Organization of Suppression in Receptive Fields of Neurons in Cat Visual Cortex

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SUMMARY AND CONCLUSIONS

1. The response to an optimally oriented stimulus of both simple and complex cells in the cat's striate visual cortex (area 17) can be suppressed by the superposition of an orthogonally oriented drifting grating. This effect is referred to as cross-orientation suppression. We have examined the spatial organization and tuning characteristics of this suppressive effect with the use of extracellular recording techniques.

2. For a total of 75 neurons, we have measured the size of each cell's excitatory receptive field by use of rectangular patches of drifting sinusoidal gratings presented at the optimal orientation and spatial frequency. The length and width of these grating patches are varied independently. Receptive-field length and width are determined from the dimensions of the smallest grating patch required to elicit a maximal response.

3. The extent of the area from which cross-orientation suppression originates has been measured in an analogous manner. Each neuron is excited by a patch of drifting grating the same size as the receptive field. The response to this stimulus is modulated by a superimposed patch of grating having an orthogonal orientation. After selecting the spatial frequency that produces maximal suppression, the response of each cell is examined as a function of the length and width of the orthogonal (suppressive) grating patch. Results from 29 cells show that the dimensions of the orthogonal grating patch required to elicit maximal suppression are similar to, or smaller than, the dimensions of the excitatory receptive field. Thus cross-orientation suppression originates from within the receptive field.

4. For some cells the spatial frequency tuning of the suppressive effect is much broader than the spatial frequency tuning for excitation. In these cases it is possible to find a spatial frequency that produces suppression but not excitation. With the use of a suppressive stimulus having this spatial frequency, we examined the strength of suppression as a function of orientation for 11 cells. These tests show that suppression occurs at all orientations, including the preferred orientation for excitation. In some cases, suppression is somewhat stronger at the preferred orientation for excitation than at any other orientation.

5. For 12 cells we varied the relative spatial phase between the optimally oriented and orthogonal gratings. In all cases the magnitude of suppression is largely independent of the relative spatial phase.

6. For three binocular cells we examined whether the suppressive effect of a grating oriented orthogonal to the optimum could be mediated dichoptically. For this purpose an optimally oriented grating stimulus is presented to one eye, while an orthogonal grating is presented to the other eye. In each case, the orthogonal grating fails to produce any suppression of the response to the optimally oriented grating. However, these same neurons exhibit strong suppression when tested monoptically through either eye. This suggests that cross-orientation suppression is generated in the visual cortex before combination of signals from the two eyes.

7. Overall, these findings suggest that suppression plays a very limited role in enhancing the orientation selectivity of cortical neurons. Instead, suppression may serve to normalize the response of cells with respect to local image contrast.

INTRODUCTION

Neurons in the visual cortex respond to stimuli with specific and limited ranges of characteristics. This selectivity is generally thought to be based on the organization of receptive-field components, as suggested in the original detailed exploration of the visual cortex (Hubel and Wiesel 1959, 1962). In addition, it has been suggested that intracortical inhibitory processes are also involved in the generation of orientation selectivity (see Ferster and Koch 1987; Martin 1988 for review; Bishop et al. 1973; Blakemore and Tobin 1972; Bonds 1989; Creutzfeldt et al. 1974b; Morrone et al. 1982; Nelson and Frost 1978; Sillito 1975, 1977b, 1979; Tsumoto et al. 1979) and spatial frequency selectivity (Bauman and Bonds 1991; DeValois and Tootell 1983; but see Ramoa et al. 1986).

The organization of inhibitory processes in the visual cortex has been studied by use of several types of visual stimulation, as well as by neurochemical manipulation. Hubel and Wiesel (1965) noted that the response of some cells can be suppressed by presentation of a long bar stimulus that extends beyond the excitatory discharge region of the receptive field. These cells were initially classified as hypercomplex (Hubel and Wiesel 1965), and they are now referred to as end stopped, end inhibited, or length tuned (e.g., Drucker 1972; Gilbert 1977; Murphy and Sillito 1987). Similarly, it has been shown that increasing either the length or width of a patch of sinusoidal grating beyond an optimum can reduce the response of many cortical cells in the cat or monkey (Born and Tootell 1991; DeAngelis et al. 1990; DeValois et al. 1985). These effects are usually called end inhibition (for the length dimension) and side inhibition (for the width dimension). A common feature of these length and width tuning effects is that the inhibition is only effective at orientations close to the cell's preferred excitatory orientation (Born and Tootell 1991; DeAngelis et al. 1990; Hubel and Wiesel 1965; Orban et al. 1979). In fact, the end- or side-inhibitory regions typically become ineffective when stimulated with a pattern oriented orthogonal to the preferred orientation for excitation.

In marked contrast, the response of some cells to a bar stimulus of optimal orientation can be suppressed by the superposition of a second bar that is oriented orthogonally...
(Bishop et al. 1973). In fact, it has been shown that the responses of most cortical cells can be suppressed by the superposition of a sinusoidal grating presented orthogonal to the cells’ preferred orientation (Bonds 1989; Morrone et al. 1982; Petrov et al. 1980). This effect, known as cross-orientation inhibition or (cross-orientation suppression)\(^1\), has been proposed as a mechanism for the generation of orientation selectivity (Morrone et al. 1982; see Ferster and Koch 1987; Martin 1988 for an overview).

When assessing the role of suppression in cortical function, one important issue involves the spatial localization of suppressive influences. Knowledge of the spatial regions from which suppression originates places important constraints on both the functional role of suppression and the neural mechanisms that underlie it. It is fairly clear that clear that end and side inhibition arise from regions located outside of the classical receptive field, although these regions may overlap the excitatory receptive field to some extent (Born and Tootell 1991; Orban et al. 1979; Sillito 1977a). In contrast, little attention has been paid to the spatial localization of cross-orientation suppression. Previous studies (Bonds 1989; Morrone et al. 1982) have used large-field patterns to investigate the suppressive interactions between stimuli of different orientations. Hence there is a lack of information concerning the spatial extent over which cross-orientation suppression is generated. The main purpose of the study we report here is to define the regions of the visual field, relative to the classical (excitatory) receptive field, from which cross-orientation suppression originates. We use sinusoidal grating patches of variable dimension to test the hypothesis that this form of suppression arises from within the excitatory receptive field. The limits of the excitatory receptive field are determined quantitatively by finding the smallest patch of sinusoidal grating that produces a maximal response from the neuron. We have also measured the spatial frequency and orientation tuning of suppression. For several cells, we have obtained complete orientation tuning measurements of the suppressive effect by finding a spatial frequency that elicited suppression without producing excitation.

Consistent with the hypothesis stated above, our results show that cross-orientation suppression is generated entirely from within the excitatory receptive field of most cortical cells. The region producing suppression is, in some cases, considerably smaller than the excitatory receptive field. This finding has important implications for the neuronal mechanism that underlies this form of suppression. Our data also suggest that suppression plays a minimal role in generating or refining the orientation selectivity of cortical cells. By using a spatial frequency that produces suppression but not excitation, we find that the suppressive mechanism is largely independent of orientation (see also Bonds 1989). When it is dependent on orientation, the suppression is somewhat stronger at the preferred excitatory orientation than at orthogonal orientations. Suppression is unlikely, therefore, to be a major factor in generating or refining the orientation tuning properties of cortical cells. Instead, suppression may serve to normalize the responses of cortical cells with respect to local image contrast (Bonds 1989, 1991; Heeger 1991; Robson 1988).

**METHODS**

**Surgical procedure**

All experiments were performed on normal adult cats, weighing between 2.2 and 2.5 kg. After initial preanesthetic doses of atropamine and atropine (subcutaneous, 1.0 and 0.2 mg kg\(^{-1}\), respectively), each cat is anesthetized with halothane (2.5--3% in O\(_2\)) for the remainder of the surgical preparation. A rectal temperature probe is inserted, electrocardiographic (ECG) electrodes are secured, and a femoral vein is catheterized. Subsequently, a tracheostomy is performed, and a tracheal tube inserted. The animal is then secured to a stereotaxic apparatus with the use of ear bars. Electroencephalographic (EEG) screw electrodes are placed over the frontal sinus, and a section of skull and dura (~5 mm diam centered on Horsley-Clark coordinates P4 L2) are removed to allow insertion of a pair of tungsten-in-glass electrodes (Levick 1972). After lowering the electrodes to the cortical surface, agar is used to seal the hole, and melted wax is applied over the agar to create a sealed chamber. The cat is then paralyzed with gallamine triethiodide (Flaxedil), which is continuously infused at a rate of 10 mg kg\(^{-1}\) h\(^{-1}\), along with 1 mg kg\(^{-1}\) h\(^{-1}\) of sodium thiamylal (Sontal). Artificial ventilation is carried out with a gas mixture of 70% N\(_2\)O, 29% O\(_2\), and 1% CO\(_2\). The respirator is set at 25 strokes/min, and stroke volume is adjusted to maintain a constant end-tidal CO\(_2\) of ~4.5%. Temperature, heart rate, ECG, and intratracheal pressure are monitored continuously. Pupils are dilated with atropine (1%), nictitating membranes are retracted with phentylephrine hydrochloride (Neo-synephrine) (10%), and corrective contact lenses with 4-mm artificial pupils are positioned on each cornea. For additional details, see Ohzawa and Freeman (1986a) and Freeman and Ohzawa (1988).

