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Modeling the observed center-surround summation in macaque visual area V1

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Abstract

The mechanisms of center-surround summation, the process by which visual cortical neurons integrate the inputs from the classical receptive field and the non-classical surround, are poorly understood. We constructed a set of 32 representative center-surround stimuli using a repertoire of four bar types, and recorded the responses of 83 neurons from visual area V1 in two awake, fixating monkeys to each of the stimuli. We then studied, for each cell individually, the extent to which the observed responses of the cell to center-surround stimuli could be accounted for by a linear regression model of center-surround summation. The model hypothesized that the response of a given cell to a given center-surround stimulus is a weighted linear sum of its responses to the four bar types. This model accurately predicted the observed responses to the center-surround stimuli for about two-thirds of V1 cells (56/83, 67%). The ability of the model to predict the observed responses of the cells was not attributable to overfitting or other modeling artifacts, a lack of surround modulation, or a lack of response modulation across different center-surround stimuli. Furthermore, for many cells, the model was able to predict the cell's responses to novel stimuli, indicating that the model captured the center-surround summation behavior of these cells adequately. Together, our results indicate that this simple bottom-up summation mechanism can account for many important

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center-surround phenomena in V1, including surround inhibition or facilitation, and selectivity for popout or collinear stimuli.

Keywords: Contextual effects; Figure-ground segregation; Linear regression models; Primary visual cortex; Surround modulation

1. Introduction

Neural responses to stimuli presented within the classical receptive field (CRF or 'center') of visual cortical cells can be substantially modulated by additional stimuli presented in the non-classical surround [1,2,4,32]. This process is referred to as surround modulation, center-surround summation, or contextual modulation. Surround modulation is believed to play an important role in many aspects of visual information processing, including feature discrimination [1,2,32], figure-ground segregation [1,2,7,19,24,32,36,67; but see 23,36,48], 'sparsening' of the neural code [62], contrast-gain control [9], filling-in of visual scotomata [45] and representation of contours, junctions, corners [11], three-dimensional surface configurations [3], and border ownership [66]. Surround modulation has been reported in many areas of the visual cortex [1–5,19,32–34,66–67] and to some extent in the somatosensory cortex [15,16].

In visual area V1, where surround modulation has been studied most intensively, the nature of the modulation varies from cell to cell. Even for a single cell, some surround stimuli can be facilitative and others suppressive, and the magnitude of this facilitation or suppression can vary depending on the stimuli in the center and the surround [35,36,46,52,55,56]. It has been suggested that the overall response of V1 cells to center-surround stimuli is a function of the relative strengths of the center vs. surround stimulation [35,55,64]. However, the mechanisms by which V1 cells integrate the inputs from the center and the surround remain largely unresolved.

We investigated the possibility that V1 cells integrate the inputs from the center and the surround as their weighted linear sum. We recorded the responses of macaque V1 neurons to a representative set of conventional center-surround stimuli. We then studied the extent to which the observed responses of each individual cell to center-surround stimuli could be accounted for by a linear regression model, distinct from the linear models of superpositional summation by simple cell CRFs in V1 (see [14,41,63]). Linear regression models, as opposed to more complex models, were used because they are among the simplest to implement and interpret. We show in this report that for about two-thirds of V1 cells, the regression model accurately predicted the observed responses to the center-surround stimuli as a weighted (i.e., scaled) linear sum of the cell's responses to individual bar types, and adequately accounted for most of the observed response variation regardless of the nature or magnitude of surround modulation. Using a series of tests, we also show that the

success of the regression model is not attributable to modeling artifacts or a lack of response modulation.

The physiological results have been described in detail elsewhere [23]. This report focuses on the modeling of the physiological results.

2. Methods

2.1. General neurophysiological procedures

In this report, responses of neurons from visual area V1 to center-surround stimuli were recorded in awake, fixating monkeys, using procedures described in detail elsewhere [23]. Briefly, the cell's CRF was mapped and its preferences were determined using a mouse driven bar on the computer's display. The cells in our sample in general had crisply delineated CRF boundaries, so that the center-surround distinction was obvious and robust. The CRF sizes were consistent with the eccentricities [54,60]. To ensure that no surround bar stimulated the CRF during fixation, stimuli were constructed so that the closest points of any two bars were >1.2 CRF diameters or $>1.2^\circ$ apart, whichever was greater. The animal's eye position was monitored throughout the trial using a scleral search coil, and the trial was aborted if the eye deviated by more than 0.5° from the fixation point at any time during the trial. Single unit recording was carried out using standard procedures. Recording coordinates were randomly chosen from within the craniotomy. Stimuli were presented one per trial for 1 s each while the animal fixated and the response of an isolated V1 unit was simultaneously recorded. The response to each stimulus was calculated from a 300 ms time window starting 50 ms after the stimulus onset, and averaged across 10 trials.

2.2. Visual stimulation

The stimulus set consisted 32 center-surround stimuli constructed from four different bar types (see Fig. 1), so that the center contained a single bar of a given bar type, and the surround was constituted using one or more of the bar types. For a given cell, all center-surround stimuli contained the same total number of bars. Surround stimuli with more than one bar type in the surround had equal, or the closest possible to equal, numbers of each bar type in the surround. The bars of the center-surround stimuli were distributed on the computer display in randomly jittered rows and columns so that no rows, columns, or center vs. surround distinctions based on spacing were apparent by visual inspection. For any given stimulus, the location of the surround bars was randomly shuffled from one presentation to the next. Together, these measures minimized the likelihood that a given subregion of the surround was consistently stimulated by the same bar across presentations.

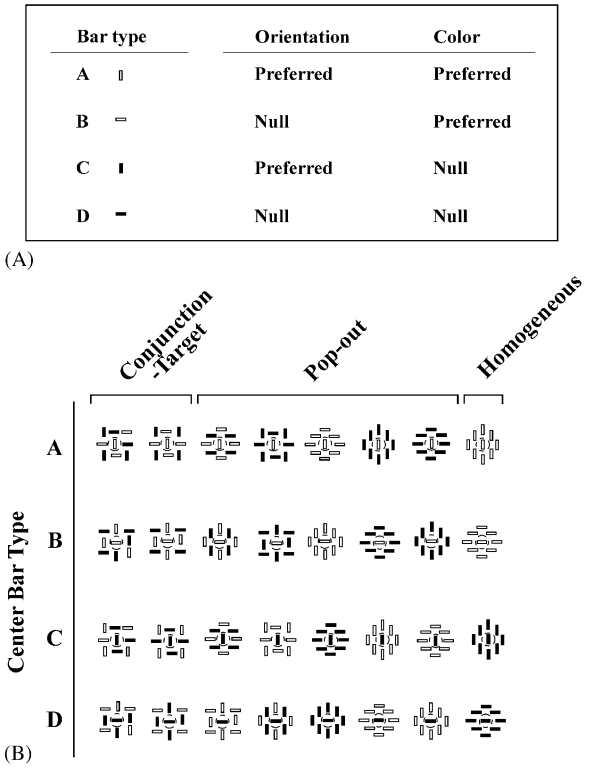


Fig. 1. Stimulus set. (A) 'Building blocks' of the stimulus set. The stimulus set was constructed using four different bar types, each which had the cell's most preferred or least preferred color and orientation. (B) Stimulus set. The center-surround stimuli consisted of a single bar of one bar type within the CRF (*dashed circle*), with many additional bars, drawn from the one or more the bar types, in the non-classical surround. Eight representative types of center-surround stimuli were constructed for each of the four types of center bar (*rows*). see Section 2 for additional details.

2.3. Modeling

The modeling was an entirely post hoc analysis; the experimental conditions described above were in no way designed to produce any given modeling result. All modeling analyses were carried out using the statistical utility S-Plus (Insightful Corp., Seattle, WA). Two linear models were constructed, each using conventional linear regression techniques, which expressed a response (or dependent) variable in terms of one or more predictor (or independent) variables (see Fig. 2B). The first model, the center-alone model, was given by the univariate linear equation:

$$Y_i = \alpha + bC_i + e_i, \tag{1}$$

where the response variable Y_i is cell's observed response to center-surround stimulus i (averaged across trials), the predictor variable C_i is the cell's observed response to the center bar of the stimulus i when presented alone in the CRF

(averaged across trials), and e_i is the residual for stimulus i. Slope b and offset α were the same for all stimuli for a given cell, and were calculated using least mean square regression so to minimize $\sum_{i=1}^{32} e_i^2$ (S-Plus routines *lm* or *glm*) [7,17,50]. Each cell was fit individually to a given model. No values, including outliers, were excluded from any model for any cell.

