Surround Modulation Measured With Functional MRI in the Human Visual Cortex

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Williams, Adrian, L., Krishna D. Singh, and Andrew T. Smith. Surround modulation measured with functional MRI in the human visual cortex. J Neurophysiol 89: 525–533, 2003; 10.1152/jn.00048.2002. Visual context profoundly influences 1) the responses of mammalian visual neurons and 2) the perceptual sensitivity of human observers to localized visual stimuli. We present data from functional MRI studies demonstrating contextual modulation in the human visual cortex. Subjects viewed a circular grating patch that was continuously present. A surround grating was added in an ON–OFF block design to reveal its effect on the central region. Stimulus-correlated activation was quantified and visualized on a flattened map of the occipital gray matter. Modulation was measured in a region of interest activated by the central grating alone. The observed effects were predominantly suppressive, consistent with the effects typically found in single neurons and perception. Suppression was greatest when the surround and center had the same orientation and was reduced or absent when it was orthogonal. When spatial phase was manipulated, suppression was greatest for in-phase center/surround gratings and much reduced or reversed (facilitation) for opposite-phase stimuli. With eccentric stimulus presentation, suppression was reduced and facilitation became more common. The findings provide a direct demonstration of the existence of powerful and stimulus-specific surround effects in human visual cortex.

INTRODUCTION

It was discovered many years ago that stimuli outside what is now called the classical receptive field (CRF) of a visual neuron in the mammalian cerebral cortex can influence the magnitude of the excitatory response to an appropriate stimulus presented inside the CRF (Blakemore and Tobin 1972; Maffei and Fiorentini 1976; Nelson and Frost 1978). Such effects were typically suppressive but in some cases facilitatory. Surprisingly little importance was attached to these effects, which tended to be regarded as minor determinants of physiological response properties. However, the 1990s saw a resurgence of interest in this topic. Many studies were conducted that together have provided detailed information about the nature of contextual effects arising from stimulation outside the CRF. There is now a growing sense that the responses of neurons are profoundly influenced by the visual context and that these influences may be of fundamental importance in understanding the operation of visual neurons.

In V1 neurons of both cats and macaque monkeys, contextual effects are typically suppressive. These are maximal when the CRF and surround orientations are the same and reduced or absent when they are very different (Gulyas et al. 1987; Levitt and Lund 1997; Li et al. 2000; Li and Li 1994; Sillitio et al. 1995). There is considerable variability among neurons (e.g., Nothdurft et al. 1999). As in the early studies, facilitation is also sometimes seen and the relative contrasts of the center and surround stimuli can be important (Polat et al. 1998). There are also some reports that the tuning properties of the CRF response can be altered (e.g., Gilbert and Weisel 1990). The relative direction of motion of center and surround stimuli is important in direction-sensitive neurons both in areas 17 and 18 of the cat (Kastner et al. 1999; Li 1999) and particularly in monkey areas MT and MST (Allman et al. 1985; Eifuku and Wurtz 1998; Tanaka et al. 1986). Influences from outside the CRF may vary with cortical lamina (Raiguel et al. 1995) and they may be asymmetric (Xiao et al. 1997).

In the context of psychophysical measurements of human perception, related phenomena have been demonstrated and a similarly complex picture emerges. One approach has been to measure the effect of contextual stimuli on contrast detection thresholds. The threshold for detecting a grating patch is elevated by the addition of flanking patches (Bowling 1985; Ejima and Takahashi 1983; Snowden and Hammett 1998) but several authors have reported facilitatory effects (e.g., Tanaka and Sagi 1998; Yu and Levi 2000) and a few have obtained both facilitation and suppression under different circumstances (e.g., Polat 1999). Another approach is to study the effect of contrast on the perceived contrast of a suprathreshold target. Ejima and Takahashi (1985) reported that perceived contrast is reduced if flanking gratings have a higher contrast than the test grating but is increased if they have a lower contrast. Others have found only suppressive effects (Cannon and Fullenkamp 1991; Olzak and Laurinen 1999; Xing and Heeger 2000).

