

Spatial frequency bandwidth of surround suppression tuning curves

Ignacio Serrano-Pedraza

Faculty of Psychology, Complutense University of
Madrid, Madrid, Spain
Institute of Neuroscience, Newcastle University,
Newcastle upon Tyne, UK



John P. Grady

Institute of Neuroscience, Newcastle University,
Newcastle upon Tyne, UK



Jenny C. A. Read

Institute of Neuroscience, Newcastle University,
Newcastle upon Tyne, UK



The contrast detection threshold of a grating located in the periphery is increased if a surrounding grating of the same frequency and orientation is present. This inhibition between center and surround has been termed surround suppression. In this work we measured the spatial frequency bandwidth of surround suppression in the periphery for different spatial frequencies (0.5, 1.1, 3, and 5 cycles/deg) of a sinusoidal grating (target) surrounded by a grating with different spatial frequencies (surround). Using a Bayesian adaptive staircase, we measured contrast detection thresholds in an 8AFC detection task in which the target (grating with a 2.3-deg Butterworth window) could appear in one of eight possible positions at 4° eccentricity. The target was surrounded by a grating (with a 18° Butterworth window) with the same or an orthogonal orientation. In each session we fixed the spatial frequency of the target and changed the spatial frequency and the orientation of the surround. When the surround was orthogonal to the target, the thresholds were similar to those obtained without surround, independent of the surrounding spatial frequency. However, when the target and surround had the same orientation and spatial frequency, the contrast threshold was increased by a factor ranging from 3 to 6 across subjects. This suppression reduced rapidly as the spatial frequency of the surround moved away from that of the target. The bandwidth of the suppressive effect depended on spatial frequency, declining from 2.9 octaves at 0.5 c/deg to 1 octave for frequencies above 3 c/deg. This is consistent with the bandwidth of individual simple cells in visual cortex and of spatial frequency channels measured psychophysically, both of which decline with increasing spatial frequency. This suggests that surround suppression may be due to relatively precise inhibition by cells with the same tuning as the target.

Keywords: spatial vision, surround suppression, inhibitory mechanisms, classical receptive fields

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Introduction

A small patch of pattern can be harder to see when it is surrounded by a larger area of the pattern than when it is presented in isolation. In particular, the contrast threshold for detecting a target grating is increased if the target is surrounded by a grating of the same frequency and orientation (Ejima & Takahashi, 1985; Lev & Polat, 2011; Petrov, Carandini, & McKee, 2005; Polat & Sagi, 1993; Snowden & Hammet, 1998; Xing & Heeger, 2000; Yu & Levi, 2000). The psychophysical properties of this surround suppression have been studied by several workers. As a result, we know that the strongest surround suppression occurs when the target stimulus is located in the periphery and

surrounded by an annular grating with a high contrast, the same orientation, and the same spatial frequency. Surround suppression tends to be weaker when the target is near the fovea (Petrov et al. 2005; Petrov & McKee, 2006; Snowden & Hammet, 1998; Xing & Heeger, 2000). It also depends on the relative orientation between the target and surround. Suppression is maximized if the surround grating has the same orientation as the target; surround gratings oriented orthogonal to the target have little or no effect on contrast detection thresholds (Petrov et al., 2005; Polat & Sagi, 1993). Under some conditions, orthogonally oriented surrounds can even improve contrast discrimination (Yu & Levi, 2000) and show a facilitation effect, enhancing the apparent contrast of the target (Cannon

