

Selectivity and Spatial Distribution of Signals From the Receptive Field Surround in Macaque V1 Neurons

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Cavanaugh, James R., Wyeth Bair, and J. Anthony Movshon. Selectivity and spatial distribution of signals from the receptive field surround in macaque V1 neurons. *J Neurophysiol* 88: 2547–2556, 2002; 10.1152/jn.00693.2001. The responsiveness of neurons in V1 is modulated by stimuli placed outside their classical receptive fields. This nonclassical surround provides input from a larger portion of the visual scene than originally thought, permitting integration of information at early levels in the visual processing stream. Signals from the surround have been reported variously to be suppressive and facilitatory, selective and unselective. We tested the specificity of influences from the surround by studying the interactions between drifting sinusoidal gratings carefully confined to conservatively defined center and surround regions. We found that the surround influence was always suppressive when the surround grating was at the neuron's preferred orientation. Suppression tended to be stronger when the surround grating also moved in the neuron's preferred direction, rather than its opposite. When the orientation in the surround was 90° from the preferred orientation (orthogonal), suppression was weaker, and facilitation was sometimes evident. The tuning of surround signals therefore tended to match the tuning of the center, though the tuning of the surround was somewhat broader. The tuning of suppression also depended on the contrast of the center grating—when the center grating was reduced in contrast, orthogonal surround stimuli became relatively more suppressive. We also found evidence for the tuning of the surround being dependent to some degree on the stimulus used in the center—suppression was often stronger for a given center stimulus when the parameters of the surround grating matched the parameters of the center grating even when the center grating was not itself of the optimal direction or orientation. We also explored the spatial distribution of surround influence and found an orderly relationship between the orientation of grating patches presented to regions of the surround and the position of greatest suppression. When surround gratings were oriented parallel to the preferred orientation of the receptive field, suppression was strongest at the receptive field ends. When surround gratings were orthogonal, suppression was strongest on the flanks. We conclude that the surround has complex effects on responses from the classical receptive field. We suggest that the underlying mechanism of this complexity may involve interactions between relatively simple center and surround mechanisms.

INTRODUCTION

The responses of neurons in visual cortex can be modulated by stimuli outside the *classical receptive field* or CRF (see Allman et al. 1985, for a review). In the preceding paper (Cavanaugh et al. 2002), we studied the influence of the re-

ceptive field surround on responses elicited by stimulation of the CRF. We showed that the surround exerted a divisive, inhibitory influence on signals from the center and that center and surround signals seem to arise from independent mechanisms with different contrast sensitivity and adaptation characteristics. In those experiments, we stimulated the surround with gratings at the orientation preferred by the neuron. This configuration is generally agreed to maximize the strength of surround inhibition (Blakemore and Tobin 1972; DeAngelis et al. 1994; Knierim and van Essen 1992; Levitt and Lund 1997). But there is a range of reports in the literature on the specificity of surround effects, both facilitatory and suppressive. Some have reported facilitation for surround targets at the preferred orientation (Kapadia et al. 1995; Nelson and Frost 1985), a puzzling contrast to the results cited in the preceding text and described in the previous paper. We suggested in the previous paper that this probably arises when stimuli intended to activate the surround encroach on subthreshold excitatory regions of the CRF. This encroachment may also explain facilitation that is evident when the surround target is oriented orthogonal to the preferred orientation (Knierim and van Essen 1992; Levitt and Lund 1997) because under some stimulus conditions, the center's sensitivity is relatively high and otherwise subthreshold regions of the CRF may become effective in driving the neuron (Cavanaugh et al. 2002). Finally, Sillito et al. (1995) reported that influence from the surround could under some circumstances adjust itself so that it was maximal for the stimulus present in the CRF (see also Allman et al. 1985). This raises the question of whether the specificity of the surround is itself dependent on stimulus context.

Surround targets are typically annular and uniformly stimulate the entire surround region. But there is no particular reason to believe that the surround itself is uniform, and several groups have reported markedly inhomogeneous distributions of surround inputs (DeAngelis et al. 1994; Nelson and Frost 1985; Walker et al. 1999).

To extend the analysis we described in the preceding paper, we explored the orientation and direction selectivity of surround influences and confirmed that these influences are maximal when the surround stimulus is at the neuron's preferred orientation. We also examined the relationship between the stimulus in the receptive field center and the surround and found that, at least for broadly tuned cells, the orientation

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selectivity of inhibition from the surround tended to match the orientation *presented* to the CRF rather than the orientation *preferred* by the CRF. We studied the effect of the contrast level presented to the CRF on the influence of the surround and found that suppression was less selective for orientation when the center contrast was reduced. Finally, we examined the spatial distribution of surround influences and found that on average the most effective inhibition from small areas of the surround occurred when the surround target was oriented along an axis that “pointed” toward the CRF. We conclude that although the receptive field surround can be modeled as a relatively simple mechanism, it modulates neuronal responses in complex ways that depend on both the orientation and spatial location of the surround targets and on their relationship to the stimulus in the center of the receptive field.

METHODS

These experiments were conducted at the same time and on the same subjects as the ones described in the previous paper (Cavanaugh et al. 2002), using methods that are detailed there.

Orientation and direction: terms and measures

The experiments described in this paper involve manipulations of the orientation and direction of movement of drifting sinusoidal gratings. Because most selectivity measurements involve stimuli moving in all possible directions, we refer to these as measuring “direction tuning,” understanding always that the stimulus orientation is orthogonal to the direction of movement. Our measure of the precision of direction and orientation tuning, described below, we term the “selectivity index.” On occasion, it is of interest to consider the relative preference for the two directions of movement of a grating at a particular orientation, which we refer to as “direction selectivity.”

To characterize direction tuning curves, we used a vector calculation to estimate a preferred direction and a selectivity index (Leventhal et al. 1995; O’Keefe and Movshon 1998). Consider the data as vectors (θ_n, R_n) , in which the angle θ_n is the direction of stimulus movement for the n th stimulus (always orthogonal to the orientation) and the magnitude R_n is the neuronal response with baseline firing subtracted. The *preferred direction* is then simply the circular mean angle

$$\arctan\left(\frac{\sum_n R_n \sin(\theta_n)}{\sum_n R_n \cos(\theta_n)}\right) \quad (1)$$

To measure a *direction selectivity index*, we first calculate the summed response vector

$$\mathbf{v} = \sum_n R_n \exp(i\theta_n) \quad (2)$$

then normalize the magnitude of \mathbf{v} by the summed magnitude of all the response vectors

$$\frac{|\mathbf{v}|}{\sum_n |R_n|} \quad (3)$$

This index has a value of 0 for a data set falling uniformly on a circle and a value of 1 for a data set with response only to a single direction.