Experiments typically last for 4 days. At the end of an experiment, the animal is given an overdose of pentobarbital sodium (Nembutal). After perfusion and fixation (with a buffered 0.9% saline solution followed by 10% Formalin), the cortex is frozen and sectioned into 40-μm-thick slices. Tissue is stained with thionin, electrode tracks are reconstructed, and laminae identified. Histological analysis confirmed that all cells were recorded from area 17, and that cells were sampled from all laminae.

**Visual stimulation**

Each cortical neuron is initially located with the use of a bar of light that is optically back projected onto a tangent screen in front of the cat. Subsequently, all visual stimulation is provided by computer-generated patterns displayed on either or both of two video monitors, one for each eye, which the cat views through half reflecting mirrors. The video monitors are refreshed at 76 Hz (non-interlaced) and display 1,024 pixels horizontally on a raster of 804 lines. Each monitor subtends an area of 28 × 22° at the cat's eye and is positioned so that the cell's receptive field falls approximately in the center of the screen. The effective lumiance of the monitor screen is 12 cd m\(^{-2}\) as viewed by the cat at a distance of 57 cm. For initial qualitative analysis of each cell, we use round gratings whose parameters are manually controlled via a joystick. During quantitative trials the patterns used for making all measurements are rectangular patches of drifting sinusoidal gratings (2 Hz temporal frequency) whose size, spatial frequency, orientation, and contrast can be automatically controlled. For experiments requiring two superimposed gratings, the component gratings are displayed on alternate scan lines (line interleaving) to

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\(^1\) On the basis of extracellular recordings, it is not possible to distinguish true synaptic inhibition from a withdrawal of excitation. For this reason, we prefer to call the effects described in this paper suppression, rather than inhibition. However, when it is not necessary to distinguish explicitly between inhibition and suppression, we shall use the terms interchangeably.
avoid any interaction of the two components resulting from the bandwidth limitation of the video amplifiers in the displays (Pelli and Zhang 1991). Frame refresh on the two displays is synchronized.

Recoding and data analysis

The action potentials of cortical neurons are detected by tungsten-in-glass microelectrodes, amplified, and recorded as binary events with 1-ms resolution. A computer controls the presentation of stimulus sequences, while simultaneously displaying peristimulus time histograms (PSTHs) of the cells' responses (see Fig. 1). Stimuli are presented for 4 s each in blocks of randomly interleaved trials. Each stimulus is typically presented 5–10 times, and successive stimuli are separated by a period of 2–3 s during which the animal views blank screens of the same mean luminance as the gratings. After presentation of the complete set of stimuli, the magnitude of the accumulated response to each different stimulus is computed by Fourier analysis. Response amplitude is taken as the mean firing rate or as the mean amplitude of the first harmonic of the response, depending on which is greater (see Fig. 1). We classify cells as simple if the first harmonic of the firing rate is larger than the mean rate for spatial frequencies higher than the optimum (De Valois et al. 1982; Skottun and Freeman 1984; Skottun et al. 1991). The remainder of the cells are classified as complex.

Preliminary procedure

Before starting detailed quantitative measurements on a cell, preliminary observations are made to determine approximately the cell's preferred orientation and spatial frequency, as well as the size and position of its receptive field for each eye. This is done by manually adjusting the parameters of a patch of grating displayed on the video screen, while subjectively assessing the strength of the cell's response. After estimating the minimum size of grating patch necessary to give a maximal response (the "optimal" patch size), the center point of the receptive field is located by carefully positioning a somewhat smaller patch of grating to give the largest response. All stimuli used subsequently are centered on this point. For many cells, we recenter the stimulus between subsequent runs as a precaution. We generally find these repeat estimates of the receptive-field center location to be highly reliable and repeatable (to within a few 10ths of a degree).

RESULTS

This report is based on measurements obtained from 75 neurons in the striate cortex of 4 cats. A complete set of measurements for each cell consists of eight to nine different runs and requires a total of 3–4 h. We were able to complete this experimental protocol for 29 cells, of which 14 were simple and 15 were complex types. For the remaining cells, we usually completed most of the necessary measurements. All cells we recorded in these experiments had receptive fields located within 5–10° of the area centralis, as determined by the location of the receptive fields with respect to the positions of the optic disks. In addition, we include results from previous measurements on 32 cells (Freeman et al. 1987).

We first measure monoptically, for each eye, the orientation tuning and the spatial frequency tuning (at the previously estimated optimal spatial frequency) and the spatial frequency tuning (at the newly determined optimal orientation) of each cell. These measurements are made with the use of a grating patch of optimal size, as estimated in the preliminary procedure. Subsequent

![FIG. 1. Measurement of receptive-field length is illustrated for a simple cell (Cell 084-19). A: peristimulus time histograms (PSTHs) are shown as obtained in response to grating patches of various lengths. The stimulus configuration is shown schematically on the left for grating patches of 2 different lengths, one shorter and one longer than the excitatory receptive field (shown as the dashed rectangle). The width of the grating patch was fixed at 6°, the orientation was 5° from horizontal, and the spatial frequency was 0.23 cycles/deg. Each different stimulus was presented 5 times, and the responses were accumulated. Stimulus length (in degrees) is shown immediately to the left of each corresponding PSTH. The PSTH marked as Null shows the cell's spontaneous discharge during interleaved control conditions in which no stimulus was presented. The scale bar at the bottom right shows a response rate of 160 spikes/s, to be used as a reference. Each PSTH shown spans 2 s. B: response level is plotted as a function of stimulus length for the same simple cell described in A. Each PSTH was Fourier analyzed to obtain the response amplitude at the drift frequency of the stimulus (1st harmonic), as well as to obtain the average (DC) response rate. The 1st harmonic values are plotted as filled triangles, whereas the DC values are plotted as filled circles.](http://jn.physiology.org/doi/10.2203/3.2 on April 14, 2017)
measurements are usually restricted to whichever eye produces the largest responses.

Excitatory summation areas

As a measure of the size of a cell's receptive field, we have adopted the extent of its excitatory summation area, that is the area over which increasing the size of a grating stimulus increases the cell's response. We measure the effect of increasing first the length (parallel to the preferred orientation) and then the width (orthogonal to the preferred orientation) of a rectangular patch of grating of optimal spatial frequency and orientation. To illustrate the data collection and analysis procedures, representative measurements of receptive-field length for a simple cell are shown in Fig. 1. In this example the width of the grating patch is fixed at the optimal value estimated in the preliminary procedure, and the length of the grating patch is varied, as shown schematically to the left of Fig. 1A, where the dashed rectangle represents the cell's excitatory receptive field. Fig. 1A shows PSTHs of the responses of this simple cell to grating patches that vary in length from 0.5 to 20°. Note that the responses are periodic at the temporal drift frequency of the grating (2 Hz), and that the response amplitude increases monotonically with the length of the grating stimulus up to ~15°. This can be seen more clearly after harmonic analysis of the PSTH data, as shown in B. Here, response rate is plotted as a function of stimulus length. Filled circles show the average firing rate (DC response component) for each length tested, and filled triangles denote the amplitude of the response at the drift frequency of the grating (1st harmonic).

The procedure for measuring receptive-field width is completely analogous to that shown in Fig. 1 for length. The only difference is that the length of the grating patch is now fixed at the optimal measured value, and the width (or number of cycles) of the grating is varied.

To illustrate the results of both types of measurement, Fig. 2 shows the effect of varying the length and width of the excitatory grating stimulus on the responses of three cells: a simple cell (A and B), a complex cell (C and D), and a simple cell (E and F), which exhibited both end and side

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**FIG. 2.** Response is shown as a function of the length and width of a sinusoidal grating stimulus. Length, L, is defined as the dimension parallel to the bars of the grating, whereas width, W, is the dimension orthogonal to the bars (see inset to A). Filled triangles represent the mean amplitude of the 1st harmonic of the firing rate, and filled circles represent the mean firing rate. A: response of a simple cell (Cell 671-09) to rectangular grating patches of variable length, L. The width of the patch is fixed at the optimal value, W0, determined by preliminary observations. The optimal grating for this cell was oriented 25° from horizontal and had a spatial frequency of 0.68 cycles/deg. Stimulus contrast was 15%, and all gratings were drifted at 2 Hz in the cell's preferred direction. The solid curve is the integral of the Gaussian that best fits the data points (see Eq. 3). The estimated receptive-field length, obtained from the best-fitting curve, is 3.7°. B: response is shown as a function of grating width for the same simple cell as depicted in A. Everything is analogous to that described above except that the solid curve is the best-fitting function described by Eq. 2. The estimated receptive-field width is 2.5°. C and D: length-response and width-response curves are presented for a complex cell (Cell 695-08). Solid curves show the bestfitting integral of a Gaussian to each data set (Eqs. 1 and 3). Everything else is analogous to A and B. The cell preferred a grating oriented 20° from vertical with a spatial frequency of 0.8 cycles/deg. Stimulus contrast was 8%. The estimated receptive-field length and width are 3.1 and 4.1°, respectively. E and F: length- and width-response curves are shown for a simple cell (Cell 695-21) that exhibits both end inhibition (E) and side inhibition (F). The solid curve in E is given by Eq. 4, whereas the curve in F is given by a similar modification to Eq. 2. The grating stimulus was oriented 30° from vertical with a spatial frequency of 0.2 cycles/deg. Contrast was 20%. The receptive-field length and width, estimated from the best-fitting curves, are 3.3 and 5.1°, respectively.
inhibition. For the simple cells, only the amplitude of the first harmonic of the response is plotted. For the complex cell, only the average firing rate is shown. In the case of the first two cells (A–D), response increases with the length and width of the grating stimulus up to some plateau level. For the third cell (E and F), increasing either the length or width of the stimulated area beyond an optimum value results in a clear reduction of the response magnitude. We generally find that the strength of end and side inhibition tend to be correlated for most cells (DeAngelis et al. 1990, 1991b).

