

Neuronal Responses to Static Texture Patterns in Area V1 of the Alert Macaque Monkey

JAMES J. KNIERIM AND DAVID C. VAN ESSEN

Division of Biology 216-76, California Institute of Technology, Pasadena, California 91125

SUMMARY AND CONCLUSIONS

1. We recorded responses from neurons in area V1 of the alert macaque monkey to textured patterns modeled after stimuli used in psychophysical experiments of pop-out. Neuronal responses to a single oriented line segment placed within a cell's classical receptive field (CRF) were compared with responses in which the center element was surrounded by rings of elements placed entirely outside the CRF. The orientations of the surround elements either matched the center element, were orthogonal to it, or were random.

2. The addition of the textured surround tended to suppress the response to the center element by an average of 34%. Overall, almost 80% of the 122 cells analyzed in detail were significantly suppressed by at least one of the texture surrounds.

3. Cells tended to respond more strongly to a stimulus in which there was a contrast in orientation between the center and surround than to a stimulus lacking such contrast. The average difference was 9% of the response to the optimally oriented center element alone. For the 32% of the cells showing a statistically significant orientation contrast effect, the average difference was 28%.

4. Both the general suppression and orientation contrast effects originated from surround regions at the ends of the center bar as well as regions along the sides of the center bar.

5. The amount of suppression induced by the texture surround decreased as the density of the texture elements decreased.

6. Both the general suppression and the orientation contrast effects appeared early in the population response to the stimuli. The general suppression effect took ~7 ms to develop, whereas the orientation contrast effect took 18–20 ms to develop.

7. These results are consistent with a possible functional role of V1 cells in the mediation of perceptual pop-out and in the segregation of texture borders. Possible anatomic substrates of the effects are discussed.

INTRODUCTION

Few surfaces in the natural visual environment are completely uniform in appearance. Rather, most surfaces contain local nonuniformities in color, luminance, motion, orientation, or other discernible characteristics. The statistical pattern of local variations across a surface is referred to as its visual texture. Textural information supplies our visual system with many important clues in determining such properties as the three-dimensional orientation of surfaces, their physical composition, and discontinuities between surfaces. As an illustration of the importance of texture cues in the natural world, the function of camouflage is to mimic the texture of the surrounding environment to escape detection by predators or prey.

Over the past decade, the study of visual texture has been

a fertile area of research in psychophysics. A major area of study has been the so-called pop-out effect, in which a subject must detect the presence, location, and/or identity of a target element embedded in a texture field of distractor elements (e.g., Bergen and Julesz 1983a,b; Treisman and Gelade 1980). If the target differs from the distractors in number or kind of certain elementary features, such as color or orientation, then human observers can effortlessly detect the presence of the target regardless of the number of distractors present. However, if the target differs from the distractors only in more complicated ways, such as in the conjunction of two elementary features, then observers must perform a serial, item-by-item search of the display to detect the presence of the target. The most common explanation of this result is based on a conceptual distinction between two modes of visual processing: a preattentive mode, which surveys the whole visual image in parallel and is sensitive to certain elementary features, and an attentive mode, which scans restricted regions of the visual image serially and is responsible for detailed visual analysis and precise form recognition (Beck 1972; Beck and Ambler 1973; Bergen and Julesz 1983a,b; Treisman and Gelade 1980). According to this explanation, when there is an area of contrast in elementary features in the image, the preattentive system detects it very quickly and automatically draws the window (or focus) of attention to that area. When there is no such contrast, then the observer must shift the window of attention serially over the individual elements until it happens to fall upon the target.

Although much is now known about the psychophysics of pop-out, little is known of the neurophysiological basis of this perceptual effect. To address this question, we recorded responses of neurons in area V1 of the alert monkey to textured stimuli modeled after those used in psychophysical experiments of