The second linear model, the center-surround model, was a multivariate model derived by adding surround factors S_1-S_3 to the center-alone model (Eq. (1)) and was given by

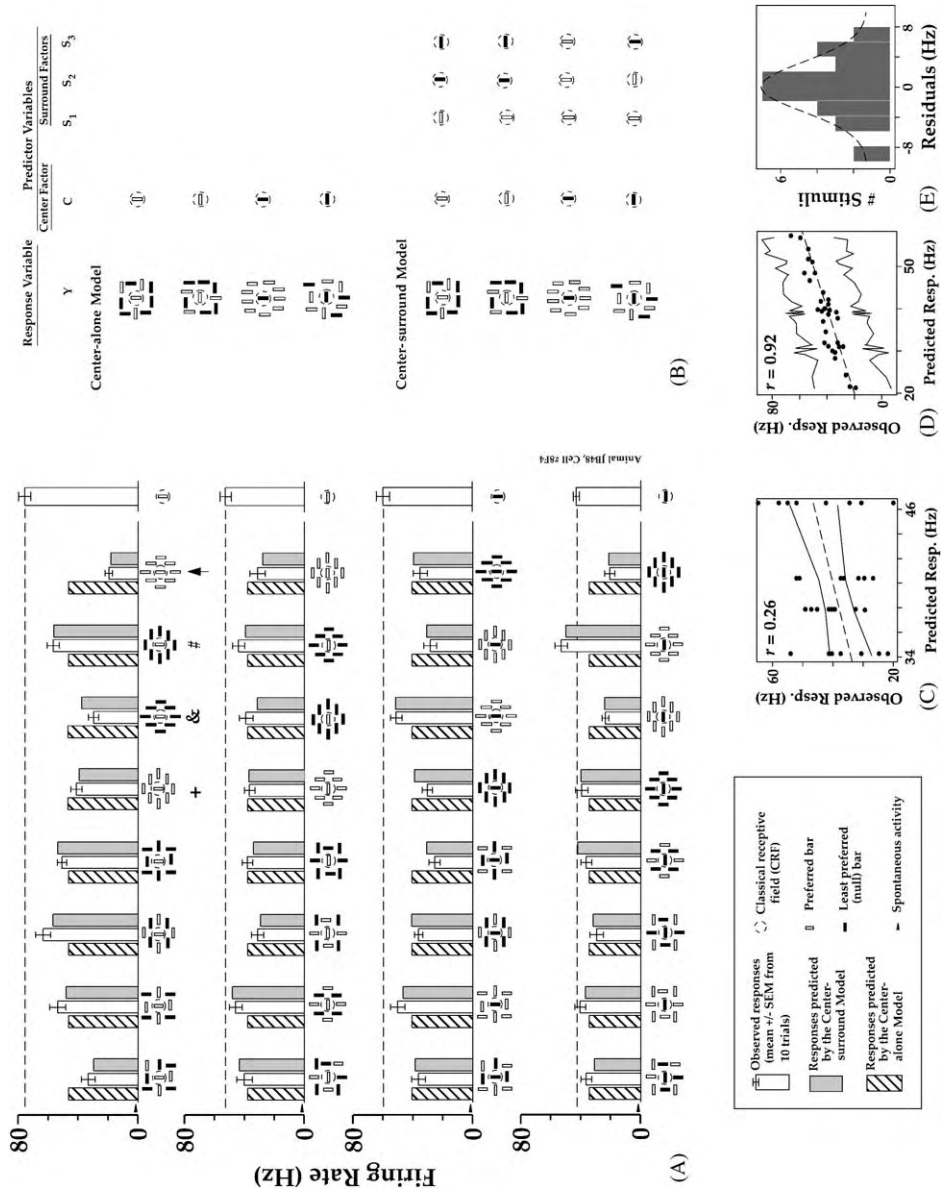
$$Y_i = \alpha + b_0 C_i + b_1 S_{i1} + b_2 S_{i2} + b_3 S_{i3} + e_i, \tag{2}$$

where Y_i is the cell's response to center-surround stimulus i and S_{ij} is the cell's response to the jth surround bar type of stimulus i when presented alone in the CRF. This model allowed for interactions among factors (subject to certain criteria, see below), so that when all possible factors and factor interactions were included, this model was described by

$$\begin{aligned} Y_i = \alpha &+ b_0 C_i + b_1 S_{i1} + b_2 S_{i2} + b_3 S_{i3} + b_4 C_i S_{i1} \\ &+ b_5 C_i S_{i2} + b_6 C_i S_{i3} + b_7 S_{i1} S_{i2} + b_8 S_{i1} S_{i3} + b_9 S_{i2} S_{i3} \\ &+ b_{10} C_i S_{i1} S_{i2} + b_{11} C_i S_{i1} S_{i3} + b_{12} C_i S_{i2} S_{i3} + b_{13} S_{i1} S_{i2} S_{i3} \\ &+ b_{14} C_i S_{i1} S_{i2} S_{i3} + e_i. \end{aligned} \tag{3}$$

The values of offset α and weight coefficients b_0–b_{14}, which applied to the cell as whole and did not vary from stimulus to stimulus, were calculated so as to minimize $\sum_{i=1}^{32} e_i^2$. Each of the three surround factors represented one of the three possible *bar types* (as opposed to individual bars) in the surround. For those stimuli for which all surround bars were of the same type, all three surround factors had the same value, and for those stimuli with two bar types in the surround, the value of the third factor represented the average of the first two. These methods of assigning values to the surround factors were equivalent, since all stimuli had the same total number of bars in the surround and, when they had more than one bar type, equal proportions of the different bar types.

As in Eq. (3), the center-surround model allowed linear interactions among factors, since such interactions are plausible given the functional architecture of V1 [8,22,31,37]. Note that interaction among factors is a commonly used feature of linear modeling and do not violate the linearity of the model (see [7,17,50]). To ensure that the interaction factors did not artifactually improve the fit [7,17,29,50,53], each of the 11 possible interaction factors was individually screened and was retained only if it significantly improved the fit of the model to the data as measured by the Mallows' *Cp* criterion [7,17,50]. This process retained an average of 2.23 interaction factors per cell. The interaction factors retained by individual screening were included in the final model only if they also collectively improved the fit of the model significantly ($p<0.05$) as measured by a partial *F*-test [7,17,50]. Note that these screening procedures increase the stringency of the model at the expense of reducing its power, in a manner analogous to increasing the criterion value in a test of significance (see [17,29,53]).


Response Variable
Predictor Variables
Center Factor
Surround Factors
Y
C
S1 S2 S3
Center-alone Model
Center-surround Model
(B)
Firing Rate (Hz)
Animal 1h48, Cell #8F4
(A)
Observed responses (mean +/- SEM from 10 trials)
Classical receptive field (CRF)
Responses predicted by the Center-surround Model
Preferred bar
Least preferred (null) bar
Responses predicted by the Center-alone Model
Spontaneous activity
r = 0.26
Observed Resp. (Hz)
Predicted Resp. (Hz)
(C)
r = 0.92
Observed Resp. (Hz)
Predicted Resp. (Hz)
(D)
Stimuli
Residuals (Hz)
(E)

The proportion of the data accounted for by a given model, or, equivalently, the fit of the model to the data, is measured by its R^2 value. This value, sometimes referred to as the coefficient of determination (or coefficient of multiple determination, for multivariate models), is defined as the variation in the data accounted for by the model divided by the total variation in the data [17,53], and ranges from 0 (no variation in the data accounted for) to 1.0 (all variation in the data accounted for). The portions of the data not accounted for by the model, or the residuals, are expected to be distributed randomly if the given model adequately accounts for the relationship between the dependent and independent variables of the data [17,50]. The conventional method of testing the significance of the fit of the model to the data is by an F-test, which measures the probability p that the R^2 value of the model is greater than zero by chance [17,29,53]. A partial F-test similarly measures the significance of the fit provided by a subset of the independent variables [15,29,50,53].

