-range surround modulation**

All the observers showed long-range surround facilitation and suppression (Figure 5). At low surround-to-center contrast ratio, the surround facilitated perceived contrast of the center. The facilitation turned into suppression with increasing surround contrast.

With the 5% center contrast, the maximum long-range facilitation was as strong, or stronger, than the maximum long-range suppression (Figure 6). With the 15% center contrast, the maximum long-range facilitation was weaker than the maximum long-range suppression.

Figure 4. The maximum strengths of the short-range suppression and facilitation. Different subjects in different panels. Error bars depict ±SE of the mean of measurements repeated in different days.

Figure 5. Normalized perceived contrast in the long-range experiment. Subjects in different panels. Points above the horizontal line indicate facilitation and those below indicate suppression. Error bars depict ±SE of the mean of measurements repeated in different days.
contrast, the maximum long-range suppression was stronger than facilitation. The maximum strength of the suppression increased with increasing the center contrast from 5% to 15%.

Computed over the subjects (Equation 1), the mean (±SE of the mean) of the maximum long-range facilitation was 0.096 (±0.013) for the 5% center contrast and 0.074 (±0.008) for the 15% center contrast. The maximum long-range suppression strengths were 0.064 (±0.013) and 0.12 (±0.013) for 5% and 15% center contrasts, respectively. We report the maximum modulation strengths only for the

5% and 15% center contrasts, because it was impossible to measure the highest surround-to-center contrast ratios with the 75% center contrast.

Increasing the center contrast from 5% to 15% decreased the surround-to-center contrast ratio at which the long-range facilitation changed to suppression (Figure 7a). Computed over the subjects, the mean (±SE of the mean) surround-to-center contrast ratio at which facilitation changed to suppression was 1.8 (±0.30) for 5% and 1.4 (±0.25) for 15%. Subject LN showed long-range facilitation with the 75% contrast. In this subject, the long-range facilitation with 75% center contrast changed to suppression at surround-to-center contrast ratio 0.62 (±0.01).

In all the observers, higher absolute surround contrast was required for the long-range facilitation to change to suppression when the center contrast was 15% compared to when it was 5% (Figure 7b). Computed over the subjects, the mean (±SE of the mean) absolute surround contrasts at suppression onset were 9.0% (±1.5%) and 22% (±3.7%) for 5% and 15% center contrasts, respectively. Subject LN showed long-range facilitation with the 75% contrast. In this subject, the long-range facilitation with 75% center contrast changed to suppression at 47% (±1.0%) absolute surround contrast.

The surround orientation had no effect on long-range surround modulation of perceived contrast (Figure 8).

The effect of gap size

This experiment reproduced the main findings of our previous short- and long-range experiments also in the naive subject (Figure 9). The strongest suppression was observed when the surround was near the center. Increasing the center-to-surround distance decreased the suppression strength. All observers showed long-range facilitation when the gap size was equal to or larger than 8.6 cycles. In observers LN and TP, the strength of the facilitation
depended on the contrast of the center. In particular, the facilitation was weaker with the 50% than with the 15% center contrast.

Discussion

We studied short- and long-range surround modulation in human vision. Our study demonstrates for the first time that surround modulation of perceived contrast involves both very long-range suppression and facilitation.

Short-range surround modulation

The short-range experiment essentially replicated the previous findings on short-range surround modulation. As in previous studies (Cai et al., 2008; Cannon & Fullenkamp, 1993; Ejima & Takahashi, 1985; Meese & Hess, 2004; Xing & Heeger, 2001), the ratio of center and surround contrasts largely determined the amount of suppression, which increased with increasing surround-to-center contrast ratio and leveled off with sufficiently high surround contrast (Cannon & Fullenkamp, 1993). We found some individual differences, as only one subject showed clear short-range facilitation in addition to suppression. The finding is in line with the previous findings by Cannon and Fullenkamp (1993) who demonstrated large individual differences in the pattern of short-range suppression and facilitation. As in previous studies (Ejima & Takahashi, 1985; Snowden & Hammett, 1998; Takeuchi & De Valois, 2000; Xing & Heeger, 2001), the short-range facilitation occurred at low surround-to-center contrast ratio. When we observed short-range facilitation, it was always much weaker than the short-range suppression (Ejima & Takahashi, 1985; Snowden & Hammett, 1998; Xing & Heeger, 2001).