To obtain quantitative estimates of the length and width of a cell’s excitatory receptive field (excitatory summation area), we have used standard procedures for fitting curves to the experimental data. Curve fitting was performed with the use of the Nelder and Mead simplex algorithm (Press et al. 1988) with a simple least-squared-error criterion. We have fitted all experimental length data and the width data for complex cells with the integral of a Gaussian function. To fit the width data from simple cells, we have assumed that the cell’s basic sensitivity profile is a Gabor function (the product of a Gaussian and a sinusoid), whose periodic component has a spatial frequency equal to the optimal spatial frequency determined experimentally (e.g., Field and Tolhurst 1986). In all cases we have taken the size of the underlying Gaussian envelope as a measure of the relevant receptive-field dimension. This dimension is referred to as a length if it is parallel to the optimal excitatory orientation and a width if it is orthogonal to this orientation.

Specifically, we assume that the response of a complex cell, \( R_c(w) \), and of a simple cell, \( R_s(w) \), are related to the width, \( w \), of the stimulus patch by

\[
R_c(w) = k \int_{-w/2}^{w/2} e^{-\left(\frac{2 \pi x}{w_0}\right)^2} dx
\]

and

\[
R_s(w) = k \int_{-w/2}^{w/2} \cos^2 \left(2 \pi f_{opt} x + \Phi\right) e^{-\left(\frac{2 \pi x}{w_0}\right)^2} dx
\]

where \( k \), \( w_0 \) and \( \Phi \) are adjusted to give the best fit of \( R(w) \) to the experimental width data (see solid curves in Fig. 2B and D). Once these parameters are adjusted independently, \( w_0 \) is taken to be the best estimate of the width of the excitatory receptive field. The form of Eq. 2 reflects the fact that the spatial frequency at which measurements are made is always the same as the optimal value, \( f_{opt} \), previously determined from the spatial frequency tuning function. Measurements from both simple and complex cells relating response to stimulus length were fitted by

\[
R(l) = k \int_{-l/2}^{l/2} e^{-\left(\frac{2 \pi y}{l_0}\right)^2} dy
\]

which is exactly analogous to Eq. 1 with length, \( l \), substituted for width, \( w \). In this case, \( k \) and \( l_0 \) are adjusted to give the best fit, and \( l_0 \) is our estimate of the receptive-field length (see Fig. 2A and C).

For cells whose responses show clear indications of either side or end inhibition, it is inappropriate to use the simple functions given above. Instead, we use a modified formulation that adds pairs of inhibitory zones at the sides or ends of the excitatory region. These inhibitory zones are themselves assumed to have Gaussian weighting functions. For an end-stopped cell, the response as a function of length, \( R_e(l) \), is assumed to be

\[
R_e(l) = k \int_{-l/2}^{l/2} e^{-\left(\frac{2 \pi y}{l_0}\right)^2} dy - k_i \int_{-l/2}^{l/2} e^{-\left(\frac{2 \pi (y-l_i)}{l_i}\right)^2} dy
\]

where \( k_i \), \( s_i \), and \( l_i \) are free parameters related to the end-inhibition zones (their strength, size, and offset from the center of the receptive field). These parameters are also optimized during the fitting procedure (see Fig. 2E). Equivalent modifications to Eqs. 1 and 2 allow for side inhibition (see Fig. 2F). This formulation assumes that the end or side inhibition is a subtractive phenomenon rather than being some type of divisive (i.e., shunting) inhibition, but the exact form of the expression is not important, and an acceptable fit to the data was obtained in almost all cases.

Length and width measurements were usually made with the use of a stimulus contrast of 10–20%, although lower and higher contrasts were used if the cells were particularly responsive or unresponsive. For a few cells we were able to make length and width measurements at more than one contrast, and, in these cases, the choice of contrast had no substantial effect on the measured receptive-field size, although some dependence of receptive-field length on contrast has been reported (Jagadeesh and Ferster 1990). For our sample of cells, the length and width of the excitatory summation areas ranges from 1.3 to 10 and 0.8 to 9°, respectively (see Fig. 5). Some summation areas are relatively long and narrow, some short and wide, and others roughly square (see Fig. 6).

Spatial frequency tuning of orthogonal suppression

Having measured the length and width of the excitatory summation area of a cell, this area is then filled with a rectangular patch of grating of optimal spatial frequency and orientation. This provides a baseline response whose reduction can be used as a measure of the suppressive effect of a superimposed grating with orthogonal orientation.

The superimposed excitatory and suppressive grating patches have identical spatial limits (see the schematic depiction of the stimulus in Fig. 3B), and their contrasts are usually 20 and 40%, respectively. These contrast values are chosen so that the response to the optimally oriented stimulus is reduced by at least 50%. This is done to produce robust suppressive effects, which can be distinguished easily from random fluctuations in a cell’s response. Note, however, that the contrast of the suppressive grating is kept low enough so that the cell’s response is not completely eliminated. It is often necessary to adjust these contrasts to compensate for variations in the relative strength of the excitatory and suppressive effects of different cells. As previously noted by Bonds (1989), use of different contrasts or contrast ratios does not have a noticeable effect on the characteristics of the suppression, but it can change the strength of the effect.

Figure 3 shows how the suppressive effect of a superimposed orthogonal drifting grating depends on spatial frequency. The spatial frequency tuning function of suppression (B, D, and F) can be compared directly with the normal excitatory tuning function (A, C, and E) for each of the
Spatial frequency tuning of excitation and orthogonal suppression is shown for 3 cells (A and B, simple; C and D, complex; E and F, simple). A: a standard spatial frequency tuning curve is presented for a simple cell (Cell 084-35). Filled triangles show the mean value of the 1st harmonic of the response to each stimulus. Gratings were oriented 35° from vertical, drifted at 2 Hz, and had a contrast of 50%. B: spatial frequency tuning of orthogonal suppression is illustrated for the simple cell shown in A. The optimally oriented grating had a contrast of 10% and a spatial frequency of 0.45 cycles/deg, whereas the superimposed orthogonal grating (see inset) had a contrast of 25% and variable spatial frequency. Both patches of grating were 4" long and 4" wide (as determined from length- and width-response curves), so that they just filled the excitatory receptive field. Filled triangles show the 1st harmonic of the response for different spatial frequencies of the orthogonal (suppressive) grating. Control conditions, in which only the optimally oriented (excitatory) patch was presented, were interleaved with the test stimuli. Dashed line indicates the response level during these control conditions. C and D: spatial frequency tuning of excitation and orthogonal suppression for a complex cell (Cell 085-13). In C the grating was oriented 10° from horizontal and had a contrast of 20%. In D the excitatory (optimally oriented) grating had a spatial frequency of 1.25 cycles/deg and a contrast of 15%, whereas the suppressive (orthogonal) grating had variable spatial frequency and a contrast of 25%. Both patches of grating measured 10" in width by 10" in length. E and F: spatial frequency tuning of excitation and orthogonal suppression is depicted for the simple cell shown in Fig. 2, E and F (Cell 695-21). In E the grating had 20% contrast and was oriented 30° from vertical. In F the optimally oriented grating had 20% contrast and a spatial frequency of 0.2 cycles/deg, whereas the orthogonally oriented grating had 40% contrast and variable spatial frequency. Both grating patches measured 7" in width by 5" in length.

For the simple cell shown in A and B, the optimal spatial frequency for excitation roughly coincides with that for suppression, and the tuning curve for suppression is just slightly broader than that for excitation. For the complex cell shown in C and D, the situation is quite different. In this case, suppression has a much broader spatial frequency tuning curve than excitation (see also Bonds 1989; Morrone et al. 1982), so that spatial frequencies that are far below the excitatory bandpass still elicit strong suppression. This type of pattern, in which suppression extends to lower frequencies than excitation, seems to be the most common among the cells that we have recorded. We have also observed cells for which the orthogonal suppression is effective at spatial frequencies higher than those that excite the cell. One such cell is shown in Fig. 3, E and F. For this cell, the optimal spatial frequency for suppression is clearly higher than that for excitation, and it is possible to elicit suppression at spatial frequencies (>0.5 cycle/deg) that will not excite the cell.

We find that the response of all cortical cells can be substantially reduced by an orthogonal grating restricted to the region of the excitatory receptive field, so long as the spatial frequency of the orthogonal grating is appropriate and its contrast sufficiently large. Unlike Morrone et al. (1982), we find no discernible difference between simple and complex cells in either the strength or the frequency of occurrence of suppression. In preliminary experiments (Freeman et al. 1987) we mainly looked at the suppressive effect of an orthogonal grating having the same contrast and spatial frequency as the excitatory grating, and we did find cells showing only minimal suppression. Such cells, in fact, can show much greater suppression when stimulus parameters are specifically optimized for the suppressive effect. This was also observed by Bonds (1989).

