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Center-surround interactions in foveal and peripheral vision

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Abstract

The perceived contrast of a central stimulus can be decreased (surround suppression) or increased (surround facilitation) by the presence of surround stimuli. In this report we examined center-surround interactions in foveal and peripheral vision using contrast-matching tasks. We found that: (1) surround suppression became markedly stronger as the center-surround stimulus was moved toward the periphery; (2) surround facilitation diminished in the periphery; and (3) the suppression in the periphery was less orientation- and frequency-specific than that in the fovea, so that significant suppression was induced even when the central and surround gratings had very different orientations and spatial frequencies. The different center-surround interactions in the fovea and periphery can not be accounted for by cortical magnification, suggesting that center-surround interactions in the fovea and periphery are incommensurable and play different functional roles in human image processing.

Keywords: Suppression; Facilitation; Masking; Peripheral vision; Lateral interactions

1. Introduction

The perceived contrast of a central visual stimulus can be changed by the presence of nearby visual stimuli. These center-surround interactions are well documented both by psychophysical and neurophysiological experiments (Cannon & Fullenkamp, 1991, 1996; Polat & Sagi, 1993, 1994; Snowden & Hammett, 1998; Solomon, Sperling, & Chubb, 1993; Polat & Norcia, 1996; Levitt & Lund, 1997). The effect of a surround is typically suppressive, although with some special manipulations, it can be facilitative (Cannon & Fullenkamp, 1993; Ejima & Takahashi, 1985; Polat & Sagi, 1993). Surround suppression is maximal when the center patch and surround stimuli have the same spatial frequency and orientation (Chubb, Sperling, & Solomon, 1989; Cannon & Fullenkamp, 1991). These effects persist even when there is a relatively large gap between the center and surround stimuli. For sinusoidal gratings, for example, the interaction region extends up to 8–12 cycles of the central grating (Polat & Sagi, 1993, 1994).

These center-surround interactions have been extensively studied for stimuli presented in the fovea. On the other hand, little is known about such interactions for stimuli presented in the periphery of the visual field. Visual performance for many discrimination and detection tasks is degraded in the periphery. For example, visual acuity falls off rapidly with eccentricity. In many cases, differences between foveal and peripheral vision can be accounted for by cortical magnification: the visual cortex devoted to each degree of visual angle decreases approximate linearly with retinal eccentricity. Thus scaling the stimulus appropriately might achieve similar cortical representations regardless of retinal eccentricity (Wilson, Levi, Maffei, Rovamo, & DeValois, 1990; Daniel & Whitteridge, 1961; Virsu & Rovamo, 1979). However, cortical magnification fails to explain degraded recognition performance for complex stimuli in peripheral vision (Strasburger, Harvey, & Rentschler, 1991; Strasburger, Rentschler, & Harvey, 1994; Juttner & Rentschler, 1996). In addition, cortical magnification fails to explain contour interactions in peripheral vision (Bouma, 1970; Jacobs, 1979; Levi, Klein, & Aitsebaomo, 1985).

In this report, we studied two questions. First, what are the differences between foveal and peripheral cen-

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ter-surround interactions? Secondly, can cortical magnification account for the differences? We addressed these questions by examining the perceived contrasts of center-surround stimuli using a contrast-matching task.

2. Method

2.1. Visual stimuli

Subjects compared the perceived contrast of an isolated, contrast-reversing (8 Hz) sine-grating circular patch (Fig. 1a) with the perceived contrast of a central patch embedded in a surround annulus of gratings (Fig. 1b). Beyond the grating patches, the screen was a uniform gray field of equal mean luminance (36.2 cd/m^2), except for a small (0.3°) high contrast square that served as a fixation mark in the center of the screen. The grating contrast was defined in the usual way, $C=(L_{max}-L_{min})/(L_{max}+L_{min})$, where L_{max} and L_{min} are the maximal and minimal luminances, respectively. The central grating patch had 6 cycles of gratings and the surround grating had 8 additional cycles of gratings on each side. A small gap was introduced between the center and the surround to help the subjects to focus their contrast judgments only on the central patch. In addition, the spatial phases of the center and surround gratings differed by 180°, although in separate experiments we found that the phase had no effect on the perceived contrast. The orientation of the central gratings was vertical. The orientation of the surround gratings was either horizontal or vertical. Spatial frequency was systematically varied from 1 to 8 cyc/deg (see Section 3). The actual size of the stimulus was scaled as a function of the spatial frequency.