To estimate analogous quantities for tuning curves with two lobes rather than one (i.e., cells with orientation selectivity but no direction selectivity), we modify the first two equations simply by substituting $2\theta_n$ for θ_n and halving the resulting angle. This results in an *orientation selectivity index* appropriate for functions with periodic peaks and troughs every 180° rather than every 360° .

Neurons that are directionally selective tend to have high values of the direction selectivity index, while nondirectional but orientation-selective neurons tend to have high values of the orientation selectivity index. We always computed both selectivity indices for each neuron, and took the larger value as the selectivity index; the preferred direction was always taken from Eq. 1.

When we had occasion to estimate the selectivity of response suppression by the surround, we used analogous methods by converting the effect of the surround stimulus into a mean vector given by

$$\mathbf{v}_{\text{dir}}^{\text{supp}} = \sum_n (R - R_n) \exp(i\theta_n) \quad (4)$$

or

$$\mathbf{v}_{\text{ori}}^{\text{supp}} = \sum_n (R - R_n) \exp(i2\theta_n) \quad (5)$$

to estimate the selectivity of suppression, where R is the reference response (typically to a center stimulus alone), and R_n is the response when the surround stimulus drifted in direction θ_n . We then normalized as in Eq. 3; as in the preceding text, we used the larger of the two computed values as the estimate of suppression selectivity.

RESULTS

Direction tuning of surround influences

Our first goal was to measure the tuning and sign of surround influences under conditions when the center and surround stimuli were carefully isolated, to resolve discrepancies in previous work about the specificity and sign of surround influences (see INTRODUCTION). Our stimuli in these and all experiments in this paper were drifting sinusoidal gratings whose spatial frequency and temporal frequency of drift were optimized based on experiments described in the previous paper. These gratings were vignetted by circular or annular contrast windows (see Fig. 1 for examples) against a mid-gray background. Grating contrast was normally 0.5. As detailed in the previous paper (Cavanaugh et al. 2002), we used a summation technique to define two diameters, a *grating summation field* (GSF), which is the diameter of the smallest central patch of grating that elicits at least 95% of the neuron’s maximum response, and an *annular minimum response field* (AMRF), which is the inner diameter of the smallest annular aperture that elicits no more than 5% of the neuron’s maximum response. Stimuli presented to the receptive field center were confined to a circular region whose diameter equaled the GSF; stimuli presented to the surround were confined to an annular region whose inner diameter equaled the larger of the GSF and the AMRF. In this way, we were as careful as we could be to prevent surround stimuli from encroaching on the center of the receptive field and vice versa. We will for convenience refer to the stimuli chosen in this way simply as “center” and “surround” stimuli, but it should be recalled from the previous paper (Cavanaugh et al. 2002) that the *mechanisms* that underlie the center and surround responses are probably more extensive than our chosen stimulation areas.

We presented 34 neurons with simultaneous center and surround grating patches in an experimental design in which we presented all possible combinations of eight evenly spaced center and surround directions as well as a control series of center- and surround-alone stimuli.

Figure 1 shows responses of a sample neuron to drifting sinusoidal gratings either restricted to the neuron’s center (horizontal shaded area), restricted to the surround (vertical shaded

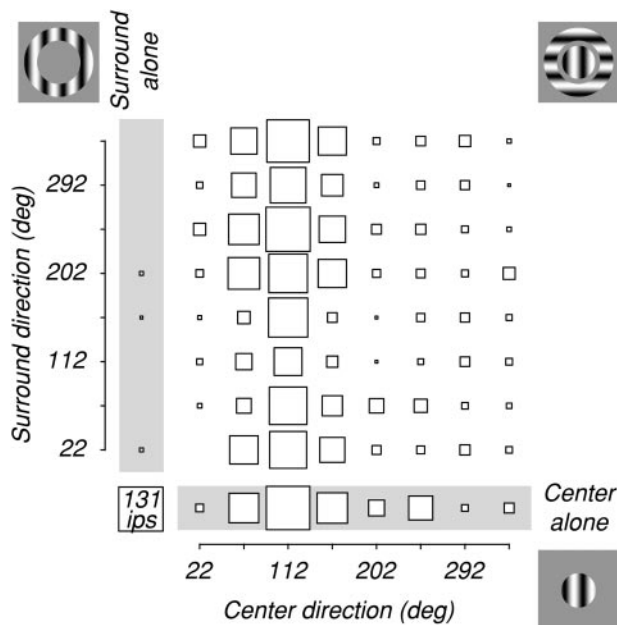


FIG. 1. Full response matrix for direction tuning of surround suppression. We have plotted response of a simple cell to compound center/surround stimuli in which directions of the center and surround were parametrically varied. Responses (in impulses per second, IPS) are proportional to the areas of the boxes. Going across a row represents a change in the direction of the center stimulus, while going up a column represents a change in the surround direction. The shaded row at the *bottom* shows responses to the center stimulus alone at all directions. The shaded column at the *left* shows responses to the surround stimulus alone at each direction. Responses to the optimal center stimulus (at 112°) were suppressed when the surround was also at 112°, indicating a suppressive surround influence tuned for orientation and direction of movement.

region) or presented together (open squares in the central region). Response is represented by the area of each box. Surround direction is constant across rows, while center direction is constant up columns. When presented with stimuli in the center alone, the neuron responded best when the direction was 112°. The neuron did not respond to a grating presented to the surround alone at any direction, but surround gratings suppressed the response to center gratings. This suppression was strongest when the direction of the surround grating was 112°, the same as the optimal direction for the center response.

Figure 2 shows three other examples of the tuning of surround suppression when the center stimulus was at the preferred direction. The thin solid curve in each plot is for the center-alone condition. The abscissa indicates the stimulus direction relative to the neuron's preferred direction. The horizontal line in each panel represents the center-alone baseline response at the preferred direction. Open circles plot responses to the center stimulus in the presence of surround stimuli at different directions. Figure 2A shows responses from a complex direction-selective cell in V1. The lowest response to the compound stimulus occurred when the surround grating was drifting in the neuron's preferred direction. At orthogonal surround directions ($\pm 90^\circ$ on the abscissa), responses to the compound stimulus were indistinguishable from the center-alone response. When the surround stimulus had the same orientation but opposite direction of drift (i.e., a direction 180° away), the neuron was also suppressed, but not as strongly as when the directions of drift in the center and surround matched.