Long-range surround modulation

The results of our long-range experiment provide novel insights into the mechanisms of surround modulation in human vision. We showed that a surround very far from the center may not only suppress but also facilitate center’s perceived contrast. Remarkably, the long-range facilitation could exceed the long-range suppression in strength. Our finding of long-range facilitation stands in contrast with the previous studies suggesting that surround facilitation of perceived contrast arises from the regions of the surround in the vicinity of the center (Cannon & Fullenkamp, 1993; Xing & Heeger, 2001). The current study shows that surround facilitates the perceived contrast of the center with a range of gap sizes and at least up to about 20-cycle (~7-degree) distance.

To our knowledge, the width of the gap between the center and the surround was much larger in the current study than in any of the previous studies on surround modulation in the fovea. Previously, Cannon and Fullenkamp (1991) have used a gap up to 9.6 cycles (1.2 degrees) between center and surround; they found only suppression. Cannon and Fullenkamp suggested that the inhibitory mechanism underlying suppression extends over a distance of more than 12 cycles. However, our results show that suppression of perceived contrast can be found at the distance of at least ~20 cycles (~7 degrees) in foveal vision.

The general pattern of short- and long-range surround modulation was similar. The strength of long-range surround suppression increased with increasing the surround-to-center contrast ratio, as does the strength of the short-range surround suppression (Cai et al., 2008; Cannon & Fullenkamp, 1993; Ejima & Takahashi, 1985; Meese & Hess, 2004; Xing & Heeger, 2001). We found that the strongest suppression occurred at the highest absolute center contrast in both the long- and short-range conditions. In addition to these similarities, interesting differences were found. First, the short-range facilitation changes to suppression at surround-to-center contrast ratio
of 1 or slightly above (Ejima & Takahashi, 1985; Snowden & Hammett, 1998; Xing & Heeger, 2001), whereas we observed long-range surround facilitation up to surround-to-center contrast ratios of \( \frac{2}{3} \). However, the contrast detection threshold is approximately two-fold higher in the eccentricity of our long-range experiment compared to the short-range experiment (Legge & Kersten, 1987). The decrease in effective surround contrast that accompanies the increase in threshold may also underlie the increased surround-to-center contrast ratio at which the long-range facilitation changes to suppression. However, the surround-to-center contrast ratio at which the long-range facilitation changed to suppression depended on the absolute center contrast. With 5% center contrast, the ratio was approximately 1.3 times higher than with 15% center contrast. One of our subjects showed facilitation with the 75% center contrast, and in this subject, the facilitation changed to suppression at 3.8 times larger surround-to-center contrast ratio with 5% than with 75% center contrast. Second, the short-range suppression is stronger than facilitation (Ejima & Takahashi, 1985; Snowden & Hammett, 1998; Xing & Heeger, 2001), but at 5% center contrast, the long-range facilitation strength exceeds the strength of the long-range suppression (Figure 6). Third, the short-range surround modulation is tuned for orientation (Cannon & Fullenkamp, 1991), whereas the strengths of the long-range suppression and facilitation were the same regardless of the surround orientation. Cannon and Fullenkamp (1991) suggested that two mechanisms, one orientation tuned and one non-orientation tuned, underlie the surround modulation of perceived contrast. Our results suggest that mainly the non-orientation-tuned mechanism contributes to the long-range surround modulation.