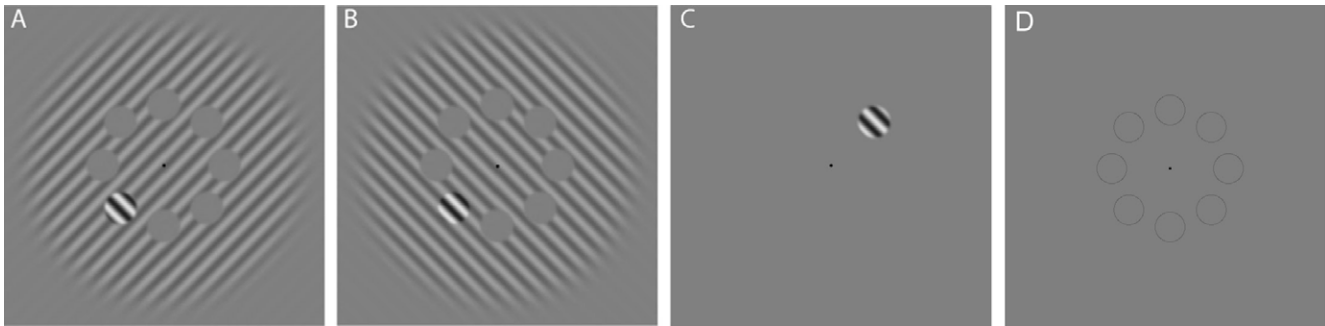


Figure 1. Example stimuli. (A) Stimulus with orthogonal surround; (B) parallel surround; and (C) no surround. In this example surround and target have the same spatial frequency. (D) Image with the eight positions outlined that appear after the stimulus.

& Fullenkamp, 1993; Ejima & Takahashi, 1985; Polat & Sagi, 1993; Yu, Klein, & Levi, 2003).

The effect (suppression or facilitation) also depends on the relative contrast of the center and surround regions. For example, surround patterns with higher contrast than the target can reduce the apparent contrast of the target (Cannon & Fullenkamp, 1991, 1993; Chubb, Sperling, & Solomon, 1989; Olzak & Laurinen, 1999; Snowden & Hammet, 1998; Xing & Heeger, 2000; Yu, Klein, & Levi, 2001; Yu et al., 2003), potentially increasing the contrast detection threshold for the target. However, if the contrast of the target is higher than the surround, a facilitation effect can occur (Cannon & Fullenkamp, 1993; Ejima & Takahashi, 1985; Yu, Klein, & Levi, 2002; Yu et al., 2003).

We also have a fair idea of the underlying neuronal mechanisms responsible for surround suppression. Analogous behavior can be seen in physiological experiments recording from single neurons. We can distinguish the effect of non-overlapping surround patterns from the masking effect produced by patterns that are spatially overlapped (overlay suppression), both psychophysically (Petrov et al., 2005) and with physiological data (DeAngelis, Robson, Ohzawa, & Freeman, 1992; DeAngelis, Freeman, & Ohzawa, 1994). Broadly, center-surround suppression seems to occur because each neuron receives inhibitory input from a pool of surrounding neurons. However, the detailed functional architecture is still not clear. For example, we do not know how closely the tuning of the inhibitory pool matches that of the center neuron. One way of assessing this psychophysically is to determine the strength of surround suppression as a function of surround frequency, keeping the center frequency constant.

The effect of surround spatial frequency on surround suppression using iso-oriented surround has been investigated by only a small number of studies (Cannon & Fullenkamp, 1991; Petrov et al., 2005; Yu & Levi, 2000; Yu et al., 2001). The results have been conflicting, complicated by the fact that center-surround interac-

tions clearly depend strongly on whether the stimulus is presented in the fovea or peripherally and on the contrasts involved. Ultimately, these psychophysical results will have to be related to the properties of visual neurons in order to gain a full understanding of the neuronal mechanisms involved.

In this paper, we contribute to this goal by measuring the effect of surround spatial frequency on the contrast detection threshold of a peripheral target grating, for both iso-oriented and cross-oriented surround gratings (Figure 1). Our objective is to determine the contrast detection thresholds of different center spatial frequencies, surrounded by gratings of different spatial frequencies, in order to measure the spatial frequency bandwidth of the suppression tuning curves.

Methods

Subjects

Four human subjects (aged between 18 and 37 years) with experience in psychophysical experiments, took part in the experiments. The subjects KL, GY, and CB were not aware of the purpose of the study. All subjects had normal or corrected-to-normal refraction and normal visual acuity. Experimental procedures were approved by Newcastle University's Faculty of Medical Sciences Ethics Committee. One author (ISP) and one experienced subject (MGC), who was not aware of the purpose of the study, took part in the control experiments. Experimental procedures were approved by Complutense University's Ethics Committee.