Figure 2B shows responses from another complex cell. This neuron was relatively unselective and responded to all directions. Suppression from the surround was maximal when it was at the neuron's preferred direction but was also unselective and was evident for all surround directions. Figure 2C shows the responses of a well-tuned directionally selective simple cell. In this case, the surround suppression was also directionally selective but was broadly tuned compared with the center.

These examples pose several questions. What is the relationship between the preferred orientations of the center and surround? Between their preferred directions? Between their degrees of tuning? To answer these, we calculated a selectivity index and direction preference for the center and surround (see METHODS). Figure 3A plots the distribution of differences between the preferred direction of drift in the center and the maximally suppressive surround direction of drift when the center was drifting in the preferred direction. Most neurons

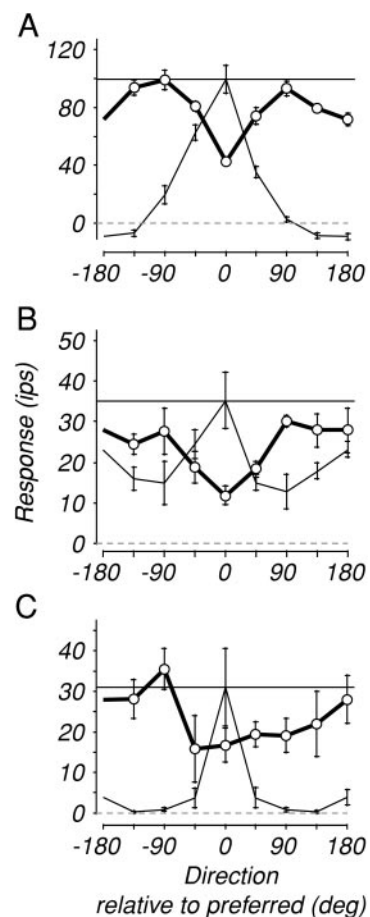


FIG. 2. Direction tuning of surround suppression for 3 example neurons, 1 simple (A) and 2 complex (B and C), to compound center/surround stimuli. The thin trace shows the response to the center drifting grating alone as a function of center direction, which is rotated to 0 for clarity. The thin horizontal line in each panel denotes the response to the preferred center stimulus alone. The thick trace shows the influence of a surround stimulus on responses to the preferred center stimulus, plotted as a function of surround direction. Error bars are ± 1 SE. Each neuron was suppressed most by oriented surround stimuli at or near the neuron's preferred direction. The responses in A show a nondirectional surround influence—the surround suppressed at the preferred orientation regardless of direction of drift (0 and 180°). The neuron in B was suppressed by surround stimuli at all directions, although suppression was greatest at the neuron's preferred direction. The responses in C show a suppressive effect broadly tuned for direction.

were maximally suppressed by surround stimulation at or near their preferred direction of drift. We compare selectivity indices for the center and surround in Fig. 3B in which surround selectivity index is plotted against center selectivity index. There was a significant correlation between the center and surround orientation selectivity indices ($r = 0.75$, $P < 0.001$), but most data fall below the diagonal—the surround was on average less selective than the center (Li and Li 1994).

A second question concerns the directional selectivity of the

surround relative to the center. By directional selectivity we mean the relative response to the two directions of drift for an optimally oriented grating. We computed a conventional directionality index for the center-alone condition as $(p-n)/(p+n)$, where p and n are the responses in the preferred and opposite directions; this index is 1 for completely directionally selective neurons and 0 for nondirectional ones. To estimate the directionality of the surround influence, we computed an index as $(p_p - p_n)/(p_p + p_n)$, where p_p is the response to a preferred center stimulus paired with a surround drifting in the same direction, and p_n is the response to a preferred center stimulus paired with an opposite direction surround stimulus. This index equals 1 when surround suppression occurs only for the preferred direction, equals -1 when suppression occurs only for the opposite surround direction, and equals 0 when preferred and opposite surround directions had the same effect. Figure 3C shows the index for the surround plotted against the index for the center alone. The first thing to note is that the index for the surround is generally positive, meaning that when the surround had a direction preference, it tended to match that of the center (this is also evident from the relative prevalence of entries in the 0–30 and 150–180° bins in Fig. 3A). But there is also no discernible relationship between the indices—directionally selective neurons are no more likely to have directionally selective surrounds than other neurons.

To summarize the relationship of surround suppression to center tuning, we normalized and averaged the direction tuning curves for center activation and for surround suppression at the optimal center direction (that is, the 2 curves in each panel of Fig. 2). Figure 3D shows these mean normalized tuning curves, which reveal that when averaged in this way, the tuning curves for excitation in the center and suppression in the surround are close to inverses of one another; only on closer inspection is it clear that the tuning of suppression is slightly broader than the tuning of the center (cf. Fig. 3B).