Our study extended the previous studies and characterized the contrast dependency of the long-range surround modulation. The long-range surround modulation of perceived contrast has been previously investigated only with two surround contrasts (12.5% and 50%) and one center contrast (25%; Cannon & Fullenkamp, 1991). We used 4 center contrasts (5, 15, 50, and 75%) and varied the surround-to-center contrast ratio from 0 to 3. Interestingly, we found that the long-range surround modulation of perceived contrast was dependent on the absolute contrast of the center. With the lowest (5%) center contrast, we found long-range facilitation that exceeded the suppression in strength. Increasing the absolute center contrast decreased the range of surround-to-center contrast ratios and gap widths that produced long-range facilitation. With the 75% center contrast, long-range facilitation was observed only with the lowest (1/3) surround-to-center contrast ratio in one subject. The high center contrast did not merely diminish the facilitation, however, but increased the strength of the long-range suppression for a given surround-to-center contrast ratio. Cannon and Fullenkamp (1991) used 25% center contrast and reported merely long-range suppression, whereas we found both suppression and facilitation. However, our results indicate that for a given surround-to-center distance and contrast ratio, the long-range facilitation diminishes with increasing the absolute contrast of the center. Thus, the apparent conflict between our results and the results of Cannon and

Figure 9. Normalized perceived contrast as a function of gap width. The surround-to-center contrast ratio was 2/3. Different subjects in different panels. Error bars depict \( \pm SE \) of the mean of measurements repeated in different days.
Fullenkamp (1991) relates, at least partly, to the center contrast used in their study. By systematically varying the center and surround contrasts, we were able to reveal that long-range surround modulation of perceived contrast involves clear facilitation at 5% and 15% center contrasts.

Long-range facilitation has often been studied by measuring the effect of flanking Gabors on the detection threshold of a central Gabor (Chen & Tyler, 2001, 2002, 2008; Kurki et al., 2006; Levi et al., 2002; Polat & Sagi, 1993, 1994; Solomon et al., 1999; Williams & Hess, 1998). However, different authors have proposed different underlying mechanisms for the facilitation. Levi et al. (2002), Petrov, Verghese, and McKee (2006), and Williams and Hess (1998) suggested that the facilitation arises largely from reduction in location uncertainty. Polat and Sagi (1993) argued that facilitation of detection arises from inhibition and Kurki et al. (2006) and Solomon et al. (1999) suggested pedestal effects. Moreover, Chen and Tyler (2001, 2002, 2008) and Wu and Chen (2010) suggested that flanks affect the gain of the mechanism responding to the target. Because uncertainty reduction is a threshold phenomenon (Williams & Hess, 1998), it cannot underlie facilitation with suprathreshold stimuli. The explanation based on inhibition (Polat & Sagi, 1993) is compatible with the current long-range suppression but not with the facilitation. If the current long-range facilitation would arise from pedestal effects, then increasing the surround contrast should either increase the facilitation strength or have no effect. However, we found that long-range facilitation changed to suppression with increasing surround contrast. Thus, although uncertainty reduction, pedestal effects, and inhibition can play a role in the facilitation of detection, the current long-range facilitation agrees with explanations based on increases in gain.

Three of our four observers knew the main purpose of the current study, which may, in principle, bias the current results. However, a naive subject replicated the main findings of the study and it seems very unlikely that our results would have arisen from the selection of observers.

Comparison to long-range surround modulation in V1 neurons

The contrast dependency of long-range facilitation in the current data shows some similarity to the contrast dependency of long-range facilitation in V1 neurons. Ichida et al. (2007) found that the proportion of V1 neurons showing long-range facilitation decreased from 61% to 4% with increasing the center contrast from low to high. Similarly, in our psychophysical data, the prominent long-range facilitation with center contrasts of 5% and 15% was nearly gone with the 75% center contrast. However, the contrast dependency of long-range suppression in our data does not entirely match to that observed in V1 neurons. The long-range suppression strengthens with increasing the surround-to-center contrast ratio in our data and in previous psychophysical studies (Cannon & Fullenkamp, 1991). Schwabe, Ichida, Shushruth, Mangapathy, and Angelucci (2010) compared the long-range suppression strength in V1 neurons, in a condition where the center contrast was low and surround contrast was high (i.e., large surround-to-center contrast ratio) to a condition in which both the center and the surround contrasts were high (i.e., small surround-to-center contrast ratio). In complete disarray with our results, they found that the long-range suppression strength was higher in the latter condition.

