Contrast-Dependent Variations in the Excitatory Classical Receptive Field and Supressive Nonclassical Receptive Field of Cat Primary Visual Cortex

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In area V1 of cat and monkey, there is a surround region beyond the classical receptive field (CRF) which alone is unresponsive but may modulate the cell’s response. This field is referred to as the “nonclassical receptive field” (nCRF). It has been reported in monkey that the extent of CRF and/or nCRF of V1 neurons is not fixed but varies with stimulus contrast. We reexamined the contrast dependence of V1 neurons in cat to determine whether this differs from previous studies in macaque. By fitting the spatial summation curves obtained at different contrasts with a difference of Gaussians model, we estimated quantitatively the effect of contrast on the spatial extent of the CRF and nCRF as well as the strength of surround suppression. Our results showed that both the CRF and nCRF expanded at low contrast, but the expansion is more marked for the CRF than for the nCRF. Although the effect of contrast on surround suppression was varied, the overall suppression increased significantly at high contrast. Moreover, the contrast-dependent change in the extent of CRF is independent of the change in suppression strength. Overall, our results in cat are in agreement with those obtained in macaque money.

Keywords: cat, contrast effect, spatial summation, surround suppression, visual cortex

Introduction

Many studies have indicated that regions beyond the classical receptive field (CRF) of neurons of the primary visual cortex (V1), although alone unresponsive to visual stimuli, can modulate a cell’s response (Hammond and MacKay 1981; Allman et al. 1985; Gulyas et al. 1987; DeAngelis et al. 1994; Hammond and Kim 1994; Li CY and Li W 1994; Sillito et al. 1995; Sengpiel et al. 1997). This modulatory effect can be facilitatory or inhibitory, and its extent can be determined from area summation characteristics (DeAngelis et al. 1994; Li CY and Li W 1994). This surround field is conventionally referred to as the “non-classical receptive field” (nCRF). There has been increasing interest in interactions between the CRF and the nCRF because together they may constitute the neural basis of a variety of psychophysical phenomena, such as contour integration (Von der Heydt and Peterhans 1989; Field et al. 1993; Kapadia et al. 1995; Xu et al. 2005), contextual effects (Li et al. 1999; Shen et al. 2007), and figure-ground segregation (Lamme 1995).

Previous investigators implicitly or explicitly assumed the size of the CRF and the extent of nCRF to be fixed (DeAngelis et al. 1994; Li CY and Li W 1994) and independent of stimulus characteristics or surrounding context. Some recent studies in primate have reported that the extent of spatial summation in V1 neurons depends on stimulus contrast (Kapadia et al. 1999; Sceniak et al. 1999; Fitzpatrick 2000; Shushruth et al. 2009; Schwabe et al. 2010). However, using empirical measures versus nonempirical, the contrast dependence of surround inhibition yields very different results (Sceniak et al. 1999; Schwabe et al. 2010). We reexamined the contrast effect on spatial summation of V1 neurons in cat and estimated the extent of the excitatory CRF and the suppressive nCRF quantitatively by fitting the spatial summation curves with a difference of Gaussians (DOG) model (Rodieck 1965; Enroth-Cugell and Robson 1966; DeAngelis et al. 1994; Sceniak et al. 1999, 2001). Our results reveal that both the excitatory CRF and the suppressive nCRF expand under low stimulus contrast but that this contrast-dependent variation is more marked for the CRF than for the nCRF. In addition, the suppression strength in nCRF was seen to decrease or even disappear under low contrast. The results we obtained in the present work are in good agreement with the monkey data in a previous study (Schwabe et al. 2010). The functional significance of these contrast-dependent variations is discussed.