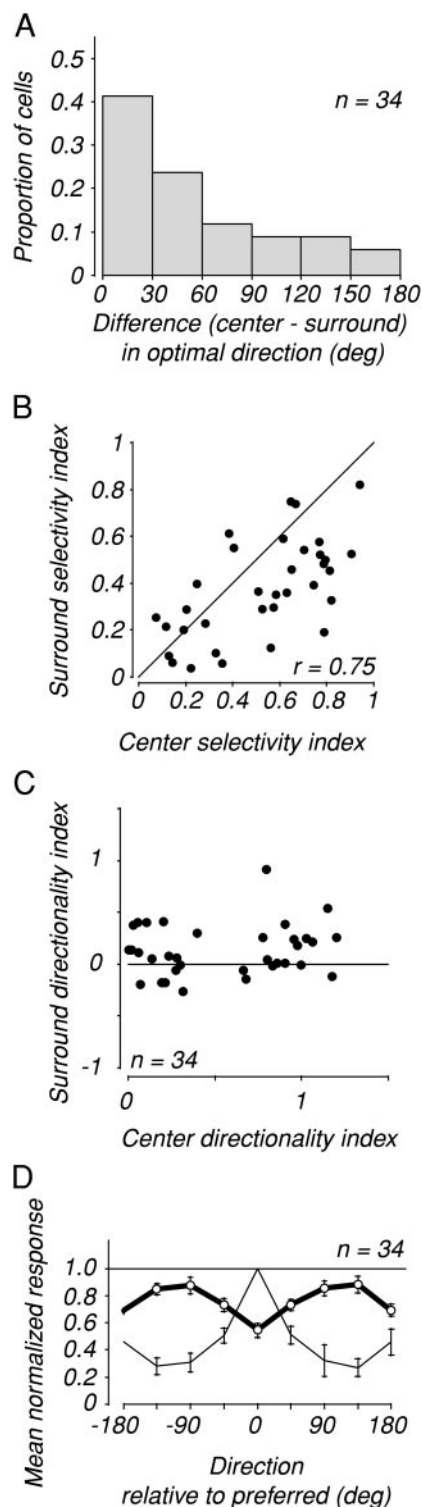


FIG. 3. Orientation and direction tuning of surround suppression. A: distribution of the difference in direction between the optimal direction for the center and the most suppressive direction for the surround. The majority of neurons were suppressed most by surround stimuli drifting at or near the preferred direction. B: relation between the selectivity indices for the center and for surround suppression. The indices correlate well ($r = 0.75$, $P < 0.001$). Most points fall below the diagonal, indicating that surrounds were less selective for stimulus orientation. For each neuron, we additionally calculated a directionality index by comparing responses in the preferred and opposite directions of drift at the preferred orientation. C: the directionality index of the surround is plotted against the directionality index of the center. Points above the horizontal line represent neurons that were more suppressed by gratings drifting in the neuron's preferred direction than in the opposite direction. Most neurons fall above the line, indicating that the surrounds of most neurons matched their centers in direction preference. Direction selectivity was typically low for the surrounds, and there appeared to be no relationship between the degree of selectivity in the center and surround. D: mean normalized center and surround responses for 34 cells. The thin trace shows the mean response of the center stimulus alone plotted as a function of center direction. Responses are normalized by the maximum response for each neuron, then averaged at each direction relative to the neuron's preferred. The thick trace shows the average suppressed response to the compound center/surround stimulus with a preferred center direction at different surround stimulus directions. On average, neurons were suppressed most (about 40%) by surround stimuli at the neuron's preferred direction. Surround stimuli drifting in the opposite direction were only about half as effective on average, while orthogonally oriented surround stimuli were the least suppressive.

Dependence of surround suppression on center stimulus direction

The analysis just presented has only considered the case of surround suppression of responses to an optimal center stimulus. But the matrix design of the experiment permits us to ask whether the surround's influence is fixed at absolute directions or whether it depends in some way on the relationship between the center and surround directions. Inspection of Fig. 1 shows a hint of specificity for relative rather than absolute surround direction, but it also shows the difficulty of the analysis—one can only pose the question when the neuron responds reliably to center stimuli at several different directions. Data from such a neuron are shown in Fig. 4, *A–C* (same cell as in Fig. 2*A*). The thin black curve in each panel shows the direction tuning curve for the center; each panel shows the effect of a surround stimulus as a function of its direction, as in Fig. 2 (Fig. 4*B* in fact reproduces the same data as Fig. 2*A*). Figure 4, *A* and *C*, plots the same comparisons but for different center stimuli; the filled symbol and asterisk mark the center direction in each case, and the horizontal line shows the center-alone reference response against which the surround effect is to be compared. In each case, the surround suppression was strongest at the orientation being presented to the center, not at a fixed preferred orientation.

For neurons like this example, which gave strong responses to the optimum direction and the two neighboring directions, we measured the most effective direction of surround suppression for the three stimulus conditions in Fig. 4, *A–C*, and plotted their distributions in Fig. 4, *D–F*. For each center stimulus orientation (indicated by the asterisk), neurons were most often maximally suppressed by surround stimuli at the direction that matched the *stimulus* in the center, not the most effective center stimulus.

We can pose the same question in the domain of directional selectivity. Is the most suppressive direction for an optimally oriented surround grating dependent on the direction of drift of an optimally oriented center grating? To examine the dependence of surround direction selectivity on center stimulation, we calculated the index for suppression of center stimuli drifting in both preferred and opposite directions (cf. Fig. 3*C*) for 17 units that had strong responses for both directions of drift. The directionality index equals 1 when the most suppressive direction for the surround matches the neuron's preferred direction. We calculated the index for suppression when the center was drifting in the neuron's preferred direction and when it was drifting in the opposite direction and plotted these values against each other in Fig. 4*G*. If the preferred direction for suppression did not depend on the direction of drift of the center grating, the data would lie near a line of unit slope. In fact, the data lie close to a line of slope -1 and are significantly negatively correlated ($r = -0.55$, $P = 0.02$), which means that the most suppressive direction of drift in the surround *reversed* when the direction of drift in the center reversed. The most suppressive surround direction matched the direction of drift in the center rather than simply the neuron's preferred direction, and the magnitude of the directional selectivity of the suppressive influence was preserved.

The results of this analysis show that the specificity of surround suppression is not fixed but instead adjusts itself adaptively to the prevailing center stimulus. The simplest way

to conceptualize this is that the surround maximally suppresses responses to what the center *sees*, not to what the center *prefers*.

Dependence of surround suppression on center stimulus contrast

In the preceding paper (Cavanaugh et al. 2002), we showed that the receptive field center and surround were well modeled by independent mechanisms that interact divisively. The balance between center and surround gains dictates the response of the neuron and can be changed by changing the stimulus contrast in either center or surround. Because the surround is tuned for stimulus direction, we can observe the dependence of this tuning on stimulus contrast and examine how the gain of the surround might change with stimulus direction. We can also ask whether the tuning of the surround depends on stimulus contrast (Levitt and Lund 1997; Polat et al. 1998). We therefore compared the effect of surround stimulation at preferred and orthogonal surround directions for different center contrasts. Figure 5*A* shows the effect of surround stimulation at different directions on the response of an example neuron to different contrasts in the center; \circ show responses in the absence of any surround stimulus. Adding a surround stimulus at an orthogonal direction caused a reduction in response (\ominus), and a surround stimulus at the neuron's preferred orientation produced even greater suppression (\bullet). While the suppressive effect of the preferred surround was similar at all center contrasts; the effect of the orthogonal surround was most pronounced for low and moderate contrasts. This suggests that the specificity of surround suppression for preferred stimuli might be more pronounced at high contrasts and reduced at lower contrasts.