We found that surround facilitation extends to at least 7-degree distance. Recent single neuron study (Ichida et al., 2007) arrived to a compatible estimate on the spatial range of surround facilitation in V1. When the inner radius of an annular surround grating is decreased to 7.7 degrees on average, the surround begins to facilitate the neural responses to the center stimulus (Ichida et al., 2007). The mechanism underlying surround suppression extends to approximately 3.5 degrees in V1 neurons (Angelucci et al., 2002; Ichida et al., 2007; Levitt & Lund, 2002). However, all of our observers showed strong suppression with the 6.6-degree gap. Thus, the spatial aspects of surround facilitation of perceived contrast, but not of suppression, agree with the average extent of the mechanisms underlying surround modulation in single V1 neurons. In accordance with broad orientation tuning of long-range surround modulation in V1 neurons (A. Angelucci, personal communication), the long-range surround modulation of perceived contrast seems to lack orientation tuning. However, further experiments are needed to fully resolve the orientation tuning of long-range surround modulation of perceived contrast.

Anatomical substrates of long-range surround modulation

The changes that context exerts upon the detection threshold of a line target have sometimes been attributed to the horizontal connections in V1 (Kapadia, Ito, Gilbert, & Westheimer, 1995). The present contrast-dependent long-range surround modulation could in principle arise from the V1 horizontal connections that form both excitatory and inhibitory synapses (McGuire, Gilbert, Rivlin, & Wiesel, 1991). However, the length of the V1 horizontal connections is ~3 mm (Angelucci et al., 2002), whereas in our long-range experiment the gap width was ~30 mm on the surface of V1. Thus, the monosynaptic reach of the horizontal connections cannot account for the spatial range of surround modulation of perceived contrast. The horizontal connections could mediate the long-range surround modulation polysynaptically (Polat & Norcia, 1996), but the temporal properties of surround modulation suggest feedback connections (Bair et al., 2003; Kilpeläinen et al., 2007).
Implications for surround modulation models

Psychophysical models of surround modulation derive from divisive gain control models (Foley, 1994; Heeger, 1992) and usually they consider only suppression (Snowden & Hammett, 1998; Solomon et al., 1993). The model of Xing and Heeger (2001) as well as models devised for surround modulation of contrast detection and discrimination (Chen & Tyler, 2001, 2002; Meese, Summers, Holmes, & Wallis, 2007) account also for facilitation. For the suppression part, all the above models suit qualitatively to the present short-range surround modulation results. However, these models do not explicitly differentiate between short- and long-range surround modulations. The model of Cannon and Fullenkamp (1996) included an explicit spatial weighting function for the surround suppression. In their model, the suppression strength decreases exponentially as a function of distance between the center and the surround. For the suppression part, the present results agree qualitatively with their model in that the short-range suppression was stronger than the long-range suppression. At quantitative level, however, our data diverge from the predictions of their model. The suppression strength falls off with 1.86-cycle space constant in the model of Cannon and Fullenkamp (1996), which predicts that only 0.002% of the suppression should be left at the center-to-surround distance (~20 cycles) that we used in the long-range experiment. Computed over the three subjects and two center contrasts (5 and 15%), the maximum short-range suppression strength was 0.385 and the maximum long-range suppression strength was 0.092. Thus, approximately 24% of the suppression that we observed with the 0.3-cycle gap was left with the 19.8-cycle gap, strongly suggesting that the mechanism underlying surround suppression is far more extensive than assumed in the model of Cannon and Fullenkamp (1996). Moreover, we found strong long-range facilitation and none of the current models of surround modulation of perceived contrast explicitly accounts for it. The contrast discrimination model of Chen and Tyler (2008) incorporates the machinery required for long-range facilitation and suppression; their model states explicitly how the center-to-surround distance affects the balance of surround excitation and inhibition. However, as Chen and Tyler (2008) point out, not only the center-to-surround distance but also the surround contrast affects the balance of surround excitation and inhibition. When the currently unknown relationship between surround contrast and the balance of surround excitation and inhibition is solved, the predictions of their model and surround modulation of perceived contrast can be quantitatively compared.