Materials and Methods

Animal Preparation

Acute experiments were performed on 21 cats (the same animals were also used for other parallel projects). All procedures were conducted according to National Institutes of Health guidelines for animal research and in compliance with the guidelines of the Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences. Detailed descriptions of procedures for animal surgery, anesthesia, and recording techniques can be found in an earlier study (Li CY and Li W 1994). Briefly, cats were anesthetized prior to surgery with ketamine hydrochloride (50 mg/kg, intravenously [iv]), and then tracheal and venous cannulations were carried out. After surgery, the animal was placed in a stereotaxic frame for performing a craniotomy and carrying out neurophysiological procedures. During recording, anesthesia and paralysis were maintained with urethane (20 mg/kg/h), gallamine triethiodide (10 mg/kg/h), respectively, and glucose (200 mg/kg/h) in Ringer’s solution (3 mL/kg/h) was infused. Heart rate, electrocardiography, electroencephalography (EEG), end-expiratory CO₂, and rectal temperature were monitored continuously. Anesthesia was considered sufficient when the EEG indicated a permanent sleep-like state. Reflexes, including cornea, eyelid, and withdrawal reflexes, were tested at appropriate intervals. Additional urethane was given immediately when necessary. The nictitating membranes were retracted and the pupils dilated. Artificial pupils of 3 mm diameter were used. Contact lenses and additional corrective lenses were applied to focus the retina on a screen for stimulus presentation. At the end of the experiment, the animal was sacrificed by an overdose of barbiturate iv.

Single-Unit Recording

Extracellular recordings were made from 115 neurons of the primary visual cortex of anesthetized cats using tungsten-in-glass microelectrodes with exposed tips of 5–10 µm (Li et al. 1995). The electrode was advanced into the cortex via a step-motor micro-drive (Narishige,
Spatial Summation Test

Customized software run on a computer with a high-resolution graphics board was used to generate visual stimuli. The stimuli were circular patches of drifting sinusoidal gratings with different sizes presented on a high-resolution monitor screen (40° × 30°) at a 100 Hz vertical refresh rate. The mean luminance of the gratings was 10 cd/m². Luminance nonlinearity of the monitor was corrected by the software. The monitor was placed 57 cm from the cat’s eyes. When single-cell action potentials were isolated, the preferred orientation, spatial frequency, and temporal frequency of each cell were determined. Each cell was stimulated monocularly through the dominant eye with the nondominant eye occluded. Then, the center location of CRF was carefully determined by placing a narrow sine-wave grating patch (0.5°–1.0° width × 3.0°–5.0° length at 0.4 contrast) at successive positions along the axes perpendicular and parallel to the optimal orientation of the cell and measuring the response to its drift. The grating was set at the optimal orientation and spatial frequency and drifted in the preferred direction with the optimal speed of the recorded cells. The peak of the response profiles for both axes was defined as the center of the CRF. All the recorded cells were in the area of the visual cortex representing the central visual field ≤5°. By measuring neuronal response as a function of stimulus area, spatial summation curves were measured at a high and low contrast levels (see Results). The grating patch was centered over the receptive field center and varied in size with 11 steps or more from 0.1° to 15° in radius. Each patch size was presented for 5–10 cycles of the grating drift, and standard errors were calculated for 3–10 repeats. Outside the grating patches, the screen was kept at the same mean luminance as the stimulus patches (10 cd/m²). Cells were classified as "simple" if the first harmonic (F1) of their response to sine-wave gratings was greater than the mean firing rate (F0) of the response (F1/F0 ratio > 1) or "complex" if F1/F0 ratio was <1 (Skottun et al. 1991). For simple cells, the spatial summation tests were based on F1 of the responses, while for complex cells, the F0 of the responses.

Data Analysis: The DOG Model

The spatial summation curves for all recorded cells were fitted using a DOG model (DeAngelis et al. 1994). In this model, the narrower positive Gaussian represents the excitatory center (the CRF), while the broader negative Gaussian represents the suppressive surround (the nCRF) (Fig. 1A). The 2 Gaussians are considered to be concentrically overlapping, and the summation profile can be represented as the difference of the 2 integrals of Gaussians (Fig. 1B). The model is defined by the following equation:

\[ R(x) = R_0 + K_e \int_{-\infty}^{\infty} e^{-2y^2/a^2} dy \cdot J - K_i \int_{-\infty}^{\infty} e^{-2y^2/b^2} dy. \]

where, \( R_0 \) is the spontaneous firing rate, and each integral represents the relative contribution from putative excitatory and inhibitory components, respectively. The excitatory Gaussian is described by \( K_e \) and \( a \), and a space constant, \( a \), and the inhibitory Gaussian by its gain, \( K_i \) and space constant, \( b \). All values were optimized to provide the least mean squared error for the data. All fitting procedures were implemented with the MATLAB optimization toolbox using the CONSTR and EMINCON nonlinear least-squares functions.