Summation area for orthogonal suppression

Having determined the spatial frequency tuning of the suppressive effect produced by an orthogonally oriented grating, we then examine the extent of the summation area.
for suppression. This is done by varying one dimension of the suppressive grating patch while keeping the other dimension fixed. As mentioned earlier, the contrasts of the excitatory and suppressive components of the stimulus are chosen to produce a clear reduction of the response without completely silencing the neuron.

Figure 4 shows how increasing either the width or the length of a superimposed orthogonal grating reduces the response of the cells whose excitatory behavior was shown in Fig. 2 (A and B, simple cell; C and D, complex cell; E and F, end- and side-inhibited simple cell). In each case, increasing the size of the suppressive grating produces a monotonic decline in the cell's response until some plateau level is reached. This plateau response level is still clearly larger than the cells' spontaneous discharge rate (dashed lines in Fig. 4), indicating that the cells' firing has not been completely suppressed by the superimposed orthogonal grating. Note that the response of the cells in Fig. 4 declines rapidly as the length or width of the suppressive grating is increased from zero. In each case there is already a large reduction of the firing rate when the suppressive grating patch has a length or width of 1°. This observation holds for virtually all cells in our sample and suggests that the summation area for orthogonal suppression has its peak sensitivity very near to the center of the excitatory receptive field.

For only one cell (a strongly side-stopped simple cell, not shown) did we see any disinhibition as the width of the orthogonal suppressive grating was increased beyond an optimum. In this case the cell's response decreased as the width of the suppressive grating increased up to a certain point, after which the response level rose as width was further increased. No similar effect was seen for any other cell.

To estimate the length and width of the suppressive summation areas, we again fit the experimental data with curves described by the integral of a Gaussian (see solid curves in Fig. 4). In this case, however, we use the same functional form (with different coefficients) for the length and width of the suppressive summation areas of both simple and complex cells. It is evident from Fig. 4 that this formulation provides an acceptable fit to the experimental results. The lengths and widths of the suppressive summation areas of our sample of cells ranges from 1 to 8 and from 0.4 to 6°, respectively. These ranges are only slightly smaller than those found for the excitatory summation areas.

![Figure 4](http://jn.physiology.org/)

**FIG. 4.** Length and width summation of orthogonal suppression is shown for the same 3 cells illustrated in Fig. 2. Each panel of this figure can be compared directly with its counterpart in Fig. 2. A and B: length and width tuning of suppression are given for the simple cell shown in Fig. 2, A and B (Cell 671-09). The size of the excitatory (optimally oriented) grating patch is fixed at the optimal length, L0, and width, W0. In A the orthogonal (suppressive) grating patch has optimal width, W0, and variable length, L. In B the orthogonal patch has optimal length, L0, and variable width, W. In both cases, the optimally oriented patch has a spatial frequency of 0.68 cycles/deg and a contrast of 20%, whereas the orthogonal patch has a spatial frequency of 0.4 cycles/deg and a contrast of 40%. Solid curves show the negative integral of a Gaussian that best fits the data. Dashed line shows the cell's spontaneous activity, as measured during interleaved control conditions in which there was no stimulus present on the display. The estimated length and width of the suppressive summation area are 2.7 and 0.95°, respectively. C and D: length and width tuning of suppression are presented for the complex cell of Fig. 2, C and D (Cell 695-08). The format is identical to that described above in A and B. For this cell, the optimally oriented patch has a spatial frequency of 0.8 cycles/deg and a contrast of 10%, whereas the orthogonal patch has a spatial frequency of 0.9 cycles/deg and a contrast of 40%. The length and width of the suppression area are 1.4 and 1.1°, respectively. E and F; for this simple cell (Cell 695-21) the optimally oriented patch has a spatial frequency of 0.7 cycles/deg and a contrast of 20%, whereas the orthogonal patch has a spatial frequency of 0.7 cycles/deg and a contrast of 40%. The suppressive length and width are 3.3 and 2.6°, respectively.
**Relationship between suppressive and excitatory summation areas**

It is clear from a comparison of the ranges of dimensions of suppressive and excitatory summation areas that, at least for some cells, a substantial part of the orthogonal suppression must come from an area within the excitatory receptive field. However, to look more precisely at the relationship between excitatory and suppressive areas, it is necessary to examine the lengths and widths of these areas for individual cells.

Figure 5A shows the length of the suppressive summation area of each cell plotted against the length of its excitatory summation area. Similarly, Fig. 5B shows a scatter plot of the widths of the suppressive and excitatory summation areas. There is considerable variability in the relationship between the lengths and widths of suppressive and excitatory areas for the cells we have examined. However, there is a clear trend for the dimensions of the suppressive area of a cell to be about the same as, or smaller than, those of the excitatory area (points in the scatter plots mostly lie near or below the diagonal). This is most clearly seen in Fig. 5A, which shows the lengths of suppressive and excitatory areas (length is the dimension parallel to the bars of an optimally oriented excitatory stimulus). For only one cell (an end-stopped simple cell) is the suppressive area substantially longer than the excitatory receptive field. On the other hand, Fig. 5B shows that 40% of the cells (10/25) have suppressive areas that are somewhat wider than the excitatory receptive field. It should be noted that one-half of these (including the most extreme cases) are side-inhibited cells (open symbols). For end- and side-inhibited cells, any overlap between the excitatory summation area and the inhibitory zones (Born and Tootell 1991; Orban et al. 1979; Sillito 1977a) might make the excitatory receptive field appear to be smaller than its actual size.

Besides those cells for which the suppressive and excitatory summation areas have similar dimensions, there are many cells for which suppression originates from a region much smaller than the excitatory receptive field (points lying well below the diagonal in Fig. 5A and B). It is important to note that these cells are not due to a total elimination (i.e., complete suppression) of the cells’ responses, which could make the suppressive summation areas appear smaller than their actual size. In all cases, care was taken to ensure that the largest orthogonal grating did not completely suppress the responses to the excitatory grating. This is evident in the examples of Fig. 4, where the smallest responses (filled symbols) are still clearly larger than the cells’ spontaneous discharge (dashed lines).

Figure 5 shows the length and width dimensions separately, but it is also of interest to see how the shapes of the suppressive and excitatory areas are related. Figure 6A shows the lengths and widths of both the suppressive and excitatory regions of all cells for which we obtained a complete set of measurements. Filled symbols are plotted at coordinates corresponding to the length and width of each cell’s excitatory summation area. Open symbols are plotted at coordinates representing the length and width of each cell’s suppressive summation area. Pairs of points relating the suppressive and excitatory regions of individual cells are joined by a line, which is dashed if the cell showed clear end or side inhibition. Notice that, for most cells, the lines from the filled symbols to the open symbols point downward and to the left, indicating that the summation areas for suppression are smaller than those for excitation along both dimensions (length and width). For only one cell does the line from the filled to the open symbol point upward and to the right; this cell exhibited both end and side inhibition.
l length ratio much larger than 1.0. Also, most of the cells with width ratios >1.0 (5/9) exhibit side inhibition, end inhibition, or both. Although some cells have small suppressive areas of the same general shape as the excitatory receptive field (points lying near the diagonal in Fig. 6B), other cells have suppressive and excitatory areas that differ in size mainly along one of the two dimensions.

**Orientation tuning of suppression**

From the results described above, it is clear that suppression from orthogonal gratings originates from approximately the same region of visual space as excitation. We now consider the orientation selectivity of this central suppressive mechanism. The major difficulty associated with this question is that a superimposed stimulus, which causes suppression when oriented orthogonal to a cell's preferred orientation, may be excitatory when its orientation is similar to the optimal orientation for excitation. This has generally been the case in previous studies (Bonds 1989; Morrone et al. 1982), where the suppressive stimulus produced some excitation at orientations near the preferred excitatory orientation. Thus it is difficult to tell how the strength of suppression varies with orientation throughout the orientation passband (see Discussion).

To overcome this problem, we have tested the orientation tuning of suppression by using gratings with spatial frequencies outside the excitatory ranges for the cells, but still effective in generating suppression. This approach allows us to assess the strength of suppression at all orientations. Figure 7 shows measurements of the orientation selectivity of excitation and suppression for one simple cell (A and B) and two complex cells (C and D, E and F). Data shown in A and B are for the same simple cell as in Fig. 3, E and F; data shown in C and D are for the complex cell also shown in Fig. 3, C and D. As described above, each cell is excited by a rectangular patch of grating having optimal orientation and spatial frequency. This produces a baseline response that is modulated by a spatially coincident patch of grating whose orientation is variable. The spatial frequency of this variable orientation grating is chosen so that it does not produce any excitation when aligned with the excitatory grating. Both grating patches have identical dimensions that are selected to contain the stimuli within the excitatory summation area of each cell.

It is clear from Fig. 7 that the suppressive stimulus, which we knew to generate suppression at an orientation orthogonal to the excitatory optimum, is actually suppressive at all orientations. Notice that the responses shown in B, D, and F are all far below the control level of response to the excitatory patch presented alone (shown by the dashed lines). Thus the strength of suppression is, to a first approximation, independent of the orientation of the inhibiting stimulus. This finding is in accord with many of the observations made by Bonds (1989), who also concludes that the dominant characteristic of suppression is its uniformity across orientation (see his Figs. 4, C and D, 5A, and 8E). The results of Fig. 7 are also consistent, for the most part, with the data of Morrone et al. (1982), except that their data exhibit strong excitation when the “suppressive” stimulus is at the preferred orientation. Hence Morrone et al. (1982)
were not able to observe that there is actually quite strong suppression at the optimal orientation for excitation.