We also attempted to fit several mixed-effects non-linear models to the data. In these models, the linear relation between the response variable and the predictor variables in Eq. (2) was replaced by a non-linear relation, such that

Exponential model:

$$Y_i = \alpha + C_i^{b0} + S_{i1}^{b1} + S_{i2}^{b2} + S_{i3}^{b3} + e_i \tag{4}$$

or

Logarithmic model:

$$Y_i = \alpha + b_0 \log_{10}(C_i) + b_1 \log_{10}(S_{i1}) + b_2 \log_{10}(S_{i2}) + b_3 \log_{10}(S_{i3}) + e_i \tag{5}$$

or

Fig. 2. Linear modeling of center-surround responses of an exemplar V1 cell. (A) Cell's actual responses and the responses predicted by two different linear models to each of the 32 center-surround stimuli (*bar array icons*), and the cell's responses to the four bars from which center-surround stimuli were constructed (*bar icons*). The *solid arrow* denotes the cell's most suppressive stimulus with the preferred bar in the center. The *ampersand*, '+' and '#' *signs* denote stimuli to which the cell's responses were progressively less suppressive. See Section 3 for details. (B) Linear models. To predict the response to a given center-surround stimulus, each model regressed the observed response of the cell to the appropriate stimulus (dependent or response variable) on one or more predictor (independent) variables. In the center-alone model (*top*), the cell's response to a given center-surround stimulus was predicted as a function of the cell's response to only the center element of each center-surround stimulus as shown for four exemplar stimuli. In the center-surround model (*bottom*), the contributions from both the center and surround were taken into account. For either model, the weight coefficients (not shown) were calculated so as to minimize the overall difference between the response variable and the weighted sum of the predictor variables across all 32 stimuli (see Section 2 for details). Correlation between the observed responses and the predicted responses for the center-alone model (C) and for the center-surround model (D). Each dot represents a single center-surround stimulus. The *dashed line* denotes the line of perfect correlation ($r = 1.0$) and the *solid lines* denote 95% confidence bands. (E) Probability density distribution of the residuals for the center-surround model. The *dashed line* is the best-fitting Gaussian curve. For this cell, the values of the coefficients of the best-fitting center-surround model were $\alpha = 0.23$, $b_0 = 15.67$, $b_1 = 6.07$, $b_2 = 0.15$, $b_2 = -13.11$, $b_3 = -0.32$. The remaining factors in Eq. (3) were not retained for this cell after the model selection procedure (see Section 2 for details).

Polynomial model:

$$Y_i = \alpha + b_0 C_i + b_1 S_{i1}^2 + b_2 S_{i2}^3 + b_3 S_{i3}^4 + e_i. \quad (6)$$

Interactions among factors were allowed (although not shown in Eqs. (4)–(6)) in a manner analogous to that illustrated for the linear model in Eq. (3). These non-linear models were chosen solely because the relevant equations were compatible with the structure of our data so that model fitting could be attempted, and not because they were necessarily representative of all possible non-linear functions or of possible summation mechanisms (see, e.g., [55,56]). These models were screened, and the fit of the models to the data evaluated, using the same procedures as for the linear models. None of these non-linear models produced a significant fit for any cell. Two quasi-linear models, previously reported to provide good descriptions of spatial summation within CRFs in area MT (see [64]), did not provide significantly better fit than the corresponding center-surround model for any cell as determined by the partial *F*-test (not shown).

2.4. Tests for modeling artifacts

Three different tests, each based on randomization procedures (for overviews, see [18,40]), were used to test the center-surround model for each cell against modeling artifacts. The *reshuffling test* was a modification of the permutation test previously described [10,44], which tests for artifacts resulting from covariance among predictor variable values. To perform the reshuffling test on a given cell, the cell's responses to the four bar types from which the stimulus set was constructed were reassigned, so that the cell's actual response to each bar was assigned to one of the three remaining bars. Nine such novel bar–response combinations are possible. The best fit of the center-surround model to the observed data was recalculated for each of the nine such combinations. For a cell to pass the reshuffling test, the R^2 value had to be no less than the R^2 value obtained from using the actual data, and the p value no greater than 0.017 for both the overall and the partial *F*-tests, for at least one of the nine rounds. The criterion value of 0.017 represents the 0.05 criterion after Bonferroni correction for multiple comparisons [26].

The *random reallocation test* was modified from the one in [39, p. 172]. To perform this test on a given cell, each of the four bar types from which the stimulus set was constructed was assigned a random value within the range of the cell's observed maximum and minimum response to these bar types. The best fit of the center-surround model to the observed data was recalculated using the modeling procedure described above. This process was repeated 1000 times for each cell. In order to pass the random reallocation test, a given cell had to have $p < 0.05$ for both the overall *F*-test and the partial *F*-test for at least 50 of the 1000 rounds.

The *test for overfitting* (see [39, p. 104]) used the original best-fitting center-surround model of the cell (constructed using the actual data as described earlier),

but with the actual values of predictor variable randomly reassigned among predictor variables. Overfitting artifacts were ruled out at a level of $p<0.05$ for a given cell if the R^2 values from the randomization rounds exceeded the actual R^2 value for no more than 50 of the 1000 rounds. Note that the reshuffling and random reallocation tests above do not address overfitting by the original center-surround model, since for those tests the model that best fit the data was recalculated during each round of randomization. The *F*-tests described above assess whether the R^2 of the given model is significantly above zero given both the model and the data [17,29,53], but do not address whether a given model by itself can produce a good fit regardless of the input data.

2.5. Using the center-surround model to predict the responses to 'novel' stimuli

A center-surround model was constructed for a given cell using the model selection procedures described above, except that only the responses to half of the 32 center-surround stimuli were used as the response variable values. The 16 center-surround stimuli were chosen either randomly or on the basis of the bar composition of (i.e., the number of bar types in) the surround, as described in Section 3. The responses to the remaining 16 'novel' stimuli, which did not contribute to the model, were calculated given only the bar compositions of the novel stimuli and the offset and the weight coefficients provided by the model, using conventional prediction procedures (see [50,53,59]; S-plus routine *predict*). Note that these procedures do not call for testing the significance of the fit of the model to the data (for details, see [50,53,59]). But in any event, given the fact that the number of response variable values (or, equivalently, sample size n) is inversely proportional to the square of standard error of estimate of Y (see [29], pp. 171–178; [53], pp. 353–354), models constructed using the responses to only half of the 32 stimuli can be expected to have correspondingly less significant and less accurate fit to the data, and have correspondingly larger prediction intervals, relative to the models constructed using responses to all 32 stimuli.

2.6. Indices

The average surround modulation (ASM) index was calculated for each cell as $\sum_{i=1}^{n}[(|S_i - C_i|/C_i]/n$, where S_i and C_i are, respectively, the cell's responses to the ith center-surround stimulus and the corresponding center element of the stimulus. We calculated the absolute, and not the signed, difference between S_i and C_i because most cells in our sample were suppressed by some center-surround stimuli and enhanced by others. The surround-factor fit increment (SFI) index was calculated for each cell as $(R_s^2 - R_c^2/R_c^2)$, where R_s^2 and R_c^2 are the R^2 values of the center-surround and the center-alone models, respectively. The response modulation index (RMI) was calculated as $s_R/\bar{R}$, where s_R and $\bar{R}$ are standard deviation and mean, respectively, of the cell's responses to all 32 center-surround stimuli.

3. Results

3.1. Responses to center-surround stimuli

We recorded the responses of individual V1 neurons to center-surround stimuli in awake, fixating monkeys (see Section 2). We used 32 representative center-surround stimuli, each consisting of a single bar presented in the cell's CRF (center) with many additional bars in the surround. Each stimulus was constructed from a repertoire of four bar types (Fig. 1A): (i) the bar with the cell's preferred orientation and color (preferred bar), (ii) the bar with the cell's preferred color but the least preferred, or null, orientation, (iii) the bar with the cell's preferred orientation but null color, and (iv) the bar with the cell's null color and orientations (null bar). The stimulus set (Fig. 1B) consisted of many popout stimuli (e.g., preferred bar in the center and null bars in the surround), homogeneous stimuli (e.g., preferred bars in the center and the surround), and 'conjunction-target' stimuli (in which the center bar was defined by a unique combination of color and orientation). All these types of stimuli have been well-studied psychophysically [58]. The neuronal responses to popout and homogeneous stimuli have been studied extensively (see [1,2]), although the responses to conjunction-target stimuli have not (but see [23]).