The goodness of each fit was accessed by calculating the mean fraction error (cf. Selenyi et al. 2001) defined as

\[ E = \frac{1}{N} \sum_{j=1}^{N} \left( \frac{\text{theory}_j - \text{data}_j}{\text{data}_j} \right)^2 \]

where \( \text{theory}_j \) and \( \text{data}_j \) are the expected response theory and experimental response data to the jth stimulus size, respectively. The fit error in the present study ranged from 0.003 to 0.25 with a mean error of 0.025 across the population.

Since the model allows the separation of the relative contributions of the center excitation and the surround suppression, it was possible to quantitatively estimate the effects of stimulus contrast on the excitatory CRF and on suppressive nCRF separately, by fitting the spatial summation curves with the model at different contrast levels. Figure 1C is an example showing the separation of center excitation and surround suppression from the fit. The square points are the original data obtained from the spatial summation test of a simple cell at high contrast (0.4). The cell increased response as the radius of the patch was increased from 0° to 1.5°. After the initial peak, the response of the cell decreased with increasing stimulus size, indicating a suppressive area (nCRF) outside the excitatory summation area (CRF). By fitting the spatial summation curve with the DOG model, the center and surround mechanisms could be separated as is indicated by the upper (dashed) and lower (dotted) curves, respectively. The bold curve shows the linear combination of these components providing the best fit for the data. As opposed to the nonempirical size (values of \( a \) and \( b \) from the DOG model), the empirical size of CRF was defined as the stimulus radius at which the curve reached its peak value (for the cells with surround suppression) or 95% of the peak value (for the cells without surround suppression). The empirical size of nCRF was defined as the stimulus radius at which the response fell to 5% of the difference between the peak response and the asymptotic response. An empirical suppression index (SI) measure was estimated from the fitted curve (Fig. 1C), defined as the amount of attenuation from the peak response.
to the asymptotic response as a percentage of the peak response amplitude (1 - asymptotic response/peak response). For comparison, a nonempirical SI deduced from the DOG model (SI') was also estimated, defined as the ratio of area under the inhibitory Gaussian to the area under the excitatory Gaussian (SI' = K_i/K_e). For the cell shown in Figure 1C, the empirical value of SI is 0.79, and the SI' is 0.86.

All population values given below are expressed as medians plus or minus standard error of the mean. All two-way comparisons were tested for significance with the Mann-Whitney U test.

Results

Selection of the High and Low Contrast Levels from the Contrast-Response Function

We first determined the contrast-response function for each individual neuron. Although the threshold location of the contrast-response curve varied from cell to cell, its form was a sigmoid curve for most V1 cells. Figure 2 shows a typical example. For this cell, the curve showed a response threshold at a contrast of 0.07 and saturated at 0.34, with a steeper slope located between the 2 points. To examine the effect of stimulus contrast on the spatial summation characteristics of V1 neurons, 2 representative contrast levels were selected. A low level was set at that contrast at which the response was just above threshold, that is, 10% of the response maximum (0.1 contrast for this cell, left arrow), and a high level was set at the contrast at which the response reached 90% of the response maximum (0.23 contrast for this cell, right arrow).

The 2 levels of stimulus contrast were determined individually for all cells, in accordance with the dynamic range of the contrast-response curves.

Categorization of Spatial Summation Characteristics Based on Contrast Dependence

Using circular patches of drifting sinusoidal gratings centered at the middle of the CRF, we determined the spatial summation characteristics of 115 cells at high and low stimulus contrast, respectively. The spatial frequency, temporal frequency, and orientation of the gratings were optimized in each case, and responses were measured as a function of the patch radius. All cells increased response as the size of the patch increased within the limit of CRF. After initial excitatory summation, most cells showed a decrease in response as the stimulus size extended into the suppressive surround (nCRF), whereas a minority of cells showed an asymptotic response without surround suppression. Of the 115 cells recorded, 61 cells showed surround suppression at both high and low contrast (type-I cells; Fig. 3A) and 22 cells exhibited surround suppression at high contrast but no suppression at low contrast (type-II cells, Fig. 3B). The remaining 32 cells did not show...
Contrast-Dependent Variations in the Spatial Extent of the CRF and nCRF

Spatial summation curves for the sample of cells under investigation were measured at high and low contrasts and were fitted with the difference of the integral of 2 Gaussians (see Materials and Methods and Fig. 1). From the fitted curves, the spatial extents of excitatory CRFs were estimated from the excitatory space constant of the Gaussians (parameter $a$ in Fig. 1A) and the spatial extent of suppressive nCRF, from the suppressive space constant of the Gaussians (parameter $b$ in Fig. 1A). Estimates of CRFs were obtained from all 115 cells and of nCRFs from 61 type-I cells. The 54 cells showing no surround suppression at low contrast (22 type-II cells) or at both low and high contrast (32 type-III cells) were not included in the population of cells for which suppressive space constants were estimated.