A closer look at the data of Fig. 7 reveals that the strength of suppression is not completely independent of orientation. We sometimes observe suppression to be strongest over a range of orientations similar to, but somewhat broader than, the range of excitatory orientations. This can be seen clearly as a pair of troughs in the orientation tuning curves for suppression shown in Fig. 7, D and F (and to a lesser extent in Fig. 7B). The depth of these troughs is variable from cell to cell, and no troughs are seen for some cells. However, if the strength of the suppressive effect varies at all with orientation, the suppression always seems to be strongest near the cell’s preferred orientation for excitation. We have observed some variation in the relative magnitude of troughs corresponding to motion in the preferred and opposite directions (i.e., troughs separated by 180° in each curve). These asymmetries are not obviously correlated with the direction selectivity, or any other characteristic, of these cells.

It should be noted that, for some cells, it is not possible to find a spatial frequency that elicits suppression without producing excitation. For these cells, we also observe suppression over a broad range of nonoptimal orientations; however, like Morrone et al. (1982), we cannot evaluate the strength of suppression at orientations within the excitatory range. Another point to emphasize is that our measurements of the orientation tuning of suppression are obtained at only a single (nonoptimal) spatial frequency. We assume that the orientation selectivity of suppression is a reasonably invariant function of spatial frequency. However, it is difficult to verify this assumption rigorously, because excitation interferes with the orientation tuning measurements at spatial frequencies within the excitatory passband. For one cell, we measured the orientation selectivity of suppression at two nonoptimal spatial frequencies, one above the
excitatory frequency range and the other below. At both frequencies, the orientation tuning of suppression was very similar.

Spatial phase sensitivity of suppression

The stimuli used in these experiments are sinusoidal gratings drifting at a fixed temporal frequency (i.e., having a linear velocity inversely related to spatial frequency). When the stimulus is a single grating of this kind, the effect of changing the orientation of the stimulus on the activity of cells with approximately circular receptive fields [i.e., those in the retina and lateral geniculate nucleus (LGN)] is simply to change the relative temporal phase of their responses. There is no change in the amplitude of the response. However, when the stimulus consists of two superimposed gratings at different orientations, the composite stimulus has the nature of, and may have the appearance of, a rigid plaid. This stimulus will have an increased effective contrast for some cells with circular receptive fields and a decreased contrast for others, depending on their exact location with respect to the path of the nodes of the pattern. This would be unimportant to cortical cells if signal transmission to the cortex were a completely linear process. However, nonlinearities could result in interference effects that appear at higher levels. Similarly, simple nonlinearities operating at the cortical level, before the processes of spatial summation, could result in interference effects that mimic suppression from within the excitatory receptive field.

It is difficult to rule out completely the possibility that the suppressive phenomena we have observed might to some extent be a reflection of this kind of nonlinear interaction. However, such effects should be markedly dependent on the relative spatial phase of the excitatory and suppressive gratings, that is, the exact positioning of the composite stimulus with respect to the receptive field.

We have therefore examined the effect of changing the relative spatial phase of suppressive and excitatory gratings on the magnitude of suppression. Results of this test are shown in Fig. 8 for two cells. Figure 8A shows the response of a complex cell as a function of the relative spatial phase between the optimally oriented and orthogonal gratings. The dashed line indicates the response level to the excitatory grating patch, when presented in isolation. Note that superposition of the suppressive (orthogonal) grating reduces the response of the cell uniformly at all spatial phases. However, when the stimulus consists of two superimposed gratings at different orientations, the composite stimulus has the nature of, and may have the appearance of, a rigid plaid. This stimulus will have an increased effective contrast for some cells with circular receptive fields and a decreased contrast for others, depending on their exact location with respect to the path of the nodes of the pattern. This would be unimportant to cortical cells if signal transmission to the cortex were a completely linear process. However, nonlinearities could result in interference effects that mimic suppression from within the excitatory receptive field.

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furred orientation but with a spatial frequency chosen to be outside the excitatory range. The result of one such test is shown in Fig. 8C. These data were obtained from the same simple cell as in Fig. 8B. Again, the strength of suppression is independent of the relative spatial phase between the excitatory and suppressive stimuli. Note, however, that suppression elicited by a stimulus at the preferred orientation (Fig. 8C) is somewhat stronger than suppression obtained at the orthogonal orientation (Fig. 8B).

Another reason for believing that the suppressive effects we have studied are not simply low-level nonlinear interference effects involves the contrast threshold for suppression. In some cases we were able to observe suppression when both the excitatory and suppressive stimuli were of very low contrast (5% or less), whereas in other cases the suppressive grating had little effect until its contrast was 20–50%. Thus there appears to be a relatively high contrast threshold for the localized suppressive effect in many cells (see also Bonds 1989). The fact that subcortical neurons, notably lateral geniculate and retinal ganglion cells, typically give large responses to contrast levels of 20–50% (Derrington and Fuchs 1979; Enroth-Cugell and Robson 1966; Lehmkuhle et al. 1980; Troy 1983) provides further evidence that suppression is not due to subcortical interference effects.

**Dichoptic suppression**

For three cells that responded well to monoptic stimulation through either eye, we examined whether suppression could be mediated dichoptically. We tested whether the response to an optimally oriented stimulus shown to one eye could be reduced by presentation of an orthogonally oriented grating to the other eye. In each case we found no measurable dichoptic suppression for an orthogonal grating of any spatial frequency or contrast (up to 80%). Data for one of these three cells are shown in Fig. 9. Response is shown as a function of the spatial frequency of the suppressive (orthogonal) grating patch. The open symbols represent tests in which both the excitatory and suppressive gratings were presented to the same eye (open circles, left eye; open squares, right eye). Broadly tuned suppression is clearly visible in both of these monoptic tests. By contrast, the filled symbols in Fig. 9 show the cell’s response when the optimally oriented grating patch was presented to the left eye and the orthogonal grating was presented to the right eye. There is no visible effect of the orthogonal grating on the response to the optimally oriented stimulus at any spatial frequency, despite the fact that the orthogonal grating had a contrast of 80%. A lack of dichoptic suppression might be expected for cells that are monocular (i.e., only excitable through 1 eye). However, the cell shown in Fig. 9 is equally excitable through either eye and clearly shows suppression in both monoptic tests.

Although we looked at just three cells in these experiments, earlier experiments suggest that cross-orientation suppression is seldom mediated dichoptically (Ohzawa and Freeman 1986a,b; Freeman et al. 1987). Ohzawa and Freeman (1986a,b) performed control experiments on many cells in which an optimally oriented grating was presented to one eye and an orthogonal grating was shown to the opposite eye. None of the simple cells examined in this manner showed discernible dichoptic suppression, although they could all be excited to some extent through either eye (for example, see Figs. 3D and 4D of Ohzawa and Freeman 1986a). Moreover, only one complex cell showed dichoptic cross-orientation suppression (see Fig. 8D of Ohzawa and Freeman 1986b). These findings were confirmed by Freeman et al. (1987), who examined cross-orientation suppression both monoptically and dichoptically for 32 cells. Most of these cells showed strong suppression monoptically but not dichoptically. Some dichoptic suppression was found for a few cells; however, the suppression was always much weaker dichoptically than monoptically. In these prior experiments, as well as those of Ohzawa and Freeman (1986a,b), dichoptic suppression was only tested with the use of excitatory and suppressive stimuli of the same spatial frequency. Moreover, the stimuli in these previous experiments were large sinusoidal gratings that were not confined to the excitatory receptive field.

**DISCUSSION**

Previous studies (Bonds 1989; Morrone et al. 1982; Petrov et al. 1980) have shown that the responses of most visual cortical cells can be suppressed by the presentation of a grating stimulus oriented orthogonal to the cell’s preferred orientation. To clarify the functional role of this phenomenon, we have studied the spatial organization and tuning characteristics of suppression for a population of neurons in the cat’s striate cortex. Our findings can be summarized as three major points. First, the extent of the region...
from which cross-orientation suppression originates is typically coextensive with the excitatory receptive field. For some cells, the region producing suppression is significantly smaller than the receptive field. Second, the strength of suppression is generally independent of the orientation of the suppressive stimulus, although this may be observed only in cases for which there is a spatial frequency that produces suppression without eliciting excitation. For some cells, the suppressive effect is somewhat stronger at the preferred orientation for excitation than at an orthogonal orientation.

Third, cross-orientation suppression is not mediated dichoptically, despite the fact that it is always elicited monoptically.

It should be noted that the suppression we have studied can be distinguished from end and side inhibition in each of the three respects described above. End and side inhibition seem to arise from regions that extend beyond the excitatory receptive field (Hubel and Wiesel 1965), although these regions may overlap the receptive field to some extent (Born and Tootell 1991; Orban et al. 1979; Sillito 1977a). Moreover, end and side inhibition are only effective at orientations around the optimal excitatory orientation (Born and Tootell 1991; DeAngelis et al. 1990; Hubel and Wiesel 1965; Orban et al. 1979). And these inhibitory effects can be mediated dichoptically in most cells (DeAngelis et al. 1990, 1991b). These differences suggest that the mechanisms that produce end and side inhibition are distinct from those that underlie the localized suppression studied here.