It has been recently shown that a simple neural model can account for area summation in human vision (Nurminen et al., 2009). Thus, it is worthwhile to consider the neural models also in the context of perceived contrast. Standard single neuron models cater for surround modulation with spatially overlapping excitatory and inhibitory mechanisms that have Gaussian envelopes in space (Cavanaugh et al., 2002a; Sceniak et al., 2001). In these models, short-range facilitation arises naturally if the addition of a surround stimulus increases the response of the excitatory mechanism more than the response of the inhibitory mechanism (Cavanaugh et al., 2002b). However, because these models assume much wider spatial spread for the inhibition than for the excitation (Cavanaugh et al., 2002a; Sceniak et al., 2001), the net effect of adding a distant surround is suppressive. In our psychophysical data, the long-range facilitation could even exceed the long-range suppression in strength. Thus, although the two antagonistic Gaussian types of models can account for area summation in the human vision (Nurminen et al., 2009), they cannot account for the long-range surround modulation of perceived contrast.

Recently, Schwabe, Obermayer, Angelucci, and Breslof (2006) developed a recurrent network model of surround modulation in macaque V1 that accounts for short- and long-range facilitation and suppression. In their model, the surround modulation arises from the interplay of feedforward, horizontal, and inter-areal feedback connections. Schwabe et al. suggested that surround grating affects the neurons responding to the center grating directly by feedback excitation and via feedback that excites the horizontal connections. The horizontal connections in turn excite the neurons responding to the center but, importantly, also inhibit them via local inhibitory neurons. In Schwabe et al.’s (2006) model, the inhibitory neurons have higher threshold and gain than the excitatory neurons. When the local inhibitory neurons receive sufficient input to cross their threshold, the surround grating suppresses the responses of the neurons in the center. If the net input to the local inhibitory neurons is below threshold, a surround grating merely excites the neurons responding to the center grating and the effect is facilitation. For example, the same surround grating may facilitate when the center grating has a low contrast and suppress when the center contrast is high, because with high center contrast the local inhibitory neurons cross their threshold (Schwabe et al., 2006).

The results of this study parallel the modeling results of Schwabe et al. (2006) in some aspects. First, surround with 7-degree inner radius and 8-degree outer radius (our center radius: 0.4, their center radius: 0.5 degree) produced facilitation and suppression both in our psychophysical data and in Schwabe et al.’s model. Second, with 85% center contrast, Schwabe et al.’s model produces long-range suppression but not facilitation. Similarly, in our data, the long-range facilitation abolished with the 75% center contrast. Long-range facilitation was observed with 15% absolute center contrast both in our data and in Schwabe et al.’s modeling results. However, critical differences between their neural model and our psychophysical data were found. In the model of Schwabe et al. (2006), the drive from the surround required for suppression is higher the lower the center contrast. In our data,
however, the absolute surround contrast required for the facilitation to change to suppression was lower the lower the center contrast (Figure 7b). In addition, we noticed that at low absolute surround contrast the suppression changed to facilitation with increasing the center contrast from 5% to 15%, whereas in Schwabe et al.’s model the suppression changes to facilitation with decreasing the center contrast. Thus, the neural model of Schwabe et al. (2006) captures well the extensive spatial range of surround suppression and facilitation in human vision but not the contrast dependencies. Although perceived contrast can be considered a relatively low-level visual property, the current models of surround modulation in V1 neurons do not account for it in any simple way.

Conclusions

Contrary to previous suggestions, the surround modulation of perceived contrast involves very long-range facilitation, in addition to suppression. The mechanisms underlying these long-range interactions are contrast-dependent and spatially extensive ranging at least to 20-cycle distance in foveal vision.

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