Taking the complex cell in Figure 4 as an example, the spatial summation curves were measured at a high (0.4, upper curve) and a low (0.1, lower curve) contrast, respectively (Fig. 4A). From the shift in peak position (indicated by arrows), it is possible to estimate the variation in the spatial extent of the excitatory CRF but it is difficult to estimate the variation in extent of the suppressive nCRF. While the spatial summation curves were approximated with the DOG model, the individual excitatory and suppressive components could be separated, respectively, at high and low contrast. In Figure 4B,C, the dashed and dotted curves represent integrals of excitatory and suppressive components and the solid curve the fit of the original data. From the fitting, the spatial extent of the CRF estimated from excitatory space constant was $2.8^\circ$ (radius) at high contrast, and it increased to $3.8^\circ$ at low contrast. By comparison, the spatial extent of the nCRF estimated from the suppressive space constant was $4.3^\circ$ and $4.7^\circ$ at the high and low contrast, respectively.

In order to confirm that the contrast dependence of receptive-field size estimated from the excitatory space constant, $a$, and inhibitory space constant, $b$, of the DOG model agreed with those from the empirical estimates of the peak and asymptote positions of the spatial summation curves, we compared the contrast effect with the 2 measures (Fig. 5). Changes in either space constant ($a$ or $b$) or the empirical size of CRF and nCRF are defined as the ratio of their estimates at low to high contrast. For the sample of cells, significant correlation was observed between $\text{CRF}_{\text{low}} / \text{CRF}_{\text{high}}$ and $\alpha_{\text{low}} / \alpha_{\text{high}}$ (Fig. 5A, $r^2 = 0.72$, $P < 0.001$) and between $\text{nCRF}_{\text{low}} / \text{nCRF}_{\text{high}}$ and $b_{\text{low}} / b_{\text{high}}$ (Fig. 5B, $r^2 = 0.79$, $P < 0.001$). Since the 2 measures correlated well with one another, we used the excitatory space constant, $a$, and the suppressive space constant, $b$, to quantify the contrast effect on the spatial extent of CRF and nCRF in the following sections.

In Figure 6, the contrast-dependent variations in the spatial extent of the excitatory CRF and suppressive nCRF are further compared by an index. Here, the ratio $\alpha_{\text{low}} / \alpha_{\text{high}}$ is used to describe the variation in the excitatory space constant and ratio $b_{\text{low}} / b_{\text{high}}$ for describing the variation in the suppressive space constant. A ratio greater than unity means that the space constant is greater at low contrast than at high contrast. The greater the ratio, the greater is the enlargement of the spatial extent. Figure 6A shows the histogram for the ratio $\alpha_{\text{low}} / \alpha_{\text{high}}$ of the entire population ($n = 115$), representing the contrast-dependent variation in the spatial extent of the excitatory CRF, while Figure 6B is the population histogram (type-I cells, $n = 61$) for ratio $b_{\text{low}} / b_{\text{high}}$, representing the variation in the extent of the suppressive nCRF. It is obvious that the low-contrast induced enlargement in the spatial extent is greater in the excitatory CRF than in suppressive nCRF. The arrows indicate...
the average for the population. The figure shows that, compared with the estimates at high contrast, the mean value for enlargement at low contrast was 1.93 times (±0.12) for the CRFs and 1.24 times (±0.14) for the nCRFs.

Moreover, we specially analyzed the contrast dependence of the excitatory space constant in 32 type-III cells in which no or negligible (SI < 0.05) surround suppression was observed at high contrast. Our results revealed that, even for this type of neurons, the excitatory space constant also exhibits remarkable contrast-dependent changes. Comparing a_{low} with a_{high} for each of the type-III cells (Fig. 7A), the great majority of data points were located above the unity ratio line, indicating that the CRFs are larger at low than at high contrast for most of the type-III cells. In addition, the distribution histogram of excitatory space constant ratio (a_{low}/a_{high}) for the type-III cells (Fig. 7B) also follows the same trend observed for the type-I and type-II populations. Comparing Figure 7B with Figure 6A, a strong resemblance between the population of cells with surround suppression and those without surround suppression becomes apparent. In both cases, the peak position and the mean ratio of the a_{low}/a_{high} (1.94 ± 0.15 in type-I and type-II cells and 1.92 ± 0.16 in type-III cells) were quite similar.