To explore this question, we presented center gratings of high and low contrast at the neuron's preferred direction in combination with surround stimuli of high contrast at either the preferred or orthogonal direction. High-contrast stimuli were at 50% contrast, whereas low-contrast stimuli were at 12% contrast or the lowest contrast of the stimulus that elicited a response that was at least 20% of the response to the high contrast stimulus. For center stimuli at high contrast (Fig. 5*B*) and low contrast (Fig. 5*C*), we compared responses to the two different surround orientations. We normalized responses by the response to the preferred center stimulus alone, so responses less than 1 indicate suppression from the surround, while responses greater than 1 indicate response facilitation. For each of 60 neurons, we plotted the response with preferred surround against response for the orthogonal surround. Points on the diagonal represent neurons for which the preferred and orthogonal surround stimuli had identical effects, while points falling below indicate a smaller response (more suppression) with the preferred direction in the surround. With a high contrast grating in the center (Fig. 5*B*) the points fall predominantly below the diagonal because suppression is stronger for surround stimuli at the preferred orientation. In fact, a substantial number of cells showed no suppression by orthogonal stimuli or even a modest enhancement (cf. Knierim and van Essen 1992; Levitt and Lund 1997). For a low center contrast (Fig. 5*C*), points are more evenly spread above and below the diagonal and there are fewer cases of facilitation for orthogonal surrounds. As can be seen from the marginal distributions in

Fig. 5, *B* and *C*, the main difference between the two cases is the increase in suppression for center stimuli at low contrast. Although the suppression afforded by both preferred and orthogonal surround stimuli is greater when the center stimulus is at low contrast, this increase in suppression is more pronounced for the orthogonal surround. One way to think of this finding is that suppression from a preferred surround is strong enough to overcome excitation from center stimuli at high *and* low contrasts, whereas the weaker suppression from the or-

thogonal surround is only strong enough to suppress the weaker excitation from center stimuli at low contrast. This is the behavior of the example neuron of Fig. 5*A* and is consistent with the results of Levitt and Lund (1997).

We examined distributions by cortical lamina of surround suppression selectivity for both high- and low-contrast center stimuli. Cells in deeper layers exhibited less orientation selectivity for surround suppression of responses to center stimuli at high contrast, although the homogeneity of distributions across layers could not be rejected on the basis of a χ^2 test. For low-contrast center stimuli, the distributions across laminae were indistinguishable.

Dependence of surround suppression on stimulus location

Up to this point we have treated the receptive field surround as radially uniform, implicitly assuming that suppression comes equally from all surround regions. But there is ample reason to believe that this is incorrect (DeAngelis et al. 1994; Nelson and Frost 1985; Walker et al. 1999). So while stimulating the receptive field center with a patch of grating at the neuron's preferred orientation, we placed two patches of grating in the surround, across the receptive field from each other, in a "dumbbell" configuration (Fig. 6). Peripheral patches contained grating at either the neuron's preferred direction or at the orthogonal direction. The radial position and diameter of the surround patches was set by the same criteria as the dimensions of the surround annulus and generally matched the width of that annulus; the diameters of the surround patches were typically set so that adjacent patch positions had little or no overlap. The contrast of center and surround patches of grating was 0.5.

Figure 6 illustrates the configuration of the stimuli and shows responses of a simple cell to surround stimulation at different peripheral locations. We presented peripheral patches in four different configurations: aligned with the neuron's axis

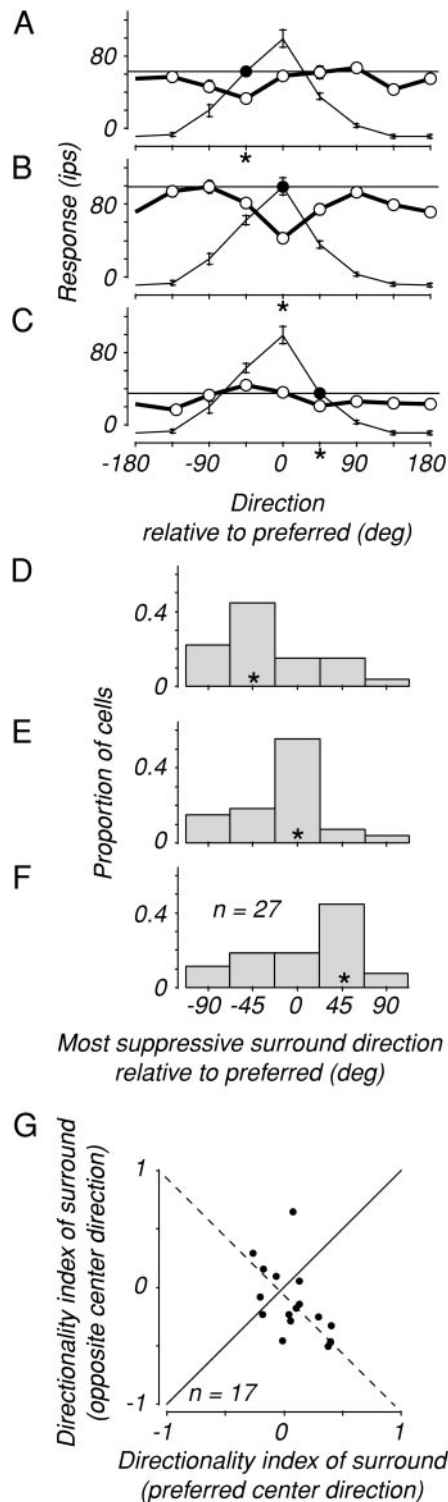
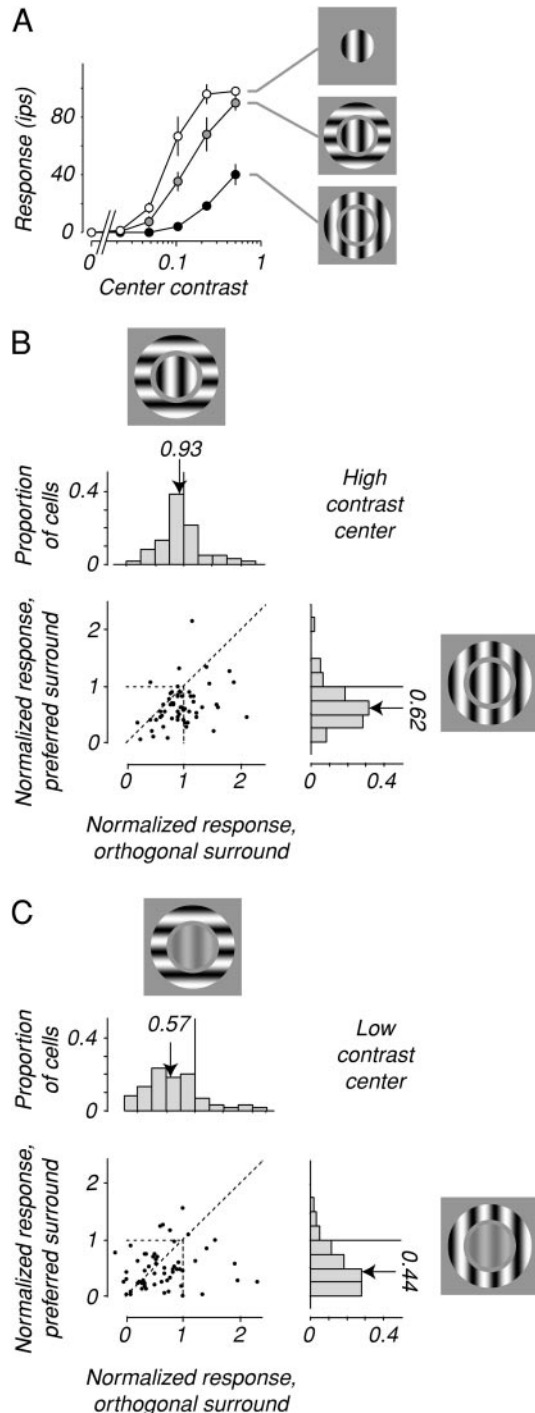