We recorded the responses of 83 V1 neurons to the 32 center-surround stimuli from two macaque monkeys (see Section 2). We also recorded the response of each cell's CRF to each of the four bar types from which the stimulus set was constructed. Fig. 2A shows the responses of a V1 cell to these stimuli. The response of the cell to each of the four center stimuli (Fig. 2A, *right*) was substantially suppressed in most cases by the addition of surround stimuli (Fig. 2A, *left*). To quantify the degree of this surround modulation, we calculated an ASM index (see Section 2). The ASM value for this cell was 0.34, indicating that the response of the cell to center-surround stimuli was modulated (mostly suppressed) by an average of 34% relative to the response to the corresponding center bar alone. The surround suppression was statistically significant for all but six center-surround stimuli (pairwise Mann–Whitney tests, $p<0.05$). Furthermore, the responses were significantly modulated from one center-surround stimulus to the next for each of the four center stimuli (*rows* in Fig. 2A; one-way ANOVA, $p<0.05$).

3.2. Linear modeling of the observed responses

We first tested whether the responses of this cell could be accounted for as a linear function of the stimulation of the CRF alone, using the center-alone model. This model predicted, using conventional linear regression (see Section 2), the cell's responses to center-surround stimuli as a linear function of only the cell's responses to the appropriate center element of the center-surround stimulus while ignoring any contributions of the surround stimuli to the cell's response (Fig. 2B, *top*). Note that while the definition of linearity that linear regression models use is formally appropriate (see [7,17,50]), it is nonetheless different from that used by the linear

models of superpositional spatial summation by V1 simple cells [14,41,63], an issue we will address in Section 4.

The responses predicted by this model were poorly correlated with the observed responses of the cell (Fig. 2A and C), while the residuals were highly correlated with the observed responses ($r = 0.97$, not shown). The percentage of the cell's response variation accounted for by the model, measured by its R^2 value, was small and statistically insignificant ($R^2 = 0.068$; F-test, $p = 0.19$). Thus, the center-alone model failed to accurately predict the responses of this cell to center-surround stimuli, consistent with the fact that the cell was substantially surround modulated.

We next tested a more detailed linear regression model, the center-surround model, which predicted the responses to center-surround stimuli as a weighted linear sum of the contributions from the various bar types from the center and the surround (see Section 2). We used the cell's response to the center element when presented alone as an estimate of the input from the CRF during center-surround stimulation. Obtaining independent estimates of the surround inputs is considerably more difficult, since V1 cells usually do not respond to stimuli presented alone in the surround [32,35,38,46,52]. We therefore used the cell's response to the given surround bar type when presented alone within the CRF as an estimate of the response of the non-classical surround to that element during center-surround stimulation (Fig. 2B, bottom). Thus, the center-surround model tested the hypothesis that a given cell's responses to the center-surround stimuli were predictable as a linear weighted sum of the cell's responses to individual bar types presented individually within the CRF.

A few qualitative observations suggest such an approach might be feasible. For the exemplar cell illustrated in Fig. 2A, the cell's responses to nearly all center-surround stimuli (*open bars*) were suppressed relative to the corresponding center-alone stimuli (*dashed lines*). The response to the center-surround stimuli depended primarily on the center bar (*rows* in Fig. 2A) and to a lesser extent on the surround stimuli, consistent with a modulatory role for the surround. If the stimulus strengths of the surround were to account for the modulatory effect of the surround, then the modulatory effect of the surround should correspond to the strengths of the bar types of the surround. A detailed examination of the responses suggests that this was largely (but not always) the case. For instance, when the cell's preferred bar was in the center (*top row* in Fig. 2A), the surround that consisted entirely of bars of the cell's preferred bars (*open vertical bars*) was the most suppressive (*filled arrow*). The surround consisting entirely of the bars with the preferred orientation but null color (*filled vertical bars*, *ampersand*) was slightly less suppressive (*ampersand*), and surrounds consisting of the two least effective bar types (*open* and *filled horizontal bars*) were correspondingly even less suppressive ('+' and '#' *signs*, respectively). These observations suggest, but by no means prove, that surround strength corresponded to the magnitude of surround suppression for this cell. If these observations were valid, then the center-surround model, which represented a quantitative implementation of these notions, should adequately predict the cell's responses to the center-surround stimuli.

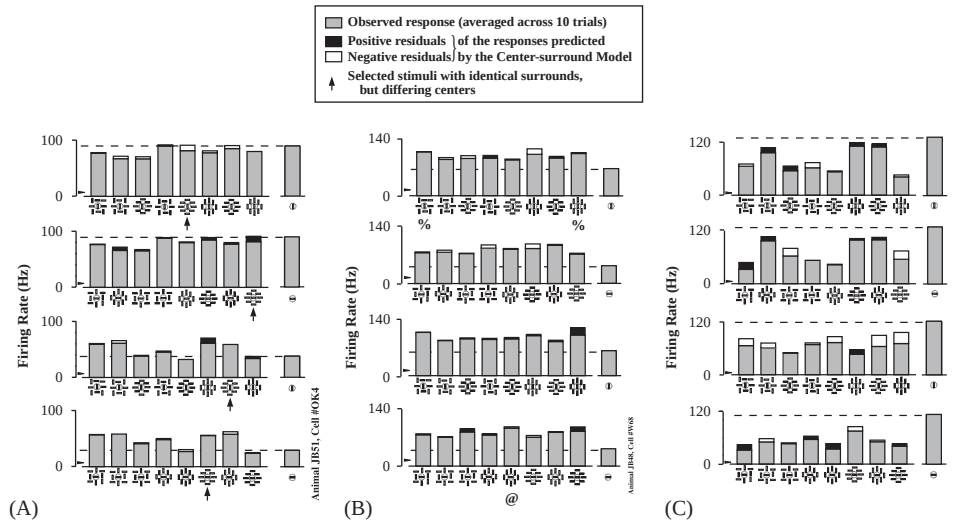


Fig. 3. Linear center-surround models can account for a diversity of surround modulation profiles. (A–C) Individual V1 cells. (A) $R^2 = 0.95$, (B) $R^2 = 0.72$, and (C) $R^2 = 0.79$. For each cell, the overall fit of the center-surround model and the contribution of the surround factors to the fit were significant ($p < 0.05$, overall and partial F-tests) and the distribution of the residuals was random (Kolmogorov–Smirnov test, $p > 0.05$) (not shown). Also, the observed responses were within the 95% confidence band of the predicted responses for all 32 center-surround stimuli for each cell (not shown). In panel B, the '%' and '@' *signs* denote the cell's most effective center-surround stimuli with the preferred and the null bars, respectively, in the center. The coefficients of the center-surround models were: (A) $\alpha = 1.23$, $b_0 = 0.97$, $b_1 = -1.54$, $b_2 = -3.17$, $b_3 = 3.18$; (B) $\alpha = 0.73$, $b_0 = -1.70$, $b_1 = -0.78$, $b_2 = -3.52$, $b_3 = 1.57$, $b_4 = 0.30$; (C) $\alpha = 2.38$, $b_0 = -3.97$, $b_1 = 1.24$, $b_2 = -12.11$, $b_3 = 10.54$, $b_6 = 0.42$.

In general, the responses predicted by the center-surround model matched the cell's observed responses well, regardless of the nature of the center-surround feature discontinuities, or the sign or the degree of surround modulation (Fig. 2A and D). Overall, the model accounted for 84% of the variation in the cell's center-surround responses ($R^2 = 0.84$), and this fit of the predicted responses to the observed responses was statistically significant ('overall' F-test, $p < 0.05$). The residuals were poorly correlated with the observed responses ($r = 0.22$, $p > 0.05$; not shown), indicating that the predicted responses matched the observed responses regardless of the response magnitude. Furthermore, the residuals were distributed randomly (Kolmogorov–Smirnov test for goodness of fit, $p > 0.05$, Fig. 2E), indicating that the model provided an adequate and unbiased description of the data for this cell. Together, the above results indicate that the center-surround model accurately predicted the responses of this cell to center-surround stimuli.