To quantify the relative change in the spatial extent of CRF and nCRF, we compared the excitatory space constant and the suppressive space constant using the ratio b/a at the 2 contrast levels for 61 type-I cells. The population results are given in Figure 8. The scatter plot shows that the overwhelming majority of data points are distributed above the unity ratio line, indicating that for most cells, the ratio is larger at high contrast than it is at low contrast. Specifically, the area ratio b/a ranged from 1.01 to 3.03 times (mean 1.21 ± 0.05) at low contrast and from 1.02 to 7.0 (mean 2.06 ± 0.17) at high contrast (P < 0.001).

**The Effect of Contrast on the Strength of Surround Suppression**

The analysis using the model also allows an estimate to be made of the contrast-dependent variation in the strength of surround suppression. The surround suppression was expressed by SI with 2 different measures, the empirical measure, SI, and the nonempirical measure, SI′ (see Materials and Methods). When the value of SI (or SI′) is 1.0, the cell’s response is completely counteracted by surround suppression. In Figure 9A, SI estimates of 61 type-I and 22 type-II cells are compared for low versus high stimulus contrast. The scatter plot of the estimates shows that most of the points are distributed above the unity ratio line, indicating that most cells exhibited higher surround suppression at high contrast than at low contrast. The mean value of SI at high contrast was 0.49 ± 0.02 (arrow at y-axis) and 0.33 ± 0.03 at low contrast (arrow at x-axis). The difference between high and low contrast was significant (P < 0.05). In Figure 9B, SI′ was calculated from 61 type-I cells after fitting the spatial summation curves with the DOG model function. In contrast to the results of Figure 9A most points are distributed below the unity ratio line. The average of SI′ values was 0.75 ± 0.02 at high contrast and 0.80 ± 0.02 at low contrast (P = 0.041).

The effect of contrast on surround suppression is further expressed by the index ΔSI and ΔSI′, which represents the difference in suppression strength between high and low contrast:

\[
\Delta SI = (SI_{low} - SI_{high}),
\]

\[
\Delta SI' = (SI'_{low} - SI'_{high}).
\]

Positive values indicate more surround suppression at low contrast and a negative value less surround suppression at low contrast. Figure 9C shows the distribution histogram of the values of ΔSI for each cell across 83 cells (61 type-I + 22 type-II). In 67.5% (56/83) of cells, surround suppression increased at high contrast (ΔSI ≤ -0.05), and in 16.9% (14/83) of cells, surround suppression decreased at high contrast (ΔSI ≥ 0.05); the rest (15.6%, 13 cells) showed no change in ΔSI (-0.05 < ΔSI < 0.05) at different contrasts. The mean value of ΔSI (arrow) for this population is -0.167. Figure 9D shows the distribution histogram of the values of ΔSI′, estimated for each of the 61 type-I cells. There are 50.8% (31/61) of cells exhibit stronger surround suppression at low contrast (ΔSI′ ≥ 0.05) and 24.6% (15/61) of cells show weaker surround suppression at low contrast (ΔSI′ ≤ -0.05), the rest (24.6%, 15/61) showed no change in ΔSI′ (-0.05 < ΔSI′ < 0.05) at different contrasts.

Since the CRF shrunk significantly as contrast increased and, concurrently, surround suppression was enhanced remarkably,
it is crucial to know whether there is any correlation between the 2 changes. In Figure 10A, we analyzed the relationship between the change in the empirical size of CRF (CRF\textsubscript{low}/CRF\textsubscript{high}) and the changes in surround suppression estimated from the fit of empirical data (\(D\text{SI}\)) in 83 cells (61 type-I and 22 type-II). We found no correlation (\(r^2 < 0.01\)) between them, regardless of whether the values of \(D\text{SI}\) were positive (\(S\text{I}\textsubscript{low} > S\text{I}\textsubscript{high}\)), negative (\(S\text{I}\textsubscript{low} < S\text{I}\textsubscript{high}\)), or zero (\(S\text{I}\textsubscript{low} = S\text{I}\textsubscript{high}\)), the values of CRF\textsubscript{low}/CRF\textsubscript{high} remained unchanged around a mean of about 2.0. Meanwhile, we also analyzed the relationship between the change in the nonempirical size of CRF (\(a\textsubscript{low}/a\textsubscript{high}\)) and the changes in surround suppression estimated from DOG model (\(D\text{SI}'\)) in 61 type-I cells (Fig. 10B). There is also no correlation (\(r^2 < 0.01\)) between them.