The stimuli were displayed on a monochrome monitor (radius, 20 gs, 75 Hz refresh) with a 10-bit frame buffer card (radius, thunder 24 gt). The screen had 1152×870 pixels and was viewed from a distance of 50 cm, thus subtending a total of $38 \times 29°$ of visual angle.

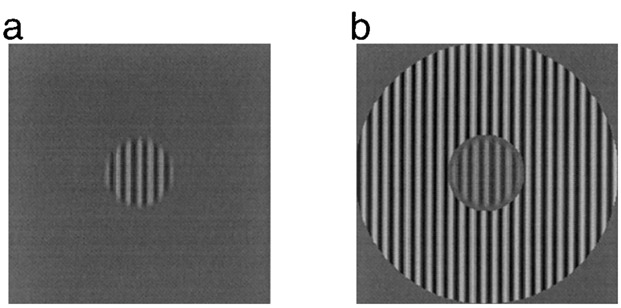

Fig. 1. Visual stimuli. (a) The isolated central patch. (b) The center-surround stimulus pattern. The embedded central patch is physically the same as the isolated patch, but it is perceived to have a different contrast.

2.2. Experimental procedures

A two-alternative-forced choice protocol was used to determine perceived contrast matches. Each trial consisted of two 500 ms stimulus intervals that were separated by a brief (300 ms) blank interval. This relatively long stimulus duration was chosen to avoid having subjects base their judgments on transient responses at stimulus onset and offset. The isolated grating patch was displayed in one stimulus interval and the center-surround stimulus was displayed in the other interval. Subjects pressed one of two buttons to indicate the interval that appeared to have a higher center contrast. The screen was blank (a uniform gray field), except for the fixation point, during both the blank and response intervals. No feedback was provided. The subjects were asked to pay attention only to the central patches and to compare the contrasts of the two central patches. When testing peripheral vision, subjects were instructed to hold their gaze on the central fixation spot throughout each trial while paying attention to the stimuli presented in the peripheral visual field.

The perceived contrast of the embedded central patch was determined using a double random staircase procedure. In this method, the 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 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 perceived contrast was defined as the matching 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.

2.3. 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.

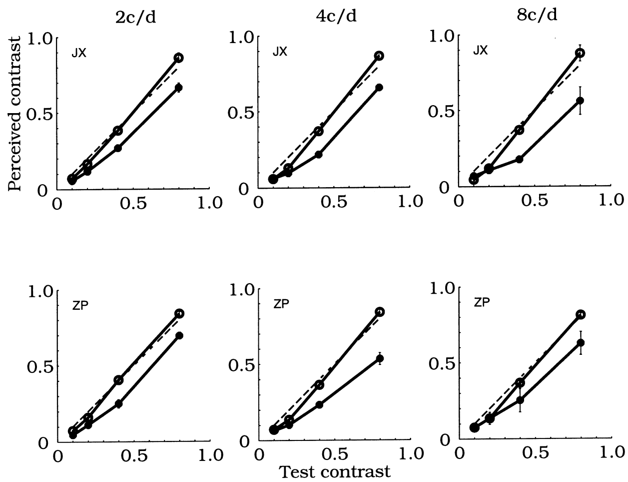

Fig. 2. Center-surround interactions in the fovea. In each graph, the horizontal axis indicates the test contrast and the vertical axis indicates the perceived, matching contrast. The dashed diagonal line indicates where a perceived contrast equals to the test contrast. Top row, subject JX. Bottom row, subject ZP. The left, middle and right panels correspond to the three spatial frequencies $f=2$, 4, 8 cyc/deg, respectively. Different plot symbols correspond to different surround contrasts: open circles are for $C_s=0.2$; filled circles are for $C_s=0.8$. Error bars, most of which are smaller than the plot symbols, represent 1 SEM.