Despite the widespread occurrence of these contextual influences, their purpose remains unclear. One function could be contrast normalization (e.g., Heeger 1992). However, the complexity and stimulus specificity of some of the observed effects suggests additional, more sophisticated functions (e.g., Sillitio et al. 1995).

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In this study, we use functional MRI (fMRI) to study the effect of a surround grating on the magnitude of the activity evoked in the visual cortex by a target grating. Contextual effects in single units vary greatly among neurons, making it difficult to assess the importance of each type of effect or to deduce their overall consequences at the population level. Psychophysical findings reveal the net result of such effects on our perception, but do not allow us to map these results onto their substrates. Potentially, fMRI can reveal the overall trends seen in large neuron populations while still allowing different visual areas to be studied separately. The purpose of the experiments in this paper is to explore the feasibility of using fMRI in this way, to establish some basic findings, and to relate them to existing psychophysical and neurophysiological results.

This work was previously published in abstract form (Williams et al. 2001a,b).

**GENERAL METHODS**

**Subjects**

The subjects were eight healthy adults including the three authors and five volunteers who were paid for their time. Some participated in more than one experiment. Subjects were screened in accordance with standard procedures and informed consent was obtained in writing.

**Visual stimulation**

Visual stimuli were generated by a computer and were projected onto a rear-projection screen by means of an LCD projector (resolution 1024 × 768 at 75 Hz). The subject lay supine in the scanner. In Experiment 1, the subject looked upwards at a mirror in which an image of the projection screen was reflected binocularly. This arrangement gave an image that was approximately circular and had a diameter of 9° (maximum) at the viewing distance of 3.5 m. In Experiment 2 (which involved peripheral stimulus presentation), the subject looked with the dominant eye into a custom-built optical device that magnified the image on the screen by a factor of three. This gave a monocular, circular image of diameter 27°. The nondominant eye was occluded. In all experiments, the mean luminance of the image was approximately 240 cd/m².

The stimuli were sine gratings that reversed in phase (counterphased) at 5 Hz. Counterphase gratings were used because they give stronger activation than static gratings in fMRI experiments. They are illustrated in Fig. 1. A block design was used in which a central grating patch was continuously present and a surround grating annulus appeared and disappeared with a squarewave temporal profile (30-s cycle; see Fig. 1). This made it possible to set up tonic activation in those parts of the retinotopic visual areas that represent the visual field locations occupied by the central patch and to observe the effect of the appearance of the surround on that activation. The central grating was always horizontal. The diameter of the central grating was always three times the period of the grating (see Fig. 1A). The spatial frequency of the annular grating was always the same as that of the

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**FIG. 1.** The stimuli used and their time courses. In each case the time profile of the center and surround stimuli are shown on the left. Each on–off cycle lasted 30 s and 8 cycles were presented (only 4 are shown). Images from the 2 phases of the block design are shown on the right. A: sample stimuli used in the main experimental conditions. A central, counterphasing grating stimulus was continuously present while the surround, which could have the same or the orthogonal orientation, appeared and disappeared. B: control stimulus. The center appeared and disappeared and there was no surround. C: ROI definition stimulus, used for defining the cortical representation of the central stimulus. The center and annulus, which were both flickering, were presented in opposite temporal phases to demarcate the boundary between them.
center and its width was always equal to the radius of the center. Its orientation could be either the same (parallel) or orthogonal.

A small central fixation spot (0.25° diam) was continuously present during all experiments. To aid fixation and to maintain attention in a constant state, the subject was given a task relating to the spot. The spot changed randomly in color at a rate of 0.5 Hz and the subject was asked to count the number of times he/she saw one particular color that had been identified beforehand.

To measure the activity produced by the central grating itself, an additional block design was used in which the central grating stimulus appeared and disappeared and there was no surround (see Fig. 1B). This was referred to as the “control stimulus” and its purpose was to make it possible to express the effects of surrounds on center activation (obtained in the main experiments) as a proportion of the center activation itself.

The control stimulus could also have been used to identify the patch of visual cortex that responded to the central stimulus (the region of interest or ROI). However, to identify the ROI with maximum accuracy, a flickering central checkerboard stimulus was alternated with a flickering checkerboard surround (see Data analysis for the rationale for this choice). This stimulus is referred to as the “ROI definition stimulus”.