**Discussion**

**Variation in the Spatial Extent of the CRF and the nCRF at Different Contrast Levels**

By fitting the spatial summation curves with the DOG model at different contrasts, we were able to quantify the variation in the spatial extent of the CRF and the nCRF at different contrast levels from the estimate of the excitatory space constant and the suppressive space constant for each individual cell. Using the ratio \(a\textsubscript{low}/a\textsubscript{high}\) to describe the variation in the excitatory space constant at different contrasts and the ratio \(b\textsubscript{low}/b\textsubscript{high}\), variation in suppressive space constant, our results (Fig. 6) showed that compared with the estimates obtained at high contrast, the enlargement of the excitatory space constant at low contrast was on average 1.93 times (\(\pm 0.12\)) in (A) and 1.24 times (\(\pm 0.14\)) in (B).

Kapadia et al. (1999) reported a 4-fold increase in receptive-field length as contrast drops from high to low in the primary visual cortex of awake rhesus monkeys. For V1 of anesthetized macaque monkeys, other investigators (Sceniak et al. 1999; Cavanaugh et al. 2002a, 2002b; Shushruth et al. 2009) reported an average 1.7- to 2.5-fold increase, respectively, as contrast dropped from high to low. Studies on cat V1 (Sadakane et al. 2006; Tailby et al. 2007; Wang et al. 2009) have reported...
a smaller variation in CRF size: The increase in CRF size at low contrast was about 2.0 times that measured at high contrast. The variation in CRF size found in our study matches that previously reported in the cat.

Although both the excitatory CRF and the suppressive nCRF expanded at low contrast, the degree of expansion is more marked for the CRF than for the nCRF. This is also reflected in the variation in relative size between CRF and nCRF represented by the ratio $b/a$, at different contrasts (Fig. 8). The ratio increased from 1.21 (±0.05) at low contrast to 2.06 (±0.17) at high contrast, resulting from the more marked enlargement for CRF than for nCRF at low contrast. The variation in the ratio indicates that the size (radius) of the nCRF is about twice as large as the CRF at high contrast. In the V1 neurons of macaque monkey (Sceniak et al. 2001), the area ratio between the suppressive surround and the excitatory center is 2.2.

**Variation in Surround Suppression and Its Role in the Dynamic Property of Spatial Summation**

Our results for cat V1 neurons showed that when the strength of surround suppression (SI) is compared at different contrasts, there is a significant change in the mean value of SI. Figure 9A shows that the mean SI increased from $0.33 \pm 0.03$ to $0.49 \pm 0.02$ ($48.5\%$ increases) while the contrast varied from low to high. The contrast-dependent variation in surround suppression is more clearly illustrated by inspecting the distribution of $\Delta S$ over the population (Fig. 9B). The average value of $\Delta S$ for the entire population of cells was $-0.167$ (arrow). The negative values of $\Delta S$ for the majority of the cells indicate that suppression was larger at high contrast than at low contrast. For V1 neurons of the cat, Wang et al. (2009) also reported a significant increase in surround suppression strength as contrast increased. The SI that they estimated was, on average, $0.33 \pm 0.04$ at low contrast and $0.44 \pm 0.04$ at high contrast. The values they obtained are very close to ours.