Table 1
The mean suppression ratios

f (cyc/deg)	Fovea (%)		10° Periphery (%)	
	$C_s=0.2$	$C_s=0.8$	$C_s=0.2$	0.8
1			61	86
2	11	38	62	84
4	18	36		
8	20	40		
Orthogonal orientation	5	12	41	66
Low (0.5 cyc/deg) surround frequency	−2	14	48	69

3. Results

3.1. Center-surround interactions in the fovea

We performed a series of measurements to determine how center-surround interactions are affected by scaling the stimuli. In particular, we scaled both the spatial frequency of each grating and the size of each grating patch by the same amount so that the number of cycles within each patch was unchanged. The stimulus configuration is shown in Fig. 1. The central and the surround patches had the same orientation and spatial frequency. Three spatial frequencies ($f=2$, 4, 8 cyc/deg) were studied. For each frequency, we tested the perceived contrasts for four test contrasts ($C_t=0.1$, 0.2, 0.4, 0.8) and for two surround contrasts ($C_s=0.2$, 0.8).

Fig. 2 shows that scaling the stimuli had very little effect on the perceived contrast. The three panels in the top row are the results for subject JX, each representing one spatial frequency. The lower panels are for subject ZP. The horizontal axis represents the test contrast and the vertical axis represents the perceived, matching contrast. The dashed diagonal line indicates where the perceived contrast is equal to the test contrast. The different plot symbols correspond to different surround contrasts. For both subjects, the high surround contrast (filled symbols) produced significant suppression at all test contrasts. The low surround contrast (open symbols) produced only weak suppression at low test contrasts, with some facilitation at high contrasts (where the data cross above the dashed diagonal line).

In order to make quantitative comparisons, we computed suppression ratios, defined as $(1-C_m/C_t)$. A suppression ratio of 100% indicates that the contrast of an embedded central patch was completely suppressed by the surround patch. The ratio of 0 means that no suppression was produced. A negative value for the suppression ratio corresponds to facilitation. The maximal suppression ratios were 45, 51, and 56% for the three tested frequencies 2, 4, 8 cyc/deg. The maximal ratios for facilitation were −8, −8 and −10%. For each frequency and each surround contrast, we calculated the mean suppression ratios averaged from the four test contrasts and the two subjects (Table 1). For a surround contrast of $C_s=0.8$, the mean suppression ratios were approximately 38%, with negligible dependence on stimulus scale.

Notice that the standard errors were larger for the highest spatial frequency (8 cyc/deg) than for the lower spatial frequencies (2, 4 cyc/deg). For the 8 cyc/deg stimulus, the diameter of the central patch was only about 1°. The subjects reported that it was difficult to keep their attention focused on the central patch alone. Furthermore, the staircase tended to step slowly downward throughout the entire block; although this happened only for the highest spatial frequency stimulus condition, we take this as evidence that there was some adaptation to the stimuli throughout the block of trials. We suspect that both of these factors contributed to the larger standard errors at the highest spatial frequency.

3.2. Center-surround interactions in the periphery

When the same experiment was performed in the periphery, the results were dramatically different (Fig. 3). The stimuli were presented at 10° eccentricity in the lower-right quadrant of the visual field. Two spatial frequencies ($f=1$, 2 cyc/deg) were studied, but the stimulus configuration was otherwise unchanged. The perceived contrast of the central patch was markedly depressed by the surround. For example, with a high contrast surround ($C_s=0.8$), and for test contrasts of

$C_t = 0.4$ and 0.8, the perceived contrasts were 0.03 and 0.11, respectively.

Some visual discriminations are impaired in the periphery, so we felt that it was important to make sure that the subjects could perform the task accurately. To examine this, we ran a control condition in which the surround contrast was set to zero. The data (triangles in the top right panel of Fig. 3) fall along the diagonal line with only slight deviations, demonstrating that the matching task could be performed accurately and precisely in the periphery.