The stimulus and its time course are shown in Fig. 1C. The checkerboard had a high contrast and the frequency of contrast reversal was 8 Hz. The dimensions of the center and surround were the same as in the main experiments.

Data acquisition

Imaging was performed with a 1.5-T whole-body General Electric LX/Nvi scanner equipped with a 40 mT/m gradient system. The subject was positioned with the head in an RF receive-transmit headcoil. Local variations in blood oxygenation (BOLD response) were measured using susceptibility-based fMRI, applying gradient-recalled echo-planar imaging (EPI) sequences.

Either 20 or 24 parallel, 3-mm-thick planes were imaged using a T2*-weighted sequence (TR = 3000 ms, TE = 40 ms, field of view = 190mm, 64 × 64 voxels). The planes were axial and were chosen with the aid of a midsagittal T1-weighted scout image to include the entire occipital lobe. Each experimental run lasted for 4 min, during which time functional images were acquired continuously. Each point in the acquisition volume was sampled once every 3 s.

For each subject, a sagittal T1-weighted SPGR volume scan of the posterior third of the brain was acquired (voxel size 0.78 × 0.78 × 1.6 mm). This was used to determine the anatomical localization of functional responses. The analysis included simulated cortical flattening to obtain two-dimensional representations of cortical gray matter (Engel et al. 1997; Sereno et al., 1995).

Data analysis

Each functional volume was first processed using a 3-D motion correction program, AIR (automated image registration) (Woods et al. 1992). This realigns the functional volumes in the time series so as to compensate for movement of the head within a run and then reslices the volumes. Spatial smoothing of the functional signal was performed by convolution with a 3-D Gaussian function of SD 4 mm. This smoothing reduces spatial noise (Friston et al. 1995).

Activation profiles were analyzed and visualized using BrainTools (http://www.aston.ac.uk/~singhk/mri3dX), which was developed by the second author. The temporal activity profile of each voxel was correlated with an ideal response profile. The latter consisted of a squarewave representing the ON–OFF surround stimulus cycle, which was retarded in phase by 6 s, representing the expected hemodynamic delay, and smoothed with a Gaussian kernel (SD = 3 s). The time-course of each voxel was smoothed with the same Gaussian, to reduce temporal noise. Any linear trend over time was corrected. Cortical activation was then estimated for each 4-min run as the stimulus-correlated activation (SCA), which is the product of the correlation coefficient for the voxel and the SD of the signal, calculated over the entire run (Bandettini et al. 1993). In terms of the equivalent General Linear Model, SCA is the amplitude of the main component of interest and it is linearly related to the mean percentage signal change from baseline.

To visualize the functional activation values, a 2-D representation of occipital cortex was derived from the 3-D anatomical data set, using an algorithm developed at Stanford (Teo et al. 1997; see http://white.stanford.edu/~brian/mri/segmentUnfold.htm). This algorithm simulates a process of flattening a portion of the gray matter (typically centered in the calcarine sulcus) into a 2-D surface. Having obtained a flattened representation of the occipital cortex of each hemisphere in each subject, activations were superimposed as pseudocolor overlays.

To observe the modulatory effects of a surround stimulus on the response to a central stimulus patch, a region of interest corresponding to the central patch had to be carefully defined. Since the center and surround are spatially adjacent and fixation is always imperfect, there will inevitably be a zone of cortex around the boundary that is stimulated by both center and surround during the course of the experiment. When estimating activity caused by the center stimulus alone, it is important to exclude this zone of contamination by the surround. This was achieved with the aid of the ROI definition stimulus (see Visual stimulation). In one phase of a block design, a high-contrast flickering checkerboard filled a circular patch corresponding to the size and location of the circular grating patch used in the main experiments. In the other phase, this patch disappeared and a concentric circular checkerboard annulus was presented (see Fig. 1C). Following correlation with a model waveform describing the temporal profile of the central patch, activation by the patch itself gave a positive correlation while activation caused by the surrounding annulus gave a negative correlation. When displayed as a colored overlay on a flattened representation of the cortex, these correlations appeared as a red/orange patch surrounded by blue/purple (see Fig. 2A). To define the region of interest to be used for quantitative measurements of activation in the main experiments, a region comfortably larger than the (red) center-related activation was first defined on the flatmap. The 3-D voxels that fell within this area were identified. To strip off the surround and leave a region of cortex corresponding to the central stimulus only, any voxels that did not 1) have a positive correlation with the center stimulus and 2) have an uncorrected P value of <0.01 were eliminated. This was to avoid the blurring effect of multiple microsaccades around the fixation point. By setting a threshold well above zero correlation, voxels in the border region that may be contaminated by direct activation from the surround are largely eliminated, leaving a relatively pure, central region of interest. Figure 2B shows the flatmap of Fig. 2A after thresholding in this way. The set of voxels included in the ROI on this basis defined the central measurement zone that was used for all other experimental conditions run in the same session. For each such experimental condition, activation in the included voxels was averaged to yield a mean activation value for the central region.