To quantify the improvement in the fit of the linear model by the addition of the surround factors for this cell, we calculated an SFI index (see Section 2). The cell had an SFI value of 11.35, indicating that the center-surround model accounted for

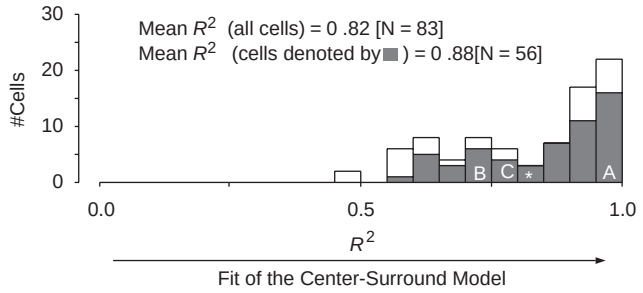


Fig. 4. Fit of the center-surround model for the V1 cell population. The distribution of R^2 values of center-surround models for 83 V1 cells are shown in histogram form. *Filled bars* denote cells with $p<0.05$ for both the overall *F*-test and the partial *F*-test; the cells denoted by *open bars* had $p>0.05$ in one or both of these tests. In this and subsequent figures, the exemplar cell shown in Fig. 2 is denoted by an *asterisk*; the cells shown in Fig. 3A, B, and C are denoted by the appropriate *letters*.

about 11-fold more response variation than the center-alone model for the cell. This improvement in the fit by the addition of surround factors (or the 'partial fit') was statistically significant (partial *F*-test, $p<0.05$), indicating that the improvement could not be attributed to artifacts arising form the inclusion of the predictor variables pertaining to the stimulus surround.

The center-surround model also accurately predicted the responses of V1 cells with other types of color and orientation tuning, surround modulation profiles and overall stimulus preferences (Fig. 3). The cell shown in Fig. 3A was a color selective cell, whereas the cell shown in Fig. 3C was modestly tuned for both color and orientation. The cell shown in Fig. 3B was exclusively surround enhanced, while the cell shown in Fig. 3C was exclusively surround suppressed. In some cases, the same surround was facilitative or suppressive, depending on the strength of the center stimulus (*arrows* in Fig. 3A). In other cases, the selectivity of the cell for the nature of the center-surround feature discontinuity (e.g., popout vs. non-popout) depended on the bar in the center. For instance, for the cell shown in Fig. 3B, a homogeneous stimulus and a conjunction-target stimulus were the two most effective stimuli with the cell's preferred bar in the center ('%' *signs*, *top row*). However, with the null bar in the center (*bottom row*), the same cell responded best to a popout stimulus ('@' *sign*). This paradoxical feature of many V1 cells has previously led to debates over whether or not V1 cells are popout selective [2,23,24,32,35,46,52,56].

For the population as a whole (Fig. 4), the overall fit of the center-surround model and the increment in the fit of the model compared to the fit of the center-alone model were both statistically significant for about two-thirds of the cells (56/83, 67%; overall *F*-test and the partial *F*-test, $p<0.05$). The model accounted for an average of 88% of the response variation for these cells (mean $R^2=0.88$, median $=0.92$), and the residuals were distributed randomly for most of these cells (53/56, 95% or 64% of the total; Kolmogorov–Smirnov test, $p>0.05$).

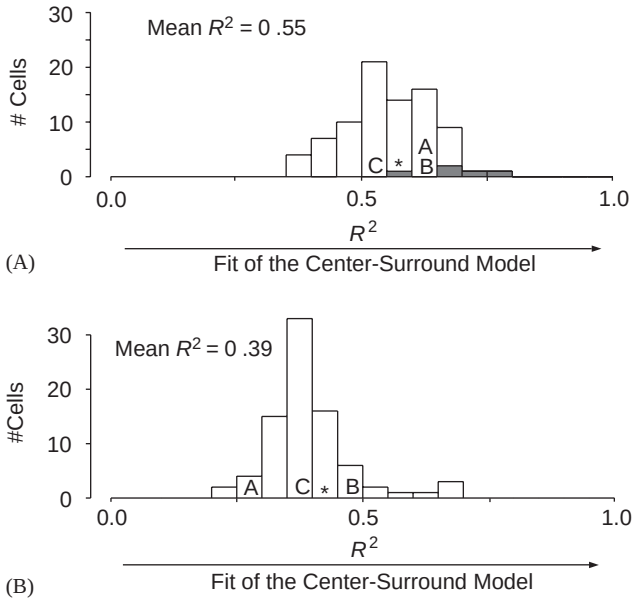


Fig. 5. Fit of the center-surround model using randomized data. (A) Distribution of the average R^2 values from the reshuffling test for each cell. The cells denoted by *filled bars* are those cells denoted by filled bars in Fig. 4 which also passed the reshuffling test. (B) Distribution of the average R^2 values from the random reallocation test for each cell. None of the cells indicated by filled bars in Fig. 4 passed the random reallocation test. See Section 2 for details.

3.3. Testing for modeling artifacts

Given the surprising efficacy of the center-surround model for V1 cells, we carried out three additional tests to determine whether the fit of the model to the data was an artifact of one or more aspects of our modeling procedure. Each test was based on randomization of the data (see Section 2), so that if the fit of the model were an artifact of the modeling procedure and not inherent in the data themselves, the randomized data should produce at least as good of a fit as the actual data.

To determine whether the performance of the center-surround model was due to a fortuitous combination of responses to the stimuli, we studied how the fit of the model was affected by either reshuffling or randomly reallocating the cell's responses to the four bar types from which the stimulus set was constructed (see Section 2). Either test involved determining whether the cell's observed responses to center-surround stimuli could be accurately predicted as an appropriate linear weighted sum of novel values for predictor variables; all procedures were otherwise identical to those used for the actual data. Either reshuffling or randomizing the input values significantly reduced the level of the fit of the model, as measured by the R^2 values (paired t-tests, $p<0.05$) (Fig. 5). The fit had a lower R^2 value, or was statistically

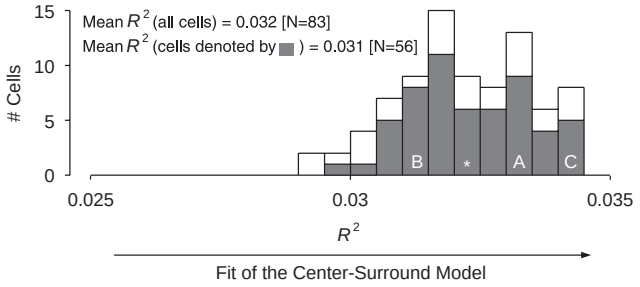


Fig. 6. Test for overfitting using randomization. The population distribution of average R^2 values, calculated from 10^3 rounds of randomization for each cell, is shown here in histogram form. *Filled bars* in this figure denote those cells for which the same center-surround model provided a significant fit when the actual data were used as input. The same set of cells were also denoted by filled bars in Fig. 4.

insignificant (overall and partial F-tests, $p > 0.05$), or both for all but five cells by the reshuffling method (Fig. 5A) and for all cells by the random reallocation method (Fig. 5B). Thus, the fit of the center-surround model to the actual data was in general much better than that expected from random chance.