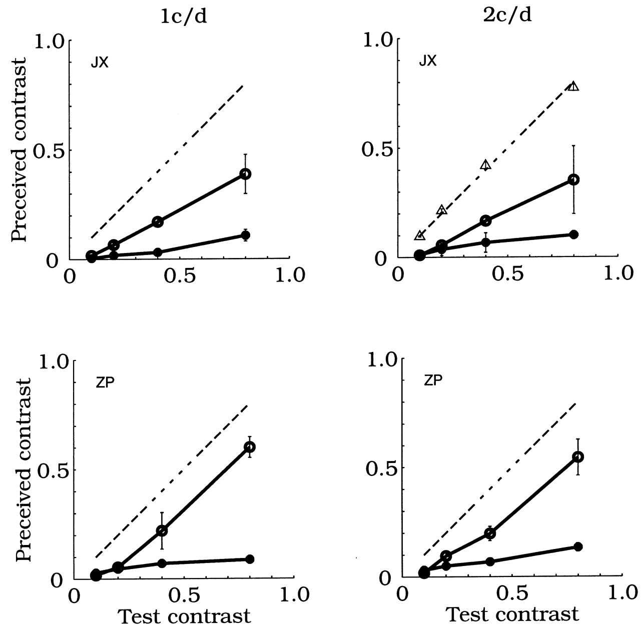

Fig. 3. Suppression is much stronger in the periphery (same format as Fig. 2). The left and right panels correspond to different spatial frequencies, $f = 1$, 2 cyc/deg. Different plot symbols correspond to different surround contrasts: triangles, $C_s = 0$; open circles, $C_s = 0.2$; filled circles, $C_s = 0.8$.

The results in Figs. 2 and 3 and in Table 1 can be summarized as follows. (1) the suppression was much stronger in the periphery than in the fovea. For the high surround contrast ($C_s = 0.8$), the mean suppression ratios were approximately 86% in the periphery but only 38% in the fovea (Table 1). In fact, the suppression induced by the lower surround contrast ($C_s = 0.2$) in the periphery (mean suppression ratios around 62%) was in general greater than that induced by higher surround contrast ($C_s = 0.8$) in the fovea (mean suppression ratios around 38%). (2) In both the fovea and the periphery, scaling the stimuli had no effect on the perceived contrast. (3) There was no evidence of facilitation in the periphery. Together these results clearly demonstrate that the center-surround interaction is different in the fovea and periphery.

3.3. *Varying the spatial configuration of the surround*

Center-surround interactions in the fovea are strongest when the orientation and frequency of the surround stimulus are equal to those of the embedded central stimulus (Chubb et al., 1989; Cannon & Fullenkamp, 1991; Polat & Sagi 1993). In particular, very little suppression is induced if the center-surround orientation difference is beyond 45° or the frequencies differ by more than two octaves. We found that changing the surround orientation or spatial frequency had much less of an impact in the periphery.

First, we explored the orientation-specificity of the center-surround interactions. We modified the configuration in Fig. 1b by changing the orientation of surround gratings to be horizontal, orthogonal to the orientation of the central gratings. The spatial frequency of the central and surround gratings were fixed at 2 cyc/deg. The perceived contrasts were measured for this configuration at the fovea and at 10° of eccentricity. The measurements were made at four test contrasts and two surround contrasts.

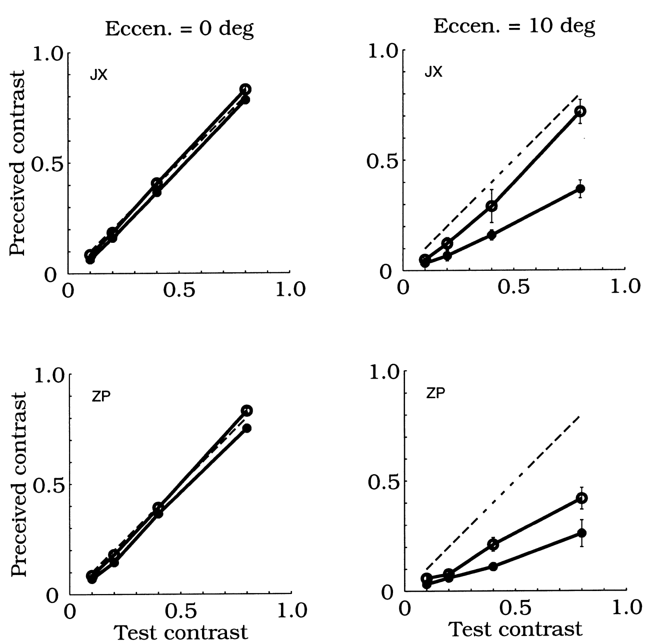

Fig. 4. Surround effects are less orientation-specific in the periphery than in the fovea (same format as Fig. 2). Orientation of the surround gratings was orthogonal to that of the central gratings. Top row, subject JX. Bottom row, subject ZP. Left column, fovea. Right column, periphery. Different plot symbols correspond to different surround contrasts: open circles, $C_s = 0.2$; filled circles, $C_s = 0.8$.