FIG. 4. Dependence of surround suppression on center direction. *A–C*: show responses of a complex cell to a center stimulus alone (thin trace) and a compound center/surround stimulus (thick trace). The thin trace is the same in *A–C*, showing the direction tuning curve for the neuron. The thick trace shows suppressed responses as a function of surround direction when the center stimulus was at the direction indicated by the large black point on the direction tuning curve and by the asterisk on the abscissa, the response to which is indicated by the horizontal line. In each panel, the most suppressive direction is at or near the direction of the center stimulus (denoted by asterisk), indicating a dependence of surround suppression on center stimulus direction. *D–F*: distributions of maximally suppressive surround directions. We calculated bias estimates of surround suppression for each center direction to indicate the most suppressive surround direction. Neurons were only included for analysis if the responses to the center stimulus alone at $\pm 45^\circ$ were at least 10% of the maximum response to the center stimulus alone (27/34 units). The asterisk in each distribution shows the direction of the center stimulus. The distributions in each panel show that the most suppressive surround direction matches the direction of the center stimulus, and not necessarily the neuron's preferred direction. *G*: relationship of surround directional preference to the direction of center stimulation. We calculated directionality indices for surround suppression when the center was drifting in the preferred direction and when the center was drifting in the opposite direction. We only included neurons for which the center drifting in the opposite direction elicited at least 10% of the neuron's maximum response. If the directionality of surround suppression is independent of center direction of drift, we would expect the points to line up on the diagonal. The points actually cluster with a slope of -1 (dashed line), indicating that the more suppressive direction of drift in the surround (preferred or opposite) was not constant, but matched the direction of drift in the center.

of preferred orientation, positioned orthogonal to it, and at the two 45° oblique positions. All data (●) have been rotated so that the preferred orientation for the neuron is vertical and duplicated around the circle (⊙) to aid in visualization.

In Fig. 6A, the surround was stimulated at the neuron's preferred direction. Responses are plotted so that the distance from the origin indicates response, and the angular deviation of each point from the vertical axis represents the position of the peripheral stimulus relative to the neuron's preferred orientation, as indicated by the stimulus icons. The neuron's response to the center stimulus alone (26 imp/s) is designated by the bounding black circle. The simple cell in Fig. 6 was suppressed by



peripheral patches in all surround locations when these patches contained a stimulus at the neuron's preferred orientation; suppression was greatest when the patches were at the receptive field ends. When the peripheral patches contained orthogonal grating (Fig. 6B), the neuron was less suppressed overall, but suppression still had a spatial pattern—suppression was greatest when the orthogonal patches were placed in the flanks of the receptive field.

We obtained tuning curves describing the magnitude and location of surround suppression for 120 neurons of which 113 showed measurable suppression from peripheral patches. We estimated the position and magnitude of maximal suppression by calculating bias estimates for the suppressive effect in a manner similar to the bias estimates of surround suppression from annular stimuli (Eq. 1–5) except we now used the position of the peripheral stimulus as the angle, rather than using the direction of the grating. Once we had the position of maximal suppression from the mean suppression vector, we determined the magnitude of suppression at that position by interpolating between measured responses with a suitable low-pass filter.

Figure 7 (A and B) shows the location and magnitude of greatest surround suppression for 113 neurons. The deviation of each point from the vertical axis represents the angular position of the most suppressive location from the receptive field ends, and the distance of each point from the origin represents the fractional suppression at that position. Fractional suppression is 0 if the patch had no effect on response and 1 if the patch suppressed response completely. In A, the patch contained stimuli at the neuron's preferred direction; in B, the patch contained stimuli orthogonal to those in A. Points near the origins in A and B represent neurons that did not show much suppression. Points in A are more displaced as a whole from the origin than in B, indicating greater suppression from peripheral stimuli at the neuron's preferred direction. The cloud of points in Fig. 7, A and B, is slightly misleading because it contains points for some neurons that had little selectivity for position and others that were strongly selective. For each surround orientation condition, we took a subgroup of neurons for which the position selectivity was at least 0.2 and the fractional suppression was at least 0.3. These neurons are plotted as ●. We adapted the selectivity index calculation

FIG. 5. Direction selectivity of the surround depends on stimulus contrast. A: contrast responses of a simple cell to a center stimulus alone (○) and compound center/surround stimuli (● and ⊙) as a function of center contrast. Adding an orthogonal surround stimulus to the center stimulus (⊙) reduced responses, while adding a surround grating at the neuron's preferred direction (●) reduced responses even more. Note that the reduction in response depended on center contrast, especially for the orthogonal surround. B: comparison of responses to high contrast center stimuli in the presence of surround stimuli at the neuron's preferred and orthogonal directions. Responses are normalized to the response to the high contrast center alone. Points on the diagonal indicate neurons for which the preferred and orthogonal surrounds had similar effects. Points falling below the diagonal represent neurons for which the preferred surround suppressed more than the orthogonal surround. The margins show the distributions of each value. For high contrast center stimuli, surrounds at the preferred orientation suppressed responses more than orthogonal surrounds did (t -test, $P \ll 0.001$). There was no mean effect from orthogonal surrounds (t -test, $P = 0.41$). C: comparison of responses to low-contrast center stimuli in the presence of surround stimuli at the neuron's preferred and orthogonal directions. For low-contrast center stimuli, there is a greater spread of points across the diagonal, resulting primarily from an increase in suppression from orthogonal surround stimuli. The marginal histograms confirm this effect—orthogonal surround stimuli were more suppressive when center stimuli were of lower contrast (t -test, $P \ll 0.001$).