Because the stimulus was usually foveal, it was not possible to distinguish the visual areas (V1, V2, and V3) with adequate reliability. The region of interest must be assumed to include the central portions of several visual areas, not just V1.

Experiment 1: Effect of an annular surround on a foveal target

In this experiment we examined the effect on the activation produced by a centrally fixated circular grating of an annular surround grating of either the same or the orthogonal orientation. The central target grating was horizontally oriented, had a contrast of 25%, and a spatial frequency of 1.0 c/°. Its diameter was 3°. The surrounding
annulus had the same spatial frequency and contrast but could be either horizontal (parallel to the center stimulus) or vertical (orthogonal). The spatial phase relationship between the two gratings was randomized. The central grating was present continuously, while the surround repeatedly appeared for 15 s and then disappeared for 15 s. The background was unpatterned and its luminance was the same as the mean luminance of the gratings.

Within a single scanner session, each of the two types of stimulus presentation (parallel and orthogonal surround grating) was repeated at least three times and the results averaged, so as to obtain accurate estimates of the effect of the surround. Control runs and ROI definition runs (see Visual stimulation) were also conducted. This first experiment, which was long and required sustained motivation, was conducted on the three authors and one experienced volunteer only.

In each hemisphere of each subject, an ROI corresponding to the cortical representation of the center stimulus was defined using the thresholding method. For each repetition of each of the two main experimental conditions (parallel and orthogonal surround), the mean activation in the central region was calculated and the results were then averaged across the three or four identical runs. Activations for the control condition were obtained using the same ROI. Data from one hemisphere had to be discarded due to signal dropout.

Figure 3 shows sample BOLD time courses for one subject along with the waveform used for correlation with the data. In the ROI definition and control conditions (Fig. 3, A and B), activation simply reflects the appearance of the center grating. These conditions gave relatively large (about 2 and 1%, respectively) signal changes that were correlated with the stimulus profile (dotted lines). In the parallel and orthogonal surround conditions (Fig. 3C–F), “activation” (better thought of as temporal modulation of activation in this case) reflects the effect of the appearance of the surround on activity in the center, since the center stimulus itself is continuously present and gives no modulation. As expected, these conditions show less systematic variation than the control conditions. What there is tends to be negatively correlated with the correlation waveform, i.e., it reflects suppression by the surround, rather than facilitation.

Figure 4 summarizes the results, averaged across subjects. Figure 4, left, shows the results in terms of SCA. The control condition gives a large positive response. A grating surround of the same orientation, contrast, and spatial frequency as the center (the parallel surround condition) causes marked suppression of activity. When the surround grating is orthogonal in orientation, however, this suppression is absent. An ANOVA showed that the difference between the parallel and orthogonal conditions was statistically significant: $F(1,12) = 5.99, P < 0.05$. Figure 4, right, shows the same results expressed as a percentage of the activation produced by the center grating itself (control condition). It shows that, for a parallel surround, the suppression is about 28%.

These results reflect activity in several visual areas (at least V1, V2, and V3). It is therefore possible that they mask important differences between these areas. Estimating the positions of the boundaries on the basis of retinotopic mapping data (see Fig. 2) and analyzing the areas separately suggests that the results are similar in all areas. However, the reliability of these estimates is low in the fovea because of corruption of temporal phase data by fixation instability.