Measurement of receptive-field size

Receptive fields of cortical neurons are often described in terms that suggest that these areas have a precise boundary within which the cell's sensitivity is uniform. However, receptive fields, as well as suppressive regions, probably have sensitivity profiles that taper away to zero along an imprecisely defined border (Jones and Palmer 1987a). Although it can be useful for some purposes to plot rectangular minimum response fields (Barlow et al. 1967), these almost certainly underestimate the area over which contributions to a cell's excitatory response are derived. In fact, it seems likely that all receptive-field plotting methods that employ small bar stimuli will underestimate the extent of the excitatory summation area. For example, Maffei and Fiorentini (1976), after taking great care to define the limits of cortical cell receptive fields with a flashing bar stimulus, still found that they could obtain facilitation of some cells' responses with the use of grating stimuli presented outside the region they had so carefully delineated. Of particular significance is their finding that, to produce facilitation, the grating stimuli placed outside the receptive field had to be spatially phase coherent with the grating located within the receptive field. The extent of the region over which Maffei and Fiorentini could obtain facilitation was as much as three times the width of the supposed receptive field determined by their initial mapping.

We suggest that a cell's excitatory receptive field is more appropriately described as the region within which a stimulus can either elicit an excitatory response or add to the response elicited by another stimulus. It is in this sense that we have employed the term receptive field in this paper. If we suppose that the facilitatory effect seen by Maffei and Fiorentini (1976) is really no more than the summation of a subthreshold response with a suprathreshold response (rather than a true multiplicative effect), then this definition of the receptive field seems justifiable (Tadmor and Tolhurst 1989). On the basis of this definition, we can measure the size of a cell's receptive field by finding the smallest patch of sinusoidal grating required to produce a maximal response from the cell. This measurement is obtained, in practice, by fitting curves to the length- and width-response data (see Eqs. 1–3) and extracting size parameters.

At this point, it is important to clarify how our receptive-field measurements made with gratings relate to the detailed internal structure of simple and complex cell receptive fields. Simple cells were initially described as having spatially alternating subregions that respond to either the onset (on regions) or offset (off regions) of a bar of light (Hubel and Wiesel 1959, 1962). Alternatively, on and off regions can be thought of as responding to bright stimuli and off regions as responding to dark stimuli (Maske et al. 1985). The response of a simple cell to a drifting sinusoidal grating thus reflects the net stimulation of both the bright-excitatory and dark-excitatory subregions. It has been suggested that simple receptive fields are well characterized by a Gabor function (Daugman 1985; DeAngelis et al. 1991a; Field and Tolhurst 1986; Jones and Palmer 1987b; Marcelja 1980; but see Stork and Wilson 1990), which is a sinusoid modulated in space by a Gaussian envelope. On the basis of this model, our estimates of the size of a simple cell receptive field probably corresponds best to the size of its Gaussian envelope and includes all bright- and dark-excitatory subregions that are contained therein.

Complex cells, on the other hand, respond to both bright and dark stimuli throughout their receptive fields (Hubel and Wiesel 1962). The line-weighting functions of complex cells do not resemble Gabor functions, but rather show a sensitivity profile that is approximately Gaussian (Movshon et al. 1978b; see also Fig. 1 of Ohzawa et al. 1990). For complex cells, the estimates of receptive-field size obtained with variable size patches of sinusoidal gratings also presumably reflect the size of their Gaussian envelopes.

Although no direct comparison appears to have been made, the extent of a receptive field measured by our method is likely to be closer to the extent predicted through Fourier analysis of the spatial frequency tuning function (Andrews and Pollen 1979; DeValois et al. 1978; Giesler et al. 1980, 1982; Kulikowski and Bishop 1981; Maffei et al. 1979; Movshon et al. 1978a), than that provided by methods using flashed or moving bars. Several researchers (Andrews and Pollen 1979; Giesler et al. 1980, 1982; Kulikowski and Bishop 1981; Tadmor and Tolhurst 1989) have shown that the predicted receptive-field profile of simple cells, on the basis of inverse Fourier transformation of the spatial frequency tuning curve, is typically larger than the receptive-field profile measured with bars (i.e., the line-weighting function). Tadmor and Tolhurst (1989) have shown that most of this discrepancy can be accounted for by a response threshold nonlinearity in simple cells. Essentially, the discrepancy between predicted receptive-field profiles and measured line-weighting functions arises be-
cause weak flanks of the receptive field cannot always be detected with a single bar stimulus because their contribution to the cell’s response is subthreshold (see Douglas et al. 1991). Our method of determining receptive-field size with gratings does not suffer from this limitation because the contribution of weak peripheral flanks is superimposed on an already suprathreshold response. When using this method, however, one must be careful to use low-contrast stimuli (10–20% contrast was used here) in order not to saturate the cells’ responses. Saturation could cause receptive-field size estimates to be erroneous. Note that this potential source of error would not affect our conclusion that suppression arises from within the excitatory receptive field, however, because saturation errors would cause an underestimation of the size of the excitatory receptive field.

Another reason for measuring receptive-field size with gratings is that the extent of a suppressive region can be measured in an exactly analogous manner. This obviates some of the problems of interpretation involved in comparing two measurements made by the use of different methods.

Nature of the suppressive effect

On the basis of the results described above, as well as those obtained by Bonds (1989) and Morrone et al. (1982), we suggest that the suppressive effect we have studied arises through inhibition from a pool of cortical neurons. Each cell in this inhibitory pool has a receptive field that overlaps the receptive field of the neuron from which we record. Moreover, members of the inhibitory pool exhibit a full range of orientation preferences and a broad range of optimal spatial frequencies (i.e., the suppression is largely non-specific). This scheme is very similar to that proposed by D. J. Heeger (1991, 1992).

Because inhibition is likely to be involved in many functions of the visual cortex, it is important to distinguish the nonspecific suppression studied here with other types of inhibition known to operate in the striate cortex. As alluded to above, it is highly unlikely that we are confusing the source of nonspecific suppression with that producing end inhibition or side inhibition. Nonspecific suppression was observed in all cells tested, regardless of whether they exhibited any end or side inhibition. In addition, we always measured the summation area for suppression with the use of a suppressive stimulus that was oriented orthogonal to the cell’s preferred orientation. This stimulus is unlikely to stimulate end or side inhibitory regions, because these regions are known to be insensitive at orientations orthogonal to the excitatory optimum (Born and Tootell 1991; DeAngelis et al. 1990; Hubel and Wiesel 1965; Orban et al. 1979). Even if end- and side-inhibitory regions overlap the summation area for suppression, they would not be included in our measurements of the size of the suppressive summation area. Contributions from end- and side-inhibitory regions may be observed, however, when the suppressive stimulus has an orientation close to the excitatory optimum, as was the case during our measurements of the orientation tuning of suppression (discussed below). In these situations it may not be possible to distinguish nonspecific suppression from end and side inhibition, because of spatial overlap.

It is also possible that our measurements of the suppressive summation area may be confounded by the presence of “inhibitory sidebands,” as described by Bishop et al. (1973) for unimodal simple cells. With the use of a conditioning stimulus to elevate the cells’ maintained discharge, Bishop et al. found regions (the sidebands) on either side of the excitatory “discharge center” that strongly inhibited the cell when stimulated with an optimally oriented light bar. When the same cell was stimulated with a non-optimally oriented bar, inhibition was observed extending throughout and beyond the excitatory discharge center (see their Fig. 3). Bishop et al. (1973) concluded that the inhibitory sidebands were not orientation selective. If so, then our measurements of the suppressive summation area should reflect the presence of these sidebands.

It is likely that the inhibition observed by Bishop et al. (1973), by stimulating with a nonoptimally oriented bar, stems from the same suppressive mechanism that we describe here. However, it is not clear how the inhibition they observed at the optimal orientation (i.e., the sidebands) relates to the nonspecific suppression we have studied. It is likely that the sidebands described by Bishop et al. (1973) are due, at least in part, to inhibition from dark-excitatory (or OFF) subregions of the simple cell’s receptive field. With the use of a binocular conditioning paradigm, Ferster (1981) observed these inhibitory sidebands to be orientation selective, appearing only when stimulated by an optimally oriented bar. Moreover, Ferster (1988) has shown that orientation-selective inhibitory postsynaptic potentials (IPSPs) can be recorded from simple cells while a dark-excitatory subregion is stimulated with a bright bar (or while a bright-excitatory subregion is stimulated with a dark bar). Thus what Bishop et al. reported may have been the combination of nonspecific suppression and orientation-selective inhibition from dark-excitatory subregions. In any case, it is likely that the inhibition observed by Bishop et al. at the nonoptimal orientation was, in fact, generated by the suppressive mechanism described here.

Orientation specificity of suppression

Previous studies of the orientation specificity of cross-orientation suppression (Bonds 1989; Morrone et al. 1982) have used, as suppressive stimuli, patterns that could cause excitation when oriented within the excitatory range for the cell. Although both studies found suppression to occur over a wide range of orientations, they were not able to determine conclusively, what happens at orientations close to the preferred excitatory orientation. The implicit assumption of Morrone et al. (1982) seems to be that suppression occurs at all orientations, excluding the range of orientations that excite the cell. By using excitatory and suppressive stimuli with different temporal frequencies, Bonds (1989) attempts to address this issue, at least for simple cells. His methodology relies on the assumption that simple cells operate linearly, both in space and time, such that the responses to the two frequencies can be decomposed by Fourier analysis. In our experiments we have made observations of the magnitude of suppression at all orientations by using a suppressive stimulus with a spatial frequency outside the excitatory range for a given cell. This approach...
has the advantage that it is applicable to both simple and complex cells, and it does not require assumptions of linearity. However, cells that have similar spatial frequency tuning for excitation and suppression cannot be studied with this method.