Sceniak et al. (1999) described a variable effect of contrast on surround suppression in V1 of the macaque monkey. Their results showed that, in $70\%$ of cells, the ratio of inhibition to excitation, SI, decreased with increasing contrast and only in $30\%$ did surround suppression increase as contrast increased. The contrast-dependent change in surround suppression, $\Delta S$ (difference between $S_{\text{high}}$ and $S_{\text{low}}$), was broadly distributed with a mean of $0.06$. Their results suggest that surround suppression strength is unaffected by contrast. In contrast to these results, Schwabe et al. (2010) found that surround suppression was significantly stronger at high than at low contrast ($84\%$ of cells are above the line). They demonstrated that the discrepancy between their results and those of Sceniak et al. is due to different methods of quantifying suppression strength. They showed that by measuring SI from the DOG model's parameters, as Sceniak et al did, they obtained with their own data the same results as Sceniak et al. We have done the same comparison as Schwabe et al. (2010) with our data on cat (Fig. 9). By calculating surround suppression strength as Sceniak et al. (1999), in which suppression index SI was estimated as a ratio ($Kb/K_{\text{exc}}$) from DOG model (see methods) and comparing the SI for low versus high stimulus contrast, the average of SI we obtained was $0.75 \pm 0.02$ at high contrast.
idea that the contrast-dependent change in CRF size is independent of surround suppression. A reasonable explanation for these observations could be the strengthening of lateral coupling among excitatory corticocortical synapses. The cellular mechanisms for changing lateral coupling are thought to be depression of excitatory corticocortical synapses at high levels of neural activity caused by higher contrast (Thomson 1997; Thomson and Deuchars 1997; Sceniak et al. 1999). Another possibility is the inactivation of high-threshold local inhibitory interneurons at low contrast (Ichida et al. 2007). Further investigation is needed to clarify the neuronal bases of the contrast-dependent changes.

**Origins of the Contrast Effects and Functional Implications**

Investigators working on the cortex mostly assume that intracortical interactions are exclusively responsible for the contrast-dependent effect in V1. This may be largely true, but a significant contribution from subcortical inputs cannot be ruled out. The enlargement of the receptive field at low contrasts has also been reported for lateral geniculate nucleus (LGN) neurons and for retinal ganglion cells (RGC). Solomon et al. (2002) have described the contrast effect of relay cells in the LGN of the marmoset. They found that LGN cells also show contrast-dependent changes in spatial summation; on average, the size (radius) of the excitatory CRF at low contrast is 1.31 times that at high contrast. Nolt et al. (2004) reported that the apparent size of the receptive-field center decreases with an increase in contrast for both LGN cells and RGCs. The center size was, on average, 1.75 times greater at low contrast than at high contrast for the LGN cells and 1.99 times greater for RGCs. By presenting different background patterns (lines or dots) over the nCRF of LGN neurons of anesthetized cat, Li and He (1987) found that these patterns caused substantial changes in CRF size and in the strength of surround suppression. The degree of variation depended on the location of the background lines and distribution of the background dots.

The data referred to above suggest that contrast-dependent variations in CRF size and strength of surround suppression seen in cortical neurons could primarily derive from subcortical input streams. Meanwhile, substantial evidence has accumulated indicating that intracortical connections within V1 (DeAngelis et al. 1994; Kapadia et al. 1995, 1999; Levitt and Lund 1997; Walker et al. 1999, 2002; Anderson et al. 2001) or feedback projections from the extrastriate cortex (Bullier et al. 2001; Angelucci et al. 2002; Levitt and Lund 2002; Bair et al. 2003; Schwabe et al. 2006; Bardy et al. 2009) play important roles in nCRF modulation of cortical neurons. There is a significant difference, however, in the nonclassical surround modulation between V1 and the LGN. As has been shown in the striate cortex of cat and monkey, the suppressive effect of nCRF stimulation is strongest when the nCRF gratings have the same orientation, spatial frequency, and spatial phase as those for CRF stimulation (DeAngelis et al. 1994; Li CY and Li W 1994; Levitt and Lund 1997; Sengpiel et al. 1997; Akasaki et al. 2002; Cavanaugh et al. 2002a; Solomon et al. 2002; Xu et al. 2005; Bardy et al. 2006; Shen et al. 2007). These results suggest that in V1 and the LGN, there are different mechanisms involved in surround suppression. It is most likely that the basic properties of surround modulation that first originate from the retina and are manifest at different stages of visual processing in the early
visual pathway are further contextually modulated and enhanced in V1, depending on the balance between excitation and inhibition in a local network within the cortex (Chen et al. 2001; Cavanaugh et al. 2002a).

The adaptive changes in the spatial summation property and in surround suppression strength as a function of contrast allow the visual system to optimize performance under changing stimulus conditions. At high contrast, both shrinkage of the excitatory CRF and an increase in surround suppression may result in an improvement in spatial resolution of visual detection and the capacity to precisely localize features of an image. At low contrast, expansion of spatial summation and a decrease in surround suppression produce increased sensitivity and a better detection capability for weak signals by sacrificing spatial resolution and localization of features of an image.

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