Another significant concern with multiple regression models such as the center-surround model is overfitting, or a good fit resulting from an unduly large number of predictor variables [7,17,29,50,53]. Thus, it is possible in principle that the performance of the center-surround model was an artifact of the mathematical fact that larger number of predictor variables result in usually higher (and never lower) R^2 values [7,17,29,50,53]. We tested this scenario for each cell using the test for overfitting (see Section 2). For each cell, we randomized the cell's observed responses to the predictor variables, so that the cell's responses to the four bar types were randomly assigned among the center-surround stimuli, regardless of the actual bar composition of the stimuli. The values of the response variable, i.e., cell's observed responses to the center-surround stimuli, were not randomized and remained unchanged. We then computed the R^2 value for the data using the given cell's original center-surround model derived using the actual data. This test differed from the random reallocation test above in that this test used the same center-surround model as used for the actual data for each cell, and in terms of the manner in which the input data were randomized (see Section 2 for details). If the performance of the center-surround model was due to the fact that there were too many predictor variables in the original model, then the model should produce comparable R^2 values from randomized vs. actual data. Fig. 6 shows the average R^2 value from 1000 rounds of randomization for each cell in histogram form. The R^2 values from randomized data were significantly lower than those obtained using the same model and the non-randomized data (paired t-test, $p < 0.05$). For the 56 cells for which the center-surround model provided a good fit to the non-randomized data (*filled bars* in Fig. 6), the average R^2 value was 0.032 (median, 0.033), and this was, on average, about 25-fold lower than the R^2 value from the actual data. Furthermore, for none of these 56 cells, the fit of the model to the randomized data was statistically

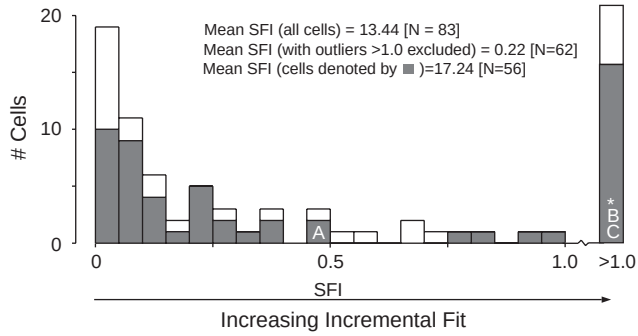


Fig. 7. Improvements in model fit when surround modulation is taken into account. SFI indexes were calculated for each cell as described in Section 2. The population distribution of SFI is shown here in histogram form. *Filled bars* denote cells with $p<0.05$ for both the overall and partial F-tests; the cells denoted by *open bars* had $p>0.05$ for one or both of these tests.

significant ($p<0.05$; data not shown). Thus, the fit of the model to the observed data was not an artifact of overfitting.

Together, the results from the randomization tests indicate that the performance of the center-surround model was not an artifact of our modeling procedures.

3.4. Degree of surround modulation and performance of the center-surround model

In principle, the performance of the center-surround model could be due to a lack of surround modulation. In such a case, the center stimulus would account for all or most of the cell's response to center-surround stimuli, and the center-surround model would successfully predict the cell's responses based largely on the contribution of the center factor alone, even if the surround factors contribute little to the fit. However, this was not the case: For the 83 cells in our sample, the responses to the center-surround stimuli on average modulated (i.e., suppressed or facilitated) 25% relative to the center-alone stimuli [23]. Importantly, the cells' R^2 values were not correlated with the magnitude of surround modulation ($r = -0.13$), indicating that the lack of fit for a given cell was not necessarily attributable to large surround modulations, nor did smaller modulations ensure a good fit. Thus, the performance of the center-surround model could not be attributed to a lack of surround modulation.

The fact that the V1 cells were substantially surround modulated, however, does not by itself ensure that the surround factors contributed significantly to the center-surround model. The SFI index described earlier measures the extent to which taking surround modulation into account improves the fit of the model (see Section 2). Fig. 7 shows the population distribution of the SFI values. The contribution of the surround factors to the overall fit of the center-surround model was statistically significant for about four-fifths of the cells (67/83, 81%) as measured by the partial F-test (data not shown). For these cells, the fit of the center-surround model

improved by an average of about 13-fold by the addition of the surround factors, as measured by the SFI (i.e., average SFI = 13.14). The 56 cells for which both the overall fit of the center-surround model and the contribution of the surround factors to the fit of the model were statistically significant (56/83, 67%; overall F-test and partial F-test, $p < 0.05$; *filled bars* in Fig. 7) had an average SFI value of 17.24, indicating that for these cells the addition of the surround factors to the center-surround model increased the fit of the model by more than 17-fold. Taken together, these results indicate not only that the surround stimuli we used substantially modulated the responses of the V1 cells, but also that the center-surround model adequately accounted for the surround modulation for a substantial majority of V1 cells.

3.5. Response modulation across center-surround stimuli

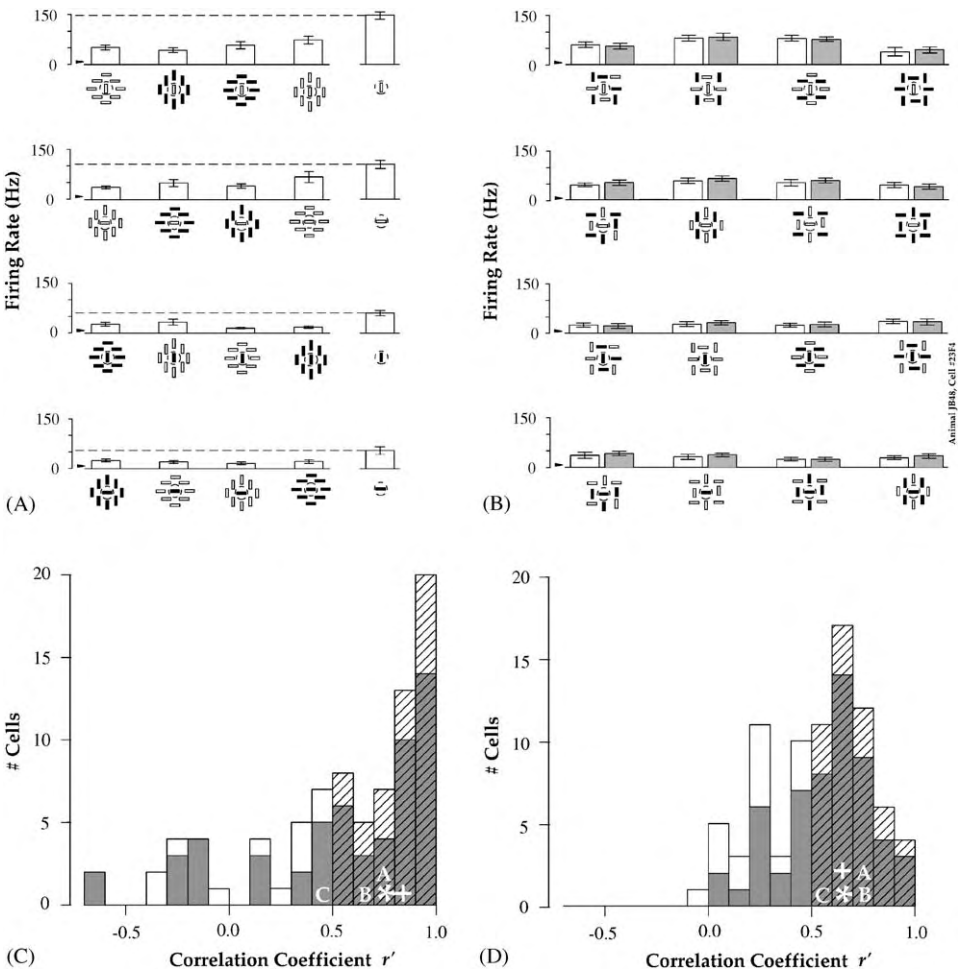
Poor response modulation across the center-surround stimuli is another potential source of artifactually good fit. In such a case, any model which accurately predicts the mean response of the cell to the center-surround stimuli would provide a good fit to the data (for additional information, see [29], pp. 174–175; [53], pp. 340–347). While the various model selection procedures we used, including the Mallows' *Cp* criterion and the F-tests, implicitly test for this possibility (see [17,29,53]; also see Section 2), a direct measure of response modulation would be desirable. We used the RMI to measure the modulation of each cell's response across the 32 center-surround stimuli (see Section 2). For the population as a whole, the mean RMI value was 0.40, indicating that the responses of V1 cells were in general substantially modulated by the center-surround stimuli, and that a model in general could not accurately predict a given cell's responses to the center-surround stimuli simply by estimating the mean response of the cell to the stimuli (data not shown). Furthermore, the RMI values were well-correlated with the R^2 values ($r = 0.62$), contrary to what would be expected if the performance of the center-surround model was due to a lack of surround modulation. The RMI values of the cells for which the center-surround model provided a good fit vs. those cells for which the model did not were statistically indistinguishable from each other (two-tailed t-test, $p > 0.05$), indicating that the differences in the performance of the model between the two sets of cells were not attributable to differences in the response modulation of the cells. We obtained qualitatively similar results when we repeated this analysis separately for each of the four groups of eight center-surround stimuli with the same center bar (see Fig. 1) (data not shown). Together, these data indicate that the performance (or lack thereof) of the center-surround model was not attributable to a lack of response modulation across the center-surround stimuli.