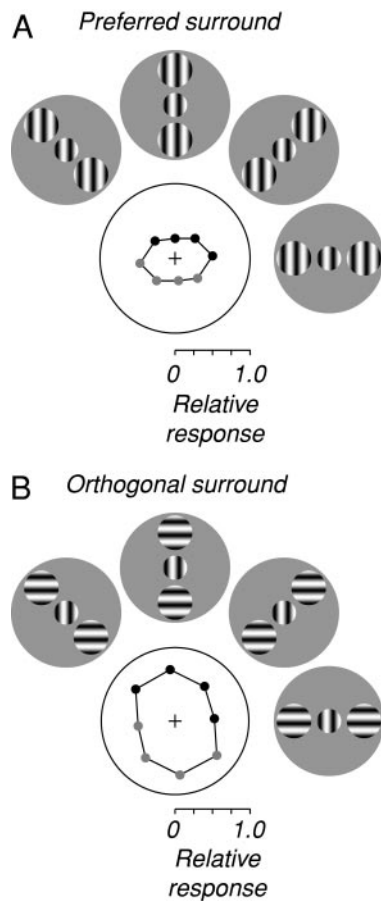


FIG. 6. Responses of a simple cell to peripheral patches of grating placed outside the CRF. The configuration of the stimulus is shown by the icons, with the central patch of grating in each icon representing the stimulus within the CRF. Peripheral patches contained grating at the neuron's preferred direction (A) or the orthogonal direction (B). The bounding circle represents the response to the center stimulus alone at the preferred direction (26 imp/s). Responses (●) are plotted in polar coordinates, with the angular deviation of points from vertical representing deviation from the ends of the receptive field and the distance from the origin representing the magnitude of the response when the stimulus was in the configuration indicated by the icon in the corresponding position. We tested four locations for each direction in the surround, and we have duplicated the responses around the circle to aid in visualization (○). When peripheral patches contained grating at the neuron's preferred direction (A), the cell was suppressed regardless of where the peripheral patches were located, although there was more suppression when the patches were at the ends of the receptive field as defined by the axis of preferred orientation. When the peripheral patches contained orthogonal grating (B), the neuron was less suppressed on average (as indicated by the spread of responses away from the origin in B). However, orthogonal patches of grating at the flanks of the receptive field suppressed more than did the same patches at the receptive field ends.

described in METHODS to ask whether the data in Fig. 7, A and B, were anisotropic, and if so, what was the axis along which they were biased. The \equiv across the two plots give the axis for this bias—near parallel to the preferred orientation for the parallel condition, near orthogonal to the preferred orientation for the orthogonal condition. The bias values for these two scatterplots were substantial, 0.25 and 0.29 for A and B, respectively.

Another way to visualize this is in Fig. 7, C and D, which shows the distributions of the most suppressive peripheral locations for each surround orientation. In the preferred surround orientation condition, suppression was most often stron-

gest from the ends of the receptive field, while in the orthogonal condition, suppression was most often strongest from the receptive field flanks.

Laminar analysis of these data suggested that for surround stimuli at the neuron's preferred orientation, cells in layers 4c and 4b were less selective for the peripheral location of these stimuli, while layers 2/3 and layer 6 contained more cells selective for peripheral location. These trends were not significant on the basis of a χ^2 test. Selectivity for the peripheral location of orthogonally oriented patches was evenly distributed across layers.

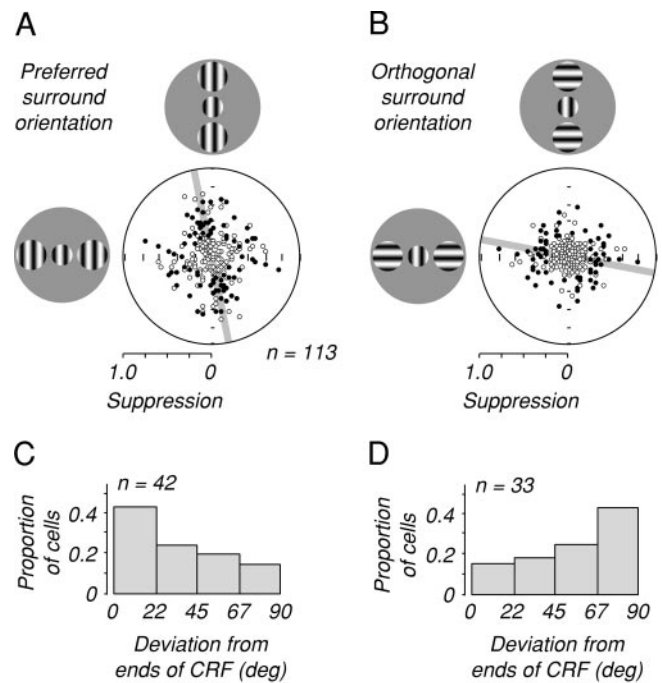


FIG. 7. Summary of the dependence of the location of suppression in the surround on stimulus orientation. We used the fractional reduction in response from bilateral surround stimuli to compute an orientation bias estimate (see METHODS) for the location of suppression in the surround. We used a low-pass interpolation to determine the magnitude of suppression in the most suppressive direction. A and B: show the magnitude of the suppressive effect and the location of greatest suppression plotted in polar coordinates for each of 113 cells. Points farther from the origin represent cells that were more suppressed than those closer to the origin, and points on the vertical axis represent neurons that were most suppressed by peripheral patches at the receptive field ends. Data are plotted for preferred (A) and orthogonal (B) surround orientations and have again been duplicated around the circle for visualization. ●, neurons with the strongest suppressive effects. Neurons were considered to have a strong effect if the magnitude of the orientation bias estimate was at least 0.2 and the maximum suppression was at least 0.3. Strong effects were determined separately for each surround orientation condition. For the preferred surround orientation, 42/113 cells matched these criteria, whereas 33/113 showed strong effects with orthogonal surround stimuli. For these selective cells, we pooled the directions and magnitudes of suppression and calculated the orientation bias of the cluster of points. The gray lines show the direction of this bias estimate for each surround orientation condition. For each selective neuron we calculated the difference between the most suppressive surround location and the neuron's axis of preferred orientation using orientation bias estimates. The distributions of these differences are shown in C (for preferred surrounds) and D (for orthogonal surrounds). More cells were suppressed by peripheral patches of grating at the neuron's preferred orientation when these patches were located at the ends of the receptive field. For orthogonal surrounds, the distribution shows a tendency for these stimuli to suppress most at the receptive field flanks.