**Experiment 2: Effects of peripheral viewing and spatial phase**

In this experiment, we investigate two separate factors that may influence the magnitude of the surround suppression that we report in Experiment 1.

First, we examine the importance of retinal location. Xing and Heeger (2000) have recently reported that the reduction of the per-
received contrast of a central grating target caused by a surrounding grating is much greater when the stimuli are presented in the peripheral visual field (eccentricity 10°) than when presented in the center. We therefore repeated our experiments with peripheral presentation of the stimuli.

Second, the fact that we randomized the spatial phase relationship of the center and surround gratings in Experiment 1 may be important. Several studies have reported that spatial phase has no effect on suppression (e.g., Solomon et al. 1993; Xing and Heeger 2001; Zenger and Sagi 1996) and it was on this basis that we randomized phase in Experiment 1. But other studies have found phase to be important. In an early study, Ejima and Takahashi (1985) reported that, when a target grating was in phase with two flanking gratings, facilitation was seen for low surround contrasts and suppression was seen for high contrasts. When they were in opposite phases, only suppression was seen and it tended to be less marked. More recently, Olzak and Laurinen (1999) measured perceived contrast of a center grating stimulus as a function of surround contrast and phase. They found that perceived contrast was reduced when the surround was in phase but not when it was in antiphase, although with plaid stimuli they found suppression in both phase relations. In view of the latter studies, and the substantial variability observed in our results with random phase, we studied two fixed phase relations separately in Experiment 2.

In a single imaging session, we separately presented circular gratings in the foveal and peripheral visual field. These were surrounded by parallel gratings that were either in the same spatial phase as the target or in the maximally different phase (180°). The contrasts of the center and surround gratings were both 25%. There was minimal separation between the two zones and so the in-phase stimulus appeared as a large, almost undifferentiated patch while the antiphase stimulus had a clearly demarcated center. We also presented control stimuli and ROI definition stimuli similar to those used in Experiment 1 but appropriately adjusted in size, location, and spatial frequency.

Different stimulus sizes and grating spatial frequencies were used...
in the foveal and peripheral conditions. There were two reasons for this. First, the cortical magnification factor (cortical extent in mm per degree of visual angle) falls sharply with increasing eccentricity. As a result, a given visual stimulus produces a much smaller area of activation on a cortical flatmap if presented in the periphery than in the fovea. It is therefore necessary to use a large stimulus in the periphery so as to obtain an active ROI large enough to give activation measurements with an acceptable signal-to-noise ratio. Second, spatial frequency sensitivity varies with eccentricity and we wished to compare stimuli of like sensitivity. Consequently, it was desirable to scale the peripheral stimulus in spatial frequency as well as size. The number of spatial cycles in the central and surround zones was held constant and the entire stimulus was scaled.

In foveal presentation conditions, the grating spatial frequency was 1.5 c/°, the center diameter was 2°, and the width of the annulus was 1°. The fixation spot was in the middle of the center grating, as in previous experiments. In the peripheral presentation condition, the grating spatial frequency was 0.375 c/°, the center diameter was 8°, and the width of the annulus was 4°. The stimulus eccentricity was 7°.

The stimulus was presented in one quadrant of the visual field (i.e., offset from the fixation point both horizontally and vertically). To obtain the best estimate of surround modulation, four center gratings were presented simultaneously, one in each quadrant, each with its own surround (the surrounds partially overlapped). Each center region was located on the flatmap and analyzed separately and then the four results were averaged. Seven subjects were tested.

A typical result for peripheral presentation is shown as a color overlay on a flatmap in Fig. 2, E and F. Within V1, two active regions can be seen in the ROI definition condition (Fig. 2E), reflecting the center stimuli in the upper and lower quadrants of the hemifield represented. Further active regions can be seen in V2 and V3. Activation was measured in these regions, defined using the thresholding procedure used in Experiment 1. Figure 2F shows the result obtained in the main experiment, using center and surround gratings in the same spatial phase, for the flatmap shown in Fig. 2E.