3.6. Ability of the center-surround model to predict the responses to 'novel' stimuli

If a given center-surround model adequately captures center-surround summation behavior of a given cell, then the model should be able to predict the cell's responses to novel center-surround stimuli. To test this hypothesis, we constructed the

center-surround model for each cell using the cell's responses to only 16 of the 32 center-surround stimuli (see Section 2). The remaining 16 stimuli are 'novel' to the model, in that the cell's responses to these stimuli played no part in the construction of the model. We then used the model to predict, using conventional procedures of multiple regression, the cell's response to the novel stimuli. Given the fact that the models were based on the responses to only one-half of the center-surround stimuli, the accuracy of the predictions and the significance of the fit (e.g., as determined by an *F*-test) can be expected to be lower relative to the earlier models which used the full complement of the cell's responses ([17,29,53]; also see Section 2).

The prediction procedure is illustrated in Fig. 8A and B using an exemplar V1 cell. The center-surround model for the cell was constructed using only the cell's



responses to the 16 center-surround stimuli which contained a single type of bar in the surround (i.e., popout or homogeneous stimuli) and the responses to the four bar types from which the stimuli were constructed (Fig. 8A). For these stimuli, the predicted responses of the model (not shown) and the actual responses of the cell (*open bars* in panel A) were significantly correlated with each other (correlation coefficient $r = 0.86$, $p < 0.05$, one-tailed Pearson product moment correlation test), indicating that it was statistically appropriate to use this model to predict the cell's responses to novel stimuli ([59], pp. 499–502). The model's predicted responses to 16 novel stimuli closely matched the cell's responses to these stimuli (correlation coefficient $r' = 0.89$, $p < 0.05$, *panel B*).

The same prediction procedure was repeated for all the remaining cells. For each cell, the predicted responses and actual responses to the original 16 stimuli (*panel A*) were significantly correlated ($r > 0.50$, $p < 0.05$; data not shown). The population distribution of the coefficients of correlation (r') between the predicted and the actual responses to the novel stimuli is shown in Fig. 8C. The r' values were statistically significant ($r' > 0.50$, $p < 0.05$) for nearly two-thirds of the V1 cells (53/83, 64%; *hatched bars* in Fig. 8C), indicating that for these cells, the center-surround model was able to accurately predict the responses to novel stimuli in panel B, given the responses to the 16 stimuli in panel A. The average correlation coefficient for these 53 cells was 0.81. For the 56 cells for which the original center-surround model using all 32 stimuli provided a significant fit to the full data set (*filled bars* in Fig. 8C), the correlation was significant for about two-thirds (37/56, 66% or 45% of the total) of the cells (*filled hatched bars*, mean $r' = 0.64$). Interestingly, the predicted responses to the novel stimuli were significantly *anti*-correlated with the observed responses ($r' < -0.50$, $p < 0.05$) for two cells, indicating that for these cells, surround

Fig. 8. Predictive ability of the center-surround model. (A) Responses ($\pm$SEM) of an exemplar V1 cell to 16 center-surround stimuli (*bar array icons, left*) and to the four bar types from which the center-surround stimuli were constructed (*bar icons, right*). A center-surround model for the cell was constructed using only the data in this panel. The correlation coefficient r between the paired observed and predicted responses to these 16 stimuli was 0.86 (not shown). (B) Center-surround model for the cell constructed using data in panel A was used to predict the cell's responses to 'novel' stimuli shown in this panel, using conventional regression prediction procedures. The predicted (*gray bars*) and the actual responses (*open bars*) are shown side by side for each stimulus. The correlation coefficient between the paired observed and predicted responses to the novel stimuli, r', was 0.89. (C) The same prediction procedure was repeated for the remaining 82 cells using the two halves of the stimulus set. The resulting correlation coefficients between the observed and the predicted responses to the novel stimuli (r') are shown here in histogram form for all 83 cells. The exemplar cell in panels A and B of this figure is denoted with a '+'. The exemplar cells in Fig. 2 (*asterisk*) and Fig. 3A–D are also denoted. Note that the r' value (0.41) for the exemplar cell in Fig. 3C was not statistically significant. (D) The same prediction procedure as above, except using randomly chosen subset of 16 cells. For each cell, 16 out of the 32 stimuli were chosen at random and center-surround model was constructed using these data. The resulting correlation coefficients between the observed and the predicted responses to the novel stimuli (r'), averaged from 10^3 rounds, are shown here in histogram form for all 83 cells. In both panels C and D, *filled bars* denote the 56 cells with $p < 0.05$ for both the overall and partial F-tests using the responses to all 32 stimuli; the *hatched bars* denote cells for which correlation was statistically significant ($p < 0.05$, $r' > 0.50$).

modulation was qualitatively different with one vs. more bar types in the surround (i.e., stimuli panel A vs. B).

In the above analysis, the two sets of 16 stimuli were chosen based on the number of bar types in the surround. To test whether the center-surround model can accurately predict responses to the center-surround stimuli regardless of the particular subsets of the stimuli chosen, we repeated the above analysis using the cell's responses to a randomly chosen 16 of the 32 center-surround stimuli and used the model to predict the responses to the remaining half of the stimuli (see Section 2). This process was repeated 10^3 times for each cell. The average r' values from 10^3 rounds of randomization are shown in Fig. 8D for all V1 cells. The mean r' value was statistically significant (i.e., mean $r' > 0.50$) for about 60% (50/83) of the cells (*hatched bars* in Fig. 8D), indicating that the center-surround model accurately predicted the responses to the novel stimuli for these cells. Of the 56 cells for which the center-surround model provided a good fit with all 32 stimuli (*filled bars* in Fig. 8B), the model was also able to accurately predict the responses to the novel stimuli for 36 cells (64% or 43% of the total; *filled hatched bars* in Fig. 8B). Together, the results of the prediction analysis indicate that the center-surround model provided a good description of the center-surround summation, and was able to predict responses to novel stimuli, for many of V1 cells.

4. Discussion

4.1. Quantitative framework for center-surround summation

Our results show that the response of many V1 cells to center-surround stimuli can be accurately described as a weighted linear sum of the cell's responses to stimuli in the center and the surround. These results represent the first demonstration that the actual responses of V1 cells to center-surround stimuli can be described by a quantitative model, linear or otherwise. The fact that a linear model provided a good account of the observed surround modulation, and non-linear models were not needed, for a majority of the cells substantially simplifies our view of center-surround modulation in V1 and neural mechanisms required to implement it. Since not all possible non-linear models were tested, our results cannot be taken to mean that linear models were better than non-linear models (also see below), but only that linear models provided a good account of center-surround summation for many V1 cells.

To the extent that the center-surround responses of many V1 cells could be quantitatively described in terms of the cell's responses to stimuli in the center and the surround, our results provide a quantitative framework of explanation for many complexities of contextual effects. For instance, it is clear that whether a given surround is facilitative or suppressive depends on the strength of the stimulation of the center vs. the surround: the same surround can be suppressive when the center stimulus is highly effective, or facilitative when the drive in the center is relatively weak (see, e.g., Fig. 3A; also see [24,46,55,56,64]). Similarly, our results demonstrate

how differential responsiveness to popout vs. non-popout stimuli can emerge in the same V1 cell as a function of the relative strengths of the stimuli in center and the surround. The questions of whether surround modulation is primarily suppressive or facilitative, or whether or not V1 cells are selective for popout stimuli, have been a matter of some debate (for overviews, see [46,55,56]; also see [23,36,48]). Our results quantitatively illustrate that these and other complex, seemingly contradictory center-surround phenomena can in many cases be accounted for by the relative strengths of the stimuli and the weights the cell uses in integrating the inputs (see [24,35,46,55,56]). That is not to say, however, that all aspects of center-surround summation can be accounted for by a linear model, an issue we will address later.