Equipment

The experiments were carried out in a dark room. The stimuli were presented on a 16-inch monitor (SONY Trinitron Multiscan G200, Sony Corp., Tokyo, Japan)

under the control of a PC running Matlab (MathWorks, Natick, MA) using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997; www.psychtoolbox.org) and Bits++ (Cambridge Research Systems Ltd., Cambridge, UK), giving 14 bits of gray-scale resolution. The monitor was gamma corrected using a Minolta LS-100 photometer (Konica Minolta Optics, Inc., Osaka, Japan). It had a resolution of 800×600 pixels (horizontal \times vertical) with vertical frame rate of 120 Hz, a mean luminance of 42 cd/m^2 , and was observed binocularly from a distance of 50 cm. A chin rest (UHCOTech HeadSpot, Houston, TX) was used to stabilize the subject's head and to control the observation distance. Stimuli were presented at the center of the monitor screen in a square of 19.5 cm per side (512×512 pixels), subtending an area of $22.1^\circ \times 22.1^\circ$, resulting in 23 pixels per degree of visual angle. The remainder of the screen was at the mean luminance. For the control experiments we used a 19-inch monitor EIZO Flexscan 720 (Eizo Corp., Japan) with a resolution of 1024×768 pixels (horizontal \times vertical) with a vertical frame rate of 120 Hz under the control of an Apple Macintosh Pro (Cupertino, CA). The rest of conditions (Psychtoolbox extensions, gray-scale resolution, mean luminance, chin rest, distance, and stimulus size) were the same as used in the main experiment.

Stimuli

The stimuli combined elements from Yoon et al. (2010), Cannon and Fullenkamp (1991), and Petrov et al. (2005). We used a Bayesian adaptive staircase to measure contrast detection thresholds in an eight-alternative spatial forced-choice (8AFC) paradigm in which the target (grating with a 2.3-deg Butterworth spatial window of order 10, see González & Wintz [1987, p. 179, 181] and Sierra-Vázquez, Serrano-Pedraza, & Luna [2006]; a formal definition can be seen in their appendix A) appeared randomly in one of eight possible positions at 4.1° eccentricity (see Figure 1). We chose this eccentricity because it has been shown that surround suppression (when target and surround have the same orientation) is stronger in the periphery than in the fovea and reaches a plateau at eccentricities greater than 4° (Petrov et al., 2005). The values of the stimulus parameters given here were altered in control experiments 1 and 2; the parameters used in the control experiments are described in the text.

We tested three general conditions in which the target could appear in a surround grating with an orthogonal orientation (Figure 1A), with the same (parallel) orientation (Figure 1B), or with no surround (Figure 1C). The surround gratings had a fixed Michelson contrast of 0.25 and a 18-deg Butterworth window of order 10. The orientation of the target and

surround was randomly $\pm 45^\circ$. The phase of the target and the surround was the same but randomized in each trial. Olzak and Laurinen (1999) found that stronger suppression occurs when targets and surrounds with same orientation are in phase, although Petrov and McKee (2006) found that surround suppression is not affected by the phase of the surround.

In order to control the target's contrast independent of the surround's contrast, we presented target and surround in different frames and temporally interleaved them (Schofield & Georgeson, 1999; Serrano-Pedraza & Sierra-Vázquez, 2006). Thus, although the frame rate of the monitor was 120 Hz, the stimuli were in practice presented at 60 Hz after frame interleaving. In the condition without surround we used the same technique but with zero contrast for the surround. Note that interleaving a grating of contrast 1 with gray frames reduces the final contrast of the grating by half (0.5). The contrast thresholds reported in the Results refer to the effective contrast after interleaving.

Procedure

Each trial started with a fixation cross displayed at the center of the screen using a Gaussian temporal function with standard deviation of $\sigma_t = 80$ ms truncated to give an overall duration of 500 ms. After the fixation cross the stimulus with the target (Figure 1) appeared modulated in time by a Gaussian temporal function with $\sigma_t = 100$ ms (duration of 200 ms, $2\sigma_t$), truncated to give an overall duration of 500 ms. We chose a Gaussian temporal function to control the temporal presentation because its Fourier transform is a Gaussian function too (Bracewell, 1986, p. 98, 130) and therefore it does not introduce high-temporal frequency components in the spatiotemporal frequency domain as other temporal windows do (i.e., Heaviside unit step or ideal temporal window). The contrast of the target was controlled by an adaptive staircase procedure. Then the stimulus was followed by an image with the eight possible positions outlined (Figure 1D), and the subject's task was to indicate the position of the target by pressing a mouse button. A new trial was initiated only after the observer's response; thus the experiment proceeded at a pace determined by the observer.

In each session we fixed the spatial frequency of the target and the spatial frequency of the surround. We measured contrast detection thresholds for targets of different spatial frequencies (0.5, 1.1, 3, and 5 cycles/deg) and for surrounds of different spatial frequencies around the frequency of the target.