Figure 5 shows quantitative results for all conditions, averaged across 14 hemispheres and including all visual areas up to V3. In Fig. 5A, the results are shown in terms of suppression/facilitation ratios, as in Fig. 4, right. For foveal presentation, there is a very large (76%) suppressive effect when the center and surround stimuli are in phase, but this completely disappears when the stimuli differ in phase by 180°. This is broadly consistent with Fig. 4, in which suppression is about 28% with phase randomized and strongly suggests that spatial phase is indeed important for contextual modulation of this kind. For peripheral presentation (Fig. 5A, right), the results are quite different. In-phase stimuli give only modest suppression and antiphase stimuli
give a marked (24%) facilitation. Thus there appears to be a marked shift from suppression to facilitation when moving from the fovea to the periphery. A two-way ANOVA shows that the effects of location (central versus peripheral; \( F(1,52) = 9.67, P < 0.003 \) and spatial phase \( F(1,52) = 23.5, P < 0.0001 \) are both statistically significant.

When peripheral stimuli are used, the different visual areas (V1, V2, etc.) are easier to distinguish than when foveal stimuli are used. This is because 1) fixation instability blurs the areal boundaries more in the fovea than in the periphery because of greater cortical magnification and 2) a foveal stimulus fills each quadrant (at low eccentricities) so there is no gap between its representations in adjacent areas. In some subjects, we were able to discern distinct peripheral activations in some or all of V1, V2d, V2v, V3, and VP (see Fig. 2E). But we were unable to do this in enough cases to obtain reliable data for all visual areas. We therefore used a region of interest that encompassed all areas in which activity was evident, as in Experiment 1. Where distinct activations were evident, the thresholding method, used to define the representation of the center stimulus, picked out and summed the different activations, excluding the inactive zones separating them. Additional measurements of the separate areas were made in cases in which this was feasible. Based on these cases, the magnitude and stimulus specificity of suppression and facilitation appear to vary little among the retinotopic visual areas up to V3.

In interpreting the difference between foveal and peripheral presentation, it is instructive to look at the raw activation levels, which are shown in Fig. 5B. For foveal presentation, the control stimulus yields about 27% of the activation produced by the ROI definition stimulus. This figure is closely consistent with the result (23%) obtained in Experiment 1 and presumably reflects the lower contrast and the single orientation and spatial frequency of the control stimulus compared with the ROI definition stimulus. But for peripheral presentation, the control stimulus gives a much higher activation, while ROI definition gives only slightly higher activation, leading to a much higher ratio of 87%. This difference is consistent across subjects. The reason for it is open to debate, but given that (in Fig. 5A) suppression/facilitation is calculated as a percentage of the response to the center stimulus alone, the high control activation has consequences for calculating suppression. In terms of raw activation levels (Fig. 5B), the difference between foveal and peripheral surround suppression looks rather less dramatic, particularly in the 0° case. However, the appearance of facilitation (peripheral presentation, 180° phase) cannot be explained away, since facilitation, as well as suppression, would be reduced (as a percentage) by an increased response to the control stimulus.

It should be borne in mind that four “centers” (targets) were presented simultaneously in the peripheral presentation condition, so as to obtain a separate measurement from each quadrant of the visual field and so as to maximize the number of measurements obtained from the dataset. It is possible that these center stimuli interacted with each other, each contributing surround modulation to the others. Despite their spatial separation. On the face of it, a larger surround should (if anything) increase the magnitude of any suppressive effect observed with a smaller surround. But there is some evidence that suppression is associated with near surrounds and facilitation with more distant surrounds (Polat 1999), which might explain the observed shift toward facilitation with peripheral viewing. It should also be borne in mind that the different visual areas (V1, V2, and V3) were activated patchily in the peripheral condition (see Fig. 2, E and F), so it is possible that the weighting of the contributions from the different areas may be slightly different in the foveal and peripheral conditions.

**Discussion**

The results described in this paper reflect a preliminary attempt to study the effects of surround stimuli on the neural activity evoked in human visual cortex by a small target stimulus, using fMRI methods. Using a simple, circular sine grating stimulus to evoke a BOLD response and a restricted set of surround gratings, we have demonstrated suppression of activity by a surround stimulus and, in one case, facilitation.