Our results also offer a simple mechanistic explanation for the role of surround modulation in many aspects of higher-order visual processing. For instance, the selectivity of many V1 cells for collinear vs. perpendicular surrounds ([30,32,35,36,42,46,52,56; also see 24]; also see Fig. 3) is believed to play an important role in the representation of many complex shape characteristics, including junctions and corners of lines [11] and of surfaces [3]. Our results demonstrate that the selectivity for junctions and corners can emerge in cells that are otherwise responsive to collinear elements from a differential efficacy of individual center-surround elements in driving the cell (also see below). Thus, a cell which prefers a right-angle (i.e., 'L' shape) over collinear lines (i.e., '–' shape) when both stimuli are presented in a given color may reverse its preferences when the stimuli are presented in a different color or orientation (this report, also see [24]), or at different luminance contrasts [46]. From a more cognitive viewpoint, the fact that surround modulation in V1 can be adequately explained in terms of bottom-up sensory inputs calls into question the notion that this modulation explicitly represents a higher-order perceptual correlate of figure-ground segregation or popout [34,67] at this level of cortex (also see [23,36,48]).

4.2. Relationship to previous work

The notion that the response of a visual neuron to center-surround stimuli represents a balance between the strengths of the stimuli in the center vs. the surround was, to our knowledge, first proposed by Levitt and Lund [35] (also see [24,55,57,64]), who showed that the response of V1 cells to center-surround stimuli varied as a function of the luminance contrasts of the stimuli in the center and the surround. Although this view of center-surround summation was supported by many later neurophysiological studies [46,51,55], the quantitative relationship between the stimulus strengths and the center-surround responses was not clear, nor was it clear whether a single quantitative framework could explain the diversity of the center-surround summation behavior in V1 cells. Somers et al. [55] have proposed a non-linear model which expresses the center-surround response of neurons as a function of the relative strengths of the inputs from the center and the surround. Similarly, Stemmler et al. [56] have proposed a neural network model which accounts for many psychophysical aspects of popout and contour integration. However, in neither case were the predictions of the model tested against the actual center-surround responses

cells in V1 or elsewhere. The difficulty in estimating the inputs from the surround is a major impediment to such testing in general, which our models address by instead using the corresponding responses to the bar types presented individually in the CRF. Many other previous models that dealt with center-surround interactions (e.g., [9,56]) did not, and were not intended to, directly address neuronal responses to different center-surround stimuli. Our results address these issues by directly comparing the predictions of a linear model to the observed responses to specific center-surround stimuli (also see [64]).

It is important to distinguish the weighted linear summation we describe in this report from the linear summation within V1 simple cell CRFs described previously [12,28,41,47]. In the context of V1 simple cells, and in the context of linear systems analysis in general, the term *linear summation* is typically used to exclusively mean *superpositional linear summation* (see, e.g., [14], pp. 20–22). Briefly, a given spatial summation is linear in this sense if and only if (a) the response of a cell to a superposition of two (or more) stimuli is an unweighted sum, usually with rectification, of its responses to the stimuli presented individually, and (b) the scaling of the stimulus results in a corresponding scaling of the response (for additional information, see [14,63]). By this definition, the weighted linear summation we describe is clearly non-linear. Indeed, the process of surround modulation itself is inherently non-linear by this definition, to the extent that the surround stimuli which by themselves elicit little or no response from the cell nonetheless inhibit or facilitate the response of the cell to the stimulus in the center. Instead, the summation we describe is linear strictly in the sense, and only to the extent, that it is adequately described by a linear model.

4.3. Neuronal mechanisms

An intriguing fact about our center-surround model is that the input by a given bar type in the surround can be effectively estimated as the response of the CRF to the given bar type. It would appear to a first approximation that the only neural mechanism consistent with this is a scenario in which center-surround summation is primarily mediated by lateral connections among cells with similar tuning profiles, so that for any given bar, the response of the unit whose receptive field is in the stimulus center is essentially the same as the responses of the units whose receptive fields are in the surround. This scenario is anatomically plausible, since nearly all of the excitatory long-range horizontal connections in V1, and about half of the inhibitory connections, are among cells with similar tuning profiles for orientation [20–22,31]. However, we wish to emphasize that our results do not rule out alternative scenarios in which the surround units with dissimilar tuning profiles also contribute substantially to the center-surround summation, but with the level of activation of the CRF gating all surround inputs. In this case, the weight coefficients of the linear model would reflect this gating. However, it is not possible to ascertain either scenario by an examination of the weight coefficients alone; further experiments, presumably at level of individual synapses, are needed (see, e.g., [25]).

Previous studies have suggested that connections across dissimilar orientation domains in V1, which are generally inhibitory, could subserve the processing of corners and T-junctions by selectively suppressing the responses to cross-oriented line segments [11,20]. The connections across similar orientation domains, on the other hand, could mediate the selectivity for collinear line segments (see [20]). Indeed, this is largely consistent with recent psychophysical studies which suggest that the selectivity for iso-orientation and cross-orientations are mediated by distinct subsystems ([65], also see [30]). While the existence of such distinct subsystems is entirely plausible, it is clear that a single V1 cell can also show selectivity for either collinear or cross-oriented line segments depending on the strength of the stimuli in the center vs. the surround ([35,46,55,56,64], this study). The two scenarios can be reconciled if one assumes that both sets of connections—across similar and dissimilar orientation domains—participate in the center-surround summation by individual V1 cells, with one set of connections dominating over the other depending on the strength of the collinear vs. cross-oriented surrounds.

4.4. Further explorations

The fact that V1 cells integrate the center-surround stimuli in a scaled linear fashion straightforwardly suggests that explorations of both additional linearities and deviations from linearity might be fruitful. Our models provide a useful point of departure for both.

To begin with, scaled linear summation of center-surround stimuli in V1 may be more extensive than our results suggest. It is possible that a different method of estimating the surround contributions, or taking into account the size, spatial heterogeneity and/or the temporal dynamics of the receptive fields [12,13,36,38,49,51,61] may uncover additional components of the scaled linear summation mechanism. For instance, it is clear that non-classical surrounds in V1 are considerably heterogeneous, in that the magnitude of surround modulation varies as a function of distance from the CRF and of the nature of the mapping stimulus, including its contrast [11,49] and that different subregions of the non-classical surround may modulate the CRF response differently [38,51,66]. Whether or not spatial summation within a given subregion is linear remains unclear. One scenario is that spatial summation within each subregion is linear, perhaps with varying weight coefficients across subregions. Alternatively, summation in some or all of these subregions may be non-linear, which may account for, at least in part, the failure of the linear model for some V1 cells. However, we believe local non-linearities are unlikely for those cells for which the linear model provides a good fit, since it requires a rather precise counterbalancing of the local non-linear effects to achieve an overall linear effect. In any event, note that the possibility of the various non-linearities notwithstanding, the fact that the summation is linear under the experimental conditions described remains a useful result.

It remains to be seen whether the linear relationship holds for more complex center-surround stimuli (e.g., stimuli constructed from a larger repertoire of bar types), or for other visual features, most notably spatio-temporal summation of

large-field motion. Many aspects of spatio-temporal summation within V1 simple cell CRFs are known to be linear [12–14,36,28]. It also remains to be seen whether or to what extent the scaled linear summation mechanism accounts for center-surround summation in other visual areas. Spatial summation of motion stimuli within MT cell CRFs is well accounted for by scaled linear summation, although allowing for modest non-linearities improves the fit even further [6].

As noted above, it is likely that non-linear mechanisms underlie, at least in part, the inability of the linear model to account for all response variation in all cells. There are many potential sources of non-linearities in center-surround summation including, but not limited to, local spatial non-linearities, temporal non-linearities, response saturation, luminance contrast effects and top-down inputs [24,27,30,35,43,46,56,65]. Many cortical phenomena believed to be mediated by center-surround summation, such as contrast-gain control, cannot be fully explained by purely linear mechanisms [9]. Thus, it is evident that non-linear models will be ultimately needed to fully account for the complexities of surround modulation. However, it may be feasible to investigate many of the non-linear effects as specific deviations from linearity under specific experimental conditions.

4.5. Concluding remarks

Ultimately, both the strength and the limitation of our model, or of any model for that matter, are that it simplifies complex realities. To the extent that the center-surround model accounts for the observed complexity and diversity of the center-surround summation behavior for a majority of V1 cells, it provides a rigorous conceptual framework for how V1 cells integrate inputs form the center and the surround. To the extent that the model does not account for the center-surround modulation of all V1 cells, and to the extent that the model itself can be refined, it offers a useful frame of reference, and a practical point of departure, for further investigations into the mechanisms of center-surround modulation.

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