The results, plotted in Fig. 4, were dramatically different in the fovea and periphery. In the fovea (left pair of graphs in Fig. 4), the high surround contrast induced only weak if any suppression and the low surround contrast induced a slight contrast facilitation at high central contrasts. In the periphery, the suppression was markedly greater (right pair of graphs in Fig. 4). Even the low surround contrast induced substantial suppression in the periphery. The mean suppression

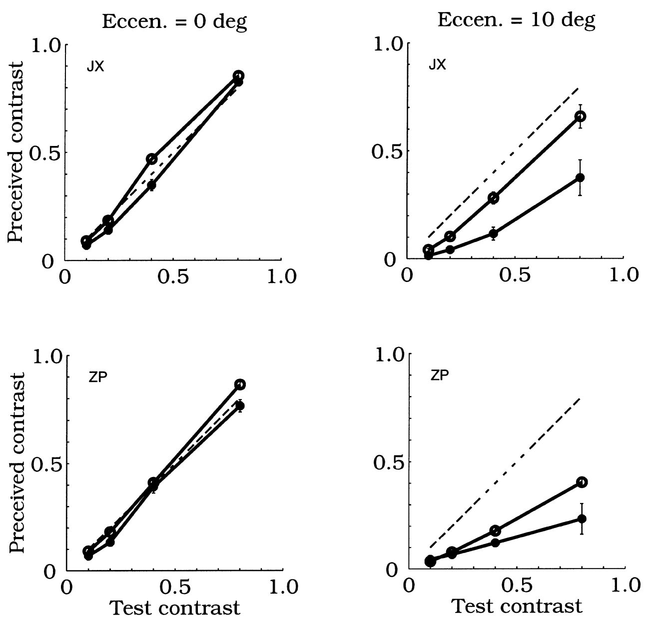

Fig. 5. Surround effects are less frequency-specific in the periphery than in the fovea (same format as Fig. 2). Spatial frequency of the surround gratings was 2 octaves lower than that of the central gratings. Top row, subject JX. Bottom row, subject ZP. Left column, fovea. Right column, periphery. Different plot symbols correspond to different surround contrasts: open circles, $C_s = 0.2$; filled circles, $C_s = 0.8$.

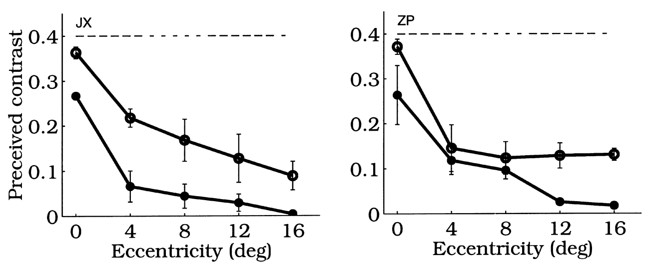

Fig. 6. Surround suppression increases dramatically from 0 to 4° eccentricity. In each graph, the horizontal axis indicates eccentricity and the vertical axis indicates the perceived, matching contrast. The dashed horizontal line indicates where the perceived contrast would equal the test contrast ($C_t = 0.4$). Left panel, subject JX. Right panel, subject ZP. Open circles, orthogonal surround gratings. Filled symbols, parallel surround gratings. Error bars represent 1 SEM.

ratios for orthogonal surrounds at 10° eccentricity were 41% at $C_s = 0.2$ and 66% at $C_s = 0.8$ while those at the fovea were 5% at $C_s = 0.2$ and 12% at $C_s = 0.8$.

Moreover, the center-surround interactions were less orientation-specific in the periphery than in the fovea. For the high surround contrast $C_s = 0.8$, the suppression ratios increased by a factor of ~ 3 (from 12 to 38%) when the surround was changed from orthogonal to parallel. In the periphery, the suppression ratios increased by only a factor of ~ 1.3 (from 66 to 84%) under the same conditions.

Next we tested spatial frequency specificity. We modified the configuration in Fig. 1b by changing the frequency of the surround gratings to 0.5 cyc/deg while keeping the frequency of the central gratings at 2 cyc/deg. Thus the frequencies in center and surround differed by 2 octaves.