Explorations of contextual effects of this kind in the realm of both perception (changes in detection thresholds and in perceived contrast) and single-unit neurophysiology are very much more comprehensive than our study and yield a rather complex picture, suggestive of an interplay of several different mechanisms with different properties (e.g., Polat 1999). We have merely sampled the resultant of these influences in a very limited set of stimulus conditions. However, our results show that contextual effects can be studied using fMRI methods, because activity arising from the target, activity arising from the surround, and modulatory effects of the surround on the target can all be distinguished and measured separately. This opens a new avenue for exploring what is increasingly seen as a fundamentally important aspect of visual function.

**Relation to other studies**

There are obvious parallels between our results and the various studies of detection thresholds, perceived contrast, and single-unit responses reviewed earlier. If we take the view that reduced activation as measured by blood oxygenation reflects reduced neural activity (see *Relationship between fMRI and neuronal activity*), the results can be compared directly.

Our two main findings are 1) that surround effects are predominantly suppressive and 2) that such effects are tuned for orientation. Both phenomena have been demonstrated clearly in single neurons, both in area 17 of the cat (e.g., Li and Li 1994; Nelson and Frost 1978) and in area V1 of the macaque monkey (e.g., Jones et al., 2001; Levitt and Lund 1997). Likewise, both results have been found repeatedly in the realm of psychophysics (e.g., Cannonad Fullenkamp 1991; Ejima and Takahashi 1983; Xing and Heeger 2000).

A third finding of our study is that suppression appears to give way to facilitation as stimulus eccentricity increases (Fig. 5). There are several reports of facilitation in single units (e.g., Gilbert and Wiesel 1990; Sillito et al., 1995), although they are less frequent and are more controversial (e.g., Walker et al., 1999) than reports of suppression. This state of affairs is paralleled by the fact that suppression is the norm in our own data. We know of no physiological evidence that facilitation increases with stimulus eccentricity, although surround effects do not appear to have been studied as a function of receptive field eccentricity in the context of single neurons. In terms of psychophysics, there also several reports of facilitation (e.g., Ejima and Takahashi 1985; Tanaka and Sagi 1998), but, again, few studies in which stimulus eccentricity was manipulated. Our results do not mirror those of Xing and Heeger (2000), who report that suppression of perceived contrast is increased, not reduced, in the periphery.

A fourth finding is that suppression occurs when the surround is in the same spatial phase as the center but not when it is in the opposite phase. This closely mirrors the effects of phase on perceived contrast found by Olzak and Laurinen (1999).

A recent attempt to summarize and model the perceptual effects of surround stimuli on the perceived contrast of gratings has been provided by Xing and Heeger (2001). Although that...
study is perhaps no more definitive than any other, it does present a coherent picture and there are many commonalities, both between their stimuli and ours and between their perceptual results and our fMRI findings. In line with previous authors, they find a predominance of suppression, but facilitation by low-contrast surrounds. Suppression is markedly reduced when the center and surround gratings are orthogonal. The only substantial difference between their perceptual results and our neuroimaging data is that they find no effect of the spatial phase of parallel center/surround gratings, whereas we find a marked effect (Experiment 2). Interestingly, however, they suggest a way of resolving the conflict in the literature on this point. Their stimuli had a small gap between center and surround, so that the two zones were always clearly demarcated, and they suggest that this may be important since previous studies reporting an effect of phase have not used a gap. It may be that when the combined stimulus is perceived as a single grating (in-phase stimuli), global or high-level factors come into play, giving a different result. One possibility is that when the two stimuli are not separated, phase-dependent brightness induction effects occur (Ejima and Takahashi 1985; Yu et al. 2001). It should be noted that in both our study and that of Xing and Heeger (2001), the surround was close to the center and had a limited spatial extent. At least one study (Polat 1999) suggests that, while local interactions may be predominantly suppressive, facilitation is the norm when there is a large separation between target and inducers.