We find that the localized suppressive effect is predominantly independent of orientation. Hence the name cross-orientation suppression is really inappropriate, because suppression occurs at all orientations including the optimum for excitation. These findings are consistent with several of the results presented by Bonds (1989) for simple cells (see his Figs. 4, C and D, 5A, and 8E). In addition, we find that some cells show increased suppression for a range of orientations similar to, but sometimes broader than, that which yields excitation (see our Fig. 7, D and F). This may reflect a genuine orientational anisotropy in the mechanism that underlies suppression. Alternatively, the “extra” suppression seen around the optimal orientation for some cells may originate in a separate process. It may be the case that this extra suppression around the preferred orientation reflects the operation of an end- or side-inhibition process that overlaps the excitatory summation area. Because end and side inhibition are thought to be tuned to the preferred orientation for excitation, the summation of these effects with an orientation-independent component of suppression might account for the data seen in Fig. 7. In fact, the cells shown in Fig. 7, C and D, and E and F, both demonstrated some degree of side inhibition. For these cells, it is plausible that the troughs in the suppressive orientation tuning curves arise through stimulation of end- or side-inhibition zones that partly overlap the excitatory receptive field (Born and Tootell 1991; Orban et al. 1979; Sillito 1977a).

Although our observations on the orientation selectivity of suppression are generally in agreement with those of Bonds (1989), there are differences worth noting. Bonds reports, for a few narrowly tuned simple cells, that suppression is strongest at orientations to either side of the optimal orientation for excitation (i.e., at the flanks of the orientation tuning curve). A similar result is illustrated in Fig. 6B of Morrone et al. (1982). In contrast, we never found suppression to be strongest on either side of the preferred orientation in tests where the suppressive stimulus had a nonexcitatory spatial frequency. It is possible that this difference is due to a cell sampling bias. Alternatively, this discrepancy may be explained by the fact that the suppressive stimuli used in these previous studies also produced excitation when oriented within the excitatory range. To illustrate this possibility, notice that a summation of the excitatory and suppressive orientation tuning functions shown in Fig. 7 (see E and F, for example) would yield a result similar to that described by Bonds (his Fig. 5, C and D) or Morrone et al. (their Fig. 6B), namely a curve in which the suppression appears to be strongest at the flanks of the excitatory tuning curve. The troughs evident in our Fig. 7 may be directly related, therefore, to the flanking inhibition observed by Bonds (1989) and Morrone et al. (1982), and it is plausible that both effects are due to some contribution of end- and side-inhibitory regions, as discussed above. Although Morrone et al. (1982) and Bonds (1989) state that they did not study cells with strong end or side inhibition, some of their cells may have had sufficiently strong inhibitory regions outside their receptive fields to generate the flanking inhibition. This is especially plausible because both Bonds and Morrone et al. used stimuli much larger than the excitatory receptive fields of most cells. Such large field stimuli are more likely to stimulate end- and side-inhibitory mechanisms than the stimuli of optimal size used here.

Origin and site of the suppressive effect

Several lines of physiological evidence suggest that the suppressive effect of superimposing stimuli of different orientations arises through intracortical inhibition. Bonds (1989) found no significant reduction of response when stimulating LGN fibers with two superimposed gratings of different orientations. He also points out that the temporal frequency bandwidth of the suppressive effect is much narrower than the temporal bandwidth of LGN cells, indicating that the signal source underlying suppression is likely to be of cortical origin. Morrone et al. (1982) found, for both simple and complex cells, that the effect of a phase-reversing superimposed orthogonal grating was manifest as a frequency-doubled modulation of the response to an excitatory stimulus. They concluded that cross-orientation suppression was probably mediated by complex cells, whose normal excitatory response is also frequency doubled (unlike that of individual simple cells). We have confirmed that the suppressive effect produced by phase-reversing gratings is a frequency-doubled modulation of the response. Further evidence for a cortical origin of suppression comes from Morrone et al. (1982), who measured cross-orientation inhibition in visual evoked potentials (VEPs) from the cat’s striate cortex. They found that application of the γ-aminobutyric acid (GABA) antagonist bicuculline eliminated cross-orientation suppression, as reflected in the VEP amplitudes. Additional evidence for a cortical origin of suppression can be found in Bonds (1989) and Morrone et al. (1982).

Most of the physiological evidence described above is consistent with the notion that suppression is mediated through inhibition by complex cells. In fact, the idea that complex cells may provide an inhibitory signal that shapes stimulus selectivity has been suggested by a number of researchers (Creutzfeldt et al. 1974a; DeValois and Tootell 1983; Hammond and MacKay 1978; Lennie 1980; Morrone et al. 1982; Singer et al. 1975). However, as pointed out by Bonds (1989), there is little direct evidence to support this notion. Intracortical inhibition is thought to be mediated by smooth stellate cells (LeVay 1973; see Martin 1988 for review), and a physiological characterization of these neurons suggests that they are simple cells (Gilbert and Wiesel 1979). In addition, cross-correlation studies find no evidence for inhibition from complex cells (Toyama et al. 1981). On the basis of this information, Bonds (1989) suggests that suppression may not be mediated directly by complex cells, but rather by a pool of simple cells having spatially incoherent receptive fields (i.e., fields with random spatial phase). We have little to add to this suggestion, except to note that all of the cells in such a pool must have receptive fields that overlap that of the cell they inhibit.
Thus far we have argued that suppression is probably mediated by intracortical inhibition. We have said little, however, about the cortical site of the inhibition or its synaptic mechanism. Our finding that the response of most cells to an optimally oriented stimulus is not affected by presentation of an orthogonal grating to the other eye places one important constraint on the cortical site of suppression. Because cross-orientation suppression is not manifested during dichoptic stimulation, the signal source that supplies the inhibition must be monocular. It seems likely, then, that suppression is generated in the visual cortex before the site of binocular convergence. This would mean that suppression originates very early in the cortical processing stream. Also, the monocular source of suppression is unlikely to be complex cells, because most of these are binocular (Gilbert 1977; Skottun and Freeman 1984). In contrast to cross-orientation suppression, we have observed that end and side inhibition can be demonstrated dichoptically in almost all cells that exhibit these effects monoptically (DeAngelis et al. 1990, 1991b), suggesting that these inhibitory effects are generated in the cortex after binocular interaction.

It is worth noting that the results of our dichoptic tests on cross-orientation suppression are consistent with some previous observations. Recording extracellularly from cortical cells, Ferster (1981) was unable to find any suppressive effect of an orthogonally oriented bar presented to one eye on the responses elicited by an optimally oriented bar presented to the other eye. Ferster (1986, 1987) has suggested that the lack of a dichoptic effect indicates that suppression is produced subcortically (i.e., in the LGN). Indeed, the observations that the source of suppression is monocular and largely nonoriented are consistent with a geniculate origin. One possibility is that cross-orientation suppression is an artifact of some nonlinear interaction between orthogonal stimuli at the level of the LGN (as described in results). Our finding that the strength of suppression is independent of the relative spatial phase between optimally oriented and orthogonal gratings makes this unlikely, however (see also Bonds 1989). Martin (1988, see his Fig. 17) also points out that cross-orientation inhibition can be observed in the responses to a single (nonoptimally oriented) stimulus, for cells that are spontaneously active. Suppression at nonoptimal orientations can also be observed with the use of a single stimulus when the background activity of cortical cells is raised by the application of an excitatory amino acid, such as glutamate (Hess and Murata 1974; Ramoa et al. 1986; Sillito 1979). Thus suppression cannot be solely an artifact of some nonlinear interaction occurring subcortically.

Several lines of evidence, described above, suggest that suppression is produced by interactions occurring within the cortex. Thus it is conceivable that suppression arises through inhibition from geniculate afferents in the cortex. However, geniculate afferents to the cortex appear to be exclusively excitatory (Cruztafeldt and Ito 1968; Garcey and Powell 1971; Tanaka 1985), and a geniculate origin for suppression would require LGN afferents to act through inhibitory interneurons in the cortex. These inhibitory interneurons would have to be insensitive to stimulus orientation. However, nonorientation-selective cortical cells are rarely encountered in the cat (Hubel and Wiesel 1959, 1962). Martin and collaborators have studied the receptive-field organization of putative inhibitory (GABAergic) interneurons and found them all to be orientation selective (Martin 1988). This makes the possibility that suppression has a geniculate origin unlikely; however, we cannot rule it out completely at this time. Instead, we favor the notion that suppression arises through a pool of cortical cells having varied selectivities for orientation and spatial frequency. Large basket cells in the cortex are a plausible anatomic substrate for mediating non-orientation-selective suppression, because these inhibitory neurons have axons that appear to contact cells of all orientation preferences (Martin 1988; Eysel and Kisvarday 1991).