The data, plotted in Fig. 5, again showed dramatic differences between the fovea and periphery. In the fovea, the surround gratings induced little suppression for any of the tested contrasts, and they induced relatively strong facilitation at some test contrasts (left pair of graphs in Fig. 5). For example, the suppression ratios for subject JX at the low surround contrast ($C_s = 0.2$) were -12% at $C_t = 0.4$ and -10% at $C_t = 0.8$. The negative ratios mean that the overall surround effect was facilitative. The mean suppression ratio at $C_s = 0.8$ was 14%. In the periphery, the suppression was again markedly greater (right pair of graphs in Fig. 5). The mean suppression ratio at 10° eccentricity was 69% at $C_s = 0.8$.

Moreover, center-surround interactions were less frequency-specific in the periphery than in the fovea. From the 2 octave frequency difference to the equal center-surround frequency, the suppression ratios increased by a factor of ~ 3 (from 14 to 38%) in the fovea, but only by a factor of ~ 1.2 (from 69 to 84%) in the periphery.

3.4. Varying stimulus eccentricity

Next, we systematically varied the stimulus locations from the fovea to the periphery. The spatial frequencies of the central and the surround gratings were 2 cyc/deg. Both parallel and orthogonal orientations between the central and surround gratings were tested. The test contrast was fixed at $C_t = 0.4$ and the surround contrast was $C_s = 0.8$. The perceived contrasts were measured at five eccentricities (0, 4, 8, 12 and 16°).

The data, plotted in Fig. 6, demonstrate that the effect varied monotonically from fovea to periphery, but that most of the change occurred by 4° of eccentricity. The perceived contrasts decreased dramatically from 0 to 4° of eccentricity. For parallel center and surround orientations (filled circles), the mean suppression ratios were 38% at 0° and 84% at 4°. Thus, at the boundary of the foveal area, the majority of the contrast was suppressed. Beyond 4°, the perceived contrast continued to decrease but at a slower rate. By 16° eccentricity, the perceived contrasts were close to zero, i.e. the grating became virtually undetectable when embedded in a parallel surround even though an isolated grating patch was readily visible. The suppression ratio changed with eccentricity, on average, by about 11% per degree of visual angle. From 4 to 16°, the suppression ratio decreased at a slower rate (about 1.3% per degree). The suppression induced by orthogonal surround gratings showed the same trend (open circles); the two curves in Fig. 6 are roughly parallel although the orthogonal orientation produced less suppression at each eccentricity.

Finally, it is worth noting that at 4 and 8° eccentricity, the effect of changing from a parallel to orthogonal surround grating was strikingly different in the two subjects; perceived contrast changed by 400% for subject JX but only by a few percent for subject ZP. Presumably, this is either because of the difficulty in performing the task in the periphery, or because of individual differences in the suppression mechanisms. We suspect the latter because each subject's contrast matches were consistent across repeated measurements on subsequent days. Cannon and Fullenkamp (1993) reported large individual differences in the strength of the facilitation induced by a surround, but there are no previous reports of individual differences in suppression.

4. Discussion

We measured center-surround interactions in the fovea and periphery using a contrast matching task. Our main findings can be summarized as follows: (1) surround suppression became stronger as the center-surround stimulus was moved toward the periphery; (2) surround facilitation diminished at peripheral locations; and (3) the center-surround interactions in the fovea were strongly orientation and spatial frequency specific but these specificities were weaker in the periphery.

Together, these results imply that the different center-surround interactions in the fovea and periphery cannot be explained by cortical magnification. Retinocortical mapping is typically described with a cortical magnification factor, measured as millimeters of cortex per degree of visual angle. At 10° eccentricity, the magnification factor measured in human visual cortex is about one-fifth that in the fovea (Engel, Glover & Wandell, 1997; Horton & Hoyt, 1991). We found that scaling the stimuli had little or no effect on the center-surround interactions, neither in the fovea (Fig. 2) nor in the periphery (Fig. 3). We varied the stimulus magnification from fovea to periphery by as much as a factor of 8, from spatial frequencies of $f = 8$ cyc/deg in the fovea to 1 cyc/deg in the periphery, that is greater than the amount that should be necessary to compensate for a cortical magnification factor of 5. Yet even when the stimuli were scaled by a factor of 8, the suppression ratios in the fovea and periphery were still dramatically different.