DISCUSSION

Complex behaviors can emerge from simple models

In the preceding paper, we proposed and tested a relatively simple model of center-surround interaction in V1 cells, based on the idea of two fixed mechanisms, interacting divisively, whose sensitivities are independently regulated by contrast and stimulation history (Cavanaugh et al. 2002). In this paper, we have presented a number of experiments that suggest more complex interactions between center and surround. We showed that signals from the surround are tuned for orientation and that this tuning is to some degree dependent on the orientation presented to the center. We showed that surround tuning depends on the contrast of the stimulus in the center. And we showed that surround suppression arises nonuniformly from different positions in the periphery of the receptive field. How can these observations be reconciled with the simple model we proposed?

We can first observe that the selectivity of the surround for orientation and stimulus location can be accommodated in the original scheme simply by allowing surround signals to be weighted according to orientation and position, requiring nothing more than parametric modifications of the model. But to explain the way that surround specificity appears to change with center stimulation at first appears to require more elaborate circuitry, but we believe this also can be explained within the simple model.

The key is to appreciate that the method we used to define the center and surround, though conservative, still allows our stimuli to activate both mechanisms. We conclude this in part because the analysis we presented in the preceding paper revealed that the center mechanism extends well beyond the limits of the GSF measured at high contrast and in part because our model similarly suggests that the surround mechanism extends well inside the border of the AMRF. All of our stimuli therefore engaged both mechanisms to some degree. How does this help explain our more complicated results?

The first problem is that in our model the surround is purely inhibitory. How do we then explain facilitation by surround stimuli? Sillito et al. (1995) showed facilitation from orthogonally oriented surround stimuli. Levitt and Lund (1997) and Polat et al. (1998) found that surround stimuli that were suppressive for high-contrast center stimuli became facilitatory for low-contrast center stimuli. We sometimes observed facilitation from surround stimuli orthogonal to the neuron's preferred orientation for responses to both high- and low-contrast center stimuli (Fig. 5). Because the surround in our model modulates the center response by gain control, we can explain surround facilitation with a modest modification to our model by allowing the surround to increase rather than to decrease center gain under some circumstances. But even this might not be necessary—we can account for response facilitation even with a purely inhibitory overlapping surround. Because of the overlap of mechanisms, responses to center stimuli are the result of stimulating both the excitatory center and the overlapping inhibitory surround. Consider a stimulus restricted to the center at the neuron's preferred orientation. Because the center and surround overlap, the response to this stimulus is a product of both the center and surround activities. If we now add an orthogonally oriented stimulus outside the receptive field, the overlapping surround mechanism will contain the center and

surround stimuli at cross-orientations. The cross-oriented stimuli in the surround will presumably inhibit each other (Bauman and Bonds 1991; Bonds 1989) and thereby reduce the surround's suppressive influence. In this case, the appearance of facilitation would be the result of disinhibition in the surround.

It would seem to be more difficult to explain the apparent dependence of surround specificity on center stimulation in a model whose mechanisms have fixed tuning characteristics. Sillito et al. (1995) claimed that the most suppressive surround orientation depended on the orientation of the center stimulus, and we have partly confirmed that observation (Fig. 4). The data show that a particular surround orientation can have a different effect at different center orientations. Consider center and surround stimuli at the same nonpreferred orientation (the conditions marked with asterisk in Fig. 4, A or C, for example). If we start with one of these conditions and then change the surround stimulus to the preferred orientation, response increases. This seems to indicate that the surround became less suppressive at the neuron's preferred orientation, contrary to expectation. But recall once more that because our stimuli engage both center and surround, all we know from the increase in response is that the *relative* effect of the center increased. Because actual center mechanisms are larger than we estimated by the GSF method, the surround stimulus probably encroached on the receptive field center mechanism. If we assume that both center and surround mechanisms have similar fixed orientation preferences, changing the orientation of the surround to the neuron's preferred would then have two effects: increasing the activation of the center and increasing the activation of the surround. All that is necessary to obtain the observed increase in response is for the added center activation to outweigh the increased suppression from the surround. And because the center is more tightly tuned for orientation than is the surround (Li and Li 1994), small changes in stimulus orientation near the neuron's preferred will have a greater effect on the center than on the surround. This could provide disparate changes in center and surround activation with surround orientation.

Consequently, a single surround orientation can have a differential effect at different center orientations, one consequence of which would be an apparent shift in orientation tuning with surround stimulation. Gilbert and Wiesel (1990) and Müller et al. (1999) have both described precisely such an effect.

Geometry of the surround and the signaling of visual context

We observed that for the population of cells with reasonably effective and spatially selective surrounds, the surround appeared to have an interesting geometric structure. Suppression was greatest at the ends of the receptive field for stimuli at the preferred orientation and greatest on the flanks of the receptive field for stimuli at the orthogonal orientation (Fig. 7). Three times as many cells were suppressed by the neuron's preferred orientation at the receptive field ends than in the flanks. And almost three times as many neurons were suppressed by orthogonally oriented patches of grating at the receptive field flanks. Thus on average, the most suppressive stimulus at any point in the surround of the receptive field would be one whose orientation axis is aligned to point toward the center of the receptive field. In the real world, stimuli that activated this

suppression would most likely be continuous contours, straight or curved, that passed through the center of the receptive field with a segment in the center near the cell's preferred orientation. This means that in general, the cortex would respond less for extended stimuli and more for more local stimuli that are distinct from the visual context. One can imagine this kind of mechanism contributing to the extraction of salience in the form of "pop-out" or other kinds of context-dependent visual segmentation. Our interest in this is not in its novelty—a role for V1 in contextual signaling has often been suggested (Knierim and van Essen 1992; Nothdurft et al. 1999; Schwartz and Simoncelli 2001). Our interest is that such a complex function can emerge from such a simple idea of how receptive fields are assembled.

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