Press et al. (2001) have recently reported fMRI results that are equivalent to one of our conditions, namely foveal stimulation with a parallel surround in the same spatial phase as the center stimulus. They measured spatial summation, i.e., they defined a small region of interest and stimulated it with patches of grating of various sizes. They report that, in V1, V2, and V3, extending the stimulus beyond the measured region resulted in 60–90% suppression but that, in V3A, V3B, and V7 there was no such suppression. It is not clear how reliably they separated these areas in the foveal representation, which we did not attempt. But our results, in which we pooled the retinotopic areas and obtained ≤76% suppression with in-phase stimuli, is in line with the mean of their results.

Relationship between fMRI and neuronal activity

The interpretation of our results is predicated on the assumption that a change in the BOLD response measured in fMRI experiments is tightly coupled to the level of neuronal activity in the region measured. This is controversial, although it is becoming less so, and the debate is now moving toward which aspects of the neural response are reflected in the BOLD response (Logothetis et al. 2001). Of particular importance here, since suppression is suggestive of inhibition from neurons responsive to the surround, is the question of whether inhibitory synaptic activity reduces the BOLD response (because it reduces net activity) or increases it (because it makes metabolic demands, including consumption of oxygen). Logothetis et al. (2001) have suggested that BOLD reflects neural input and intracortical processing rather than the spiking output of neurons. But their conclusion is based on a correlation with the spectral power of local field potentials, which could perhaps be changed in either direction by inhibition. Scannell and Young (1999) have argued that, although neural metabolic demand arises principally in synapses, so that inhibition is expected to increase oxygen consumption, in practice, levels of excitation and inhibition tend to track each other, with the result that the BOLD response reflects spike count fairly accurately. Likewise, Rees et al. (2000) have provided empirical evidence that the BOLD response is directly related to spike count in visual area V5. Boynton et al. (1999) have argued that fMRI activation is closely correlated with contrast and that this in turn is related to spike count. Logothetis et al. (2001) themselves found an extremely high correlation between local field potentials and spiking output when stimulus contrast was varied. Thus, in many cases, it may be sufficient to assume that inputs and outputs, synaptic activity and spikes, excitation, and inhibition are all highly correlated with each other. Obviously the correlation cannot be perfect or no processing could occur, but the difference may be too subtle to matter at the current stage of development of fMRI. Unfortunately, to the extent that the correlation is imperfect, it may be phenomena such as surround suppression that will most reflect the difference. Arguably, the fact that our BOLD signals mostly decrease in circumstances in which single-unit activity is typically reduced suggests that inhibition reduces, rather than increases, the BOLD signal.

Influence of adaptation effects

In our experiments, the center stimulus that provides the substrate for contextual modulation is present continuously. Inevitably, adaptation occurs during the measurement period, resulting in reduced perceived contrast and possibly reduced cortical activation. The quantitative accuracy of our data could be compromised by this fact. However, any such effects can only be secondary. A fall in stimulus-related activity will have no effect on activation as we measure it, since we measure only modulation that is correlated with the appearance of the surround. Only if the modulatory effect of a surround varies with the adaptation state of the recipient cortical region will our measurements be affected. This is quite possible, but any such effects should be similar in all conditions, since we used similar center stimuli throughout.

Mechanisms of surround modulation

Of prime interest is the origin and purpose of the modulatory signals whose influence is evident in changes in perceived contrast and fMRI signal. Various purposes have been suggested, including low-level operations such as contrast gain control and more sophisticated processes such as object segmentation. Some have suggested that multiple mechanisms may be involved (e.g., Ido et al. 2000). An important clue to their nature must lie in the extent to which interactions are local (intracortical horizontal connections) or involve feedback to the visual cortex from higher cortical areas. Several studies suggest the latter. Zipser et al. (1996) recorded responses from monkey V1 neurons and found that facilitatory contextual modulation appears only after 80–100 ms, suggesting feedback from other areas. Similarly, Hopé et al. (1998) showed that cooling MT in monkeys reduces the influence of context on responses to moving bars in V1–V3. At the same time, some cortical interactions may well be local. Certainly contextual effects are sufficiently complex to support more than one
mechanism and purpose. Because of poor temporal resolution, fMRI data do not enable us to study feedback-related delays and so other strategies will be required.

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