Synaptic mechanisms underlying suppression

Another issue that is unresolved concerns the synaptic mechanisms that underlie suppression. There are several pieces of evidence worth noting, however. On the basis of intracellular recordings, excitatory and inhibitory postsynaptic potentials (EPSPs and IPSPs, respectively) from the subregions of simple receptive fields appear to interact through linear summation (Ferster 1988). The interaction of signals from the two eyes has also been postulated to depend on postsynaptic summation (Ohzawa and Freeman 1986a, b). If cross-orientation suppression is mediated by a linear interaction of PSPs, one would expect to observe inhibitory PSPs in response to a nonoptimally oriented stimulus. Intracellular recording studies have not confirmed this expectation, however. Ferster (1986) was unable to see any PSPs in response to moving bars oriented orthogonal to the optimal orientation. More recently, Douglas et al. (1991) have confirmed this finding for simple cells. They did observe IPSPs in some complex cells while stimulating with a nonoptimally oriented stimulus; however, if this were the primary mechanism underlying suppression, it should be present in all cells.

A lack of inhibitory PSPs at the nonoptimal orientations might be expected if suppression is mediated by shunting inhibition (Fatt and Katz 1953). In the case of shunting inhibition, excitatory and inhibitory PSPs interact nonlinearly, the net effect being a reduction of the EPSP by a constant fraction (i.e., a division of the response). There is some evidence consistent with the idea that cross-orientation suppression is mediated by a shunting (i.e., divisive) mechanism. Rose (1977) finds that iontophoresis of GABA affects the orientation tuning curve of cortical cells in a manner consistent with divisive inhibition. Both Morrone et al. (1982) and Bonds (1989) find that the effect of a superimposed (suppressive) stimulus on the contrast response function of cortical cells is consistent with a divisive inhibitory process. We have also made some observations (unpublished) that support a divisive mechanism. Moreover, D. J. Heeger (1992) shows that the contrast response data of Bonds (1989) are predicted quite well by a model featuring divisive suppression. However, intracellular studies find minimal evidence to support shunting inhibition as a substrate for producing the nonspecific suppression we have studied (Berman et al. 1991; Douglas et al. 1988; Ferster 1986; Ferster and Jagadeesh 1991).
At this time, there is no strong evidence in favor of any particular synaptic mechanism that may underlie nonspecific suppression. Neither hyperpolarizing (subtractive) nor shunting (divisive) postsynaptic inhibition is consistent with the available intracellular data. This leaves the possibility that suppression may be mediated through some form of presynaptic inhibition, although there are no data that support this mechanism either. Perhaps this issue could be resolved through further intracellular studies in which cross-orientation inhibition is examined more directly by use of a pair of superimposed stimuli having different orientations.

**Function of local suppression**

It has often been suggested that inhibition contributes to the orientation selectivity of neurons in the visual cortex (see Ferster and Koch 1987; Martin 1988 for an overview; Bishop et al. 1973; Bonds 1989; Blakemore and Tobin 1972; Creutzfeldt et al. 1974b; Morrone et al. 1982; Nelson and Frost 1978; Sillito 1975, 1977b, 1979; Tsumoto et al. 1979). At one extreme, inhibition could serve as a primary mechanism for generating orientation selectivity by preventing the response of a given cell to stimuli of nonoptimal orientations. Alternatively, excitatory connections may endow a cell with rough orientation selectivity, and inhibition may serve to sharpen this selectivity.

Our findings concerning the orientation selectivity of “cross-orientation” suppression suggest that this mechanism has, at most, a very limited function in shaping the orientation tuning of cortical cells. We find, as did Bonds (1989), that suppression is typically effective at all orientations, not just those that are non-optimal for exciting the cell. Thus cross-orientation suppression must not be the primary mechanism for generating orientation selectivity. In addition, our data suggest that this suppression plays a very limited role in sharpening orientation tuning. Unlike Bonds (1989), we did not observe suppression to be strongest at orientations just outside of the excitatory orientation tuning curve. Rather, in some cases, we observed suppression to be strongest over a range of orientations similar to, but broader than, the range that produces excitation (see the “troughs” in Fig. 7, D and F). It can be argued that this component of suppression, which is more broadly tuned than excitation, serves to sharpen orientation selectivity by attenuating the flanks of the tuning curve. However, this interpretation depends on the nature of the suppressive effect. If suppression is subtractive, then the troughs seen in Fig. 7, D and F, could act to sharpen orientation tuning to a limited extent. If suppression is divisive, as suggested by the contrast-response measurements reported by Morrone et al. (1982) and Bonds (1989; see also Heeger 1992), then the troughs of suppression shown in Fig. 7, D and F, would act to broaden the orientation tuning curve, rather than sharpening it. On the basis of these observations, the suppression we have studied is likely to be of minimal consequence for generating or enhancing orientation selectivity.

If suppression does not contribute to orientation selectivity, then the orientation tuning of cortical cells may derive from excitatory connections, as proposed by Hubel and Wiesel (1962). Indeed, Ferster (1987) has used a quantititative version of the Hubel and Wiesel model to show that most of the properties of EPSPs recorded intracellularly from simple cells can be predicted on the basis of excitatory convergence of geniculate afferents. Yet, intracellular studies of simple cells reveal IPSPs that have orientation selectivity nearly identical to that of EPSPs elicited from the same cells (Ferster 1986). Ferster (1988) has also shown that EPSPs and IPSPs are spatially opponent within the receptive fields of simple cells. A light bar in a bright-excitatory (or ON) subregion evokes excitation, and a dark bar in the same subregion evokes inhibition. Similarly, for a dark-excitatory (or OFF) subregion, a dark bar elicits excitation, and a light bar produces inhibition. Thus EPSPs and IPSPs seem to interact linearly (Ferster and Jagadeesh 1991) to produce the receptive-field structure of simple cells. This evidence is consistent with the idea that simple cells are organized as mutually inhibitory, or “push-pull,” pairs (Ohzawa et al. 1990; Palmer and Davis 1981; Palmer et al. 1991; Stepnoski and Palmer 1989). The inhibition observed by Ferster (1988) in simple receptive fields is clearly distinct from the inhibition responsible for cross-orientation suppression, because the IPSPs he observed were only found at orientations near the optimum for excitation. Furthermore, the inhibition seen by Ferster is unlikely to mediate end and side inhibition, because the IPSPs were generated from within the classical receptive field.

On the basis of the available intracellular data, it would clearly be wrong to assert that inhibition is not involved in generating the orientation selectivity of simple cells. In fact, the spatially opponent interactions of EPSPs and IPSPs described by Ferster (1988) may be essential for producing the orientation and spatial frequency selectivity of these cells. However, interactions between cells that are tuned to different orientations and spatial frequencies (i.e., cross-orientation inhibition) may not be necessary to explain the tuning characteristics of cortical neurons. It has been shown that the “linear” receptive-field structure of simple cells (i.e., on the basis of linear interaction of EPSPs and IPSPs) accounts fairly well for the observed orientation and spatial frequency tuning of these neurons (Jones and Palmer 1987b). In these studies Jones and Palmer (1987a,b) obtained detailed receptive-field profiles for simple cells by taking the algebraic difference between the responses to bright and dark stimuli. This is tantamount to assuming that excitation from a dark bar is equivalent to inhibition from a bright bar, as Ferster (1988) has demonstrated. With the use of this method, Jones and Palmer (1987b) show that the receptive-field structure of simple cells can be modeled as a two-dimensional Gabor filter. Predictions of the orientation tuning of simple cells, on the basis of this model, agree fairly well with measured orientation selectivity data (Jones and Palmer 1987b). For complex cells, the receptive field is composed of subunits that largely resemble simple cells in their spatial structure (Emerson et al. 1987; Hegelund 1981; Movshon et al. 1978b; Szelborski and Palmer 1990). Moreover, predictions of complex cell orientation selectivity, on the basis of the structure of these receptive-field subunits, agree reasonably well with measured orientation tuning curves (Szelborski and Palmer 1991). These studies of linear receptive-field structure suggest that.
the spatially opponent excitation and inhibition observed by Ferster (1988) is primarily responsible for the orientation tuning of cortical neurons. They also suggest that a nonlinear interaction between neurons tuned to different orientations, namely cross-orientation suppression, is not necessary to account for the observed orientation selectivity of cortical cells.

What, then, is the function of the suppressive mechanism that we have studied? One idea is that suppression serves to normalize the response of each cell with respect to the local contrast of an image (Bonds 1989, 1991; Heeger 1991, 1992; Robson 1988). Specifically, it has been proposed that the response of a cell is normalized by the outputs of a pool of neurons located in the same region of cortex (Heeger 1991, 1992). The members of this pool exhibit a wide variety of orientations and spatial frequencies, such that the normalization signal is orientation-selective and broadly tuned for spatial frequency. Heeger (1991, 1997) has shown that this normalization scheme can explain many of the nonlinear and adaptive response characteristics of cortical cells, including cross-orientation suppression (Bonds 1989; Morrone et al. 1982; Petrov et al. 1980) and contrast gain control (Bonds 1991; Ohzawa et al. 1985).

The normalization hypothesis is strengthened by our finding that the suppressive effect originates from an area of approximately the same size as the excitatory receptive field, and that this localized suppressive effect generalizes over all orientations. The fact that suppression is broadly tuned for spatial frequency (Morrone et al. 1982; Bonds 1989) also supports the normalization hypothesis. Whether the temporal characteristics of the suppressive effect (which have received little attention) and the magnitude of the effect are consistent with this hypothesis remains to be investigated.

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