Contrast detection threshold was defined as the minimum Michelson contrast that is needed in order to achieve a performance of 55.37% correct, with chance

being 12.5%. Contrast detection thresholds were measured using adaptive Bayesian staircases (Treutwein, 1995) using a 8AFC paradigm. In general between 4 and 6 min were required per contrast detection threshold estimation. The characteristics of the Bayesian staircases were (a) the prior probability density function was uniform (Emerson, 1986; Pentland, 1980) with a starting contrast of 0.495; (b) the logistic function was used as the model likelihood function adapted from García-Pérez (1998, appendix A) with a spread value of 1 (with delta parameter equal to 0.01, a lapse rate of 0.02, and a guess rate of 0.125); (c) the value of the target contrast in each trial was obtained from the mean of the posterior probability distribution (King-Smith, Grigsby, Vingrys, Benes, & Supowit, 1994); (d) the staircase stopped after a fixed number of trials (30 trials) (Anderson, 2003; Pentland, 1980); and (e) the final threshold was estimated from the mean of the final probability density function. Two contrast threshold estimations per condition were obtained for each subject when surround was present. Four contrast thresholds were obtained when the surround was not present. A total of 48 conditions (4 target spatial frequencies \times 2 surround orientations \times 6 surround spatial frequencies) were tested in the experiments with surround and 4 (4 target spatial frequencies) in the experiments without surround. The different conditions were counter-balanced across subjects. Practice sessions were performed previous to the experiment.

Data analysis

In order to obtain the bandwidth of the surround suppression, we used least squares estimation and the multidimensional Nelder-Mead simplex search algorithm (Nelder & Mead, 1965) to fit a log-Gaussian function (blue line in Figure 2) with three free parameters (A , f_0 , and α) to the *parallel* data (red circles in Figure 2):

$$\log_{10}[m_0(f)] = L + A \exp\left[-\frac{\ln^2(f/f_0)}{2\alpha^2}\right]; \quad (1)$$

where f_0 corresponds to the peak frequency of the fit, L corresponds to the contrast threshold of the target grating without surround, and m_0 corresponds to the contrast detection threshold of the target grating surrounded by a grating of spatial frequency f . This log-Gaussian model was chosen because it matched the shape of the data and has a well-defined bandwidth. The bandwidth (full-width at half maximum, in octaves) is:

$$B_{\text{oct}} = \alpha \times \left(2\sqrt{2}/\sqrt{\ln 2}\right) \quad (2)$$

Results

Contrast detection thresholds were measured for gratings (target) presented in the visual periphery surrounded by orthogonal (cross-oriented surround) gratings, parallel (iso-oriented surround) gratings, or with no surround. Four spatial frequencies were used (0.5, 1.1, 3, and 5 cycles/deg) for the target gratings and several different spatial frequencies for the surround, centered in each case on the spatial frequency of the target.

Figure 2 shows the results for our four subjects. Each row corresponds to one subject. Each panel shows the logarithmic contrast thresholds for detecting a target of a particular spatial frequency as a function of the spatial frequency of the surround grating. The horizontal black line represents the contrast threshold for detecting the target without any surround (base line), and the dotted lines above and below represent the standard deviation. Green squares represent the contrast thresholds for detecting the target in the presence of a surround with orthogonal orientation and different spatial frequencies (orthogonal data). Red circles represent the contrast thresholds for targets with surround of the same orientation (parallel data). Blue line represents the model (see Equation 1) fitted to the parallel data points.

Strength of surround suppression at different spatial frequencies

When the surround is parallel to the target (red circles in Figure 2), contrast thresholds are substantially higher, indicating suppression. In each case, the strongest suppression occurs when the center and surround have the same spatial frequency. When the surround is orthogonal to the target, the contrast thresholds are essentially unaffected by the presence of the surround, at least for frequencies above 0.5 cycles/deg. In Figure 3, we replot this same spatial frequency data for both parallel and orthogonal surrounds and also when there is no surround. The top row shows the contrast thresholds for our four subjects, for spatial frequencies of 0.5, 1.1, 3, and 5 cycles/deg. As expected from the human contrast sensitivity function, the curves have a similar U shape. The highest sensitivity is found for spatial frequencies between 1 and 3 cycles/degree, somewhat lower than at the fovea; a result that is expected given that contrast sensitivity declines with eccentricity (Robson & Graham, 1981) more rapidly for high spatial frequencies than for low spatial frequencies (Wright & Johnston, 1983). The bottom row shows the ratio of the contrast threshold for the parallel surround to that for the no-surround condition