Snowden and Hammett (1998) reported an analogous difference between the fovea and periphery for contrast detection and discrimination. While they found no effect of a surround on thresholds in the fovea, the same stimulus configuration raised thresholds in the periphery. Note that changes in perceived contrast are not necessarily expected to have the same effect on discrimination thresholds. Discriminability is dependent on the signal-to-noise ratio of the neural responses, whereas it is widely believed that perceived contrast depends on the mean level of the responses. Nevertheless, Snowden and Hammett's results are consistent with ours in suggesting that the interactions between stimuli are stronger in the periphery. Moreover, Snowden (1998) reported that the spatial range of suppressive interactions increased in the periphery while the range of facilitation did not. This parallels our finding of increased inhibition and decreased excitation in the periphery.

Our results are consistent with the fact that visual recognition is disproportionately degraded in the periphery. Several research groups have found that recognizing a single letter flanked by other letters is more difficult in the periphery than in the fovea, even after compensating for cortical magnification (Bouma, 1970; Jacobs, 1979; Levi, Klein, & Aitsebaomo, 1985). Strasburger et al. (1991,1994) reported that cortical magnification fails to explain the degraded visual recognition of numeric characters in peripheral vision. Chung, Mansfield and Legge (1998) found that scaling print size can not compensate for the slow reading speed in peripheral vision. The strong surround suppression that we observed in peripheral vision might be the cause of these behavioral deficits.

We found no evidence for surround facilitation in the periphery. Although our experiments were not designed to produce maximal facilitation (even in the fovea), the observed lack of facilitation in peripheral vision is consistent with previous reports. Williams and Hess (1998) looked for facilitation using a stimulus configuration that was intended to produce a strong facilitation effect. They measured detection thresholds for a central patch with and without flanking patterns. In the fovea, the presence of flankers increased the sensitivity to the central patch. In the periphery, however, they found no such facilitation. Both methods, contrast detection and contrast matching, therefore lead to the consistent conclusion that surround interactions do not produce facilitation in the periphery. Nevertheless, it remains possible that some as yet untested stimulus configuration might yield facilitation in the periphery.

The lack of facilitation found in the periphery may have important consequences for perceptual organization. Neurons in the early retinotopically organized visual areas, because of their small receptive fields, respond to local image features, thereby breaking the image apart into its component parts. A number of theories suggest that excitatory interactions between neurons serve to bind, link, and group these local image features (Eckhorn, 1994; Hummel & Biederman 1992; von der Malsburg & Buhmann, 1992; Yen & Finkel, 1998). Therefore, given that surround facilitation is weak or absent in periphery, there should be little linking and grouping in the periphery. Empirical tests of this prediction may lead to new views about the distinct functional roles of foveal and peripheral vision.

It would be useful to interpret our results in terms of the known physiological and anatomical properties of V1. A number of studies have reported that the responses to a stimulus placed within a V1 neuron's receptive field could be either increased or decreased by adding a stimulus in the region surrounding the receptive field (Nelson & Frost, 1985; Kapadia, Ito, Gilbert, & Westheimer, 1995; Toth, Rao, Kim, Somers, & Sur, 1996; Levitt & Lund, 1997; Polat & Norcia, 1996, 1998; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998). Unfortunately, there is not enough information available in the published electrophysiological data to determine whether or not there is an effect of eccentricity analogous to what we have observed psychophysically.

Our results suggest that center-surround interactions may have different functional roles in the fovea and periphery. In the periphery, the suppression can be more than 90%, implying that the cortical representation of a peripheral stimulus can sometimes be completely obliterated when it is embedded in a surrounding pattern. This might serve a useful role in visual information compression. In the fovea, on the other hand, the maximum suppression ratio is only $\sim 40\%$ so that there is still a robust representation of central patch. Such partial suppression might reflect cortical gain control or response normalization (Heeger, 1992; Albrecht & Geisler, 1991; Thomas & Olzak, 1997). Further empirical and modeling work may reveal the visual processing differences that underlie these different functional roles in the fovea and periphery. For example, the strength of the suppression along with its orientation and spatial frequency tuning may all vary with eccentricity in such a way as to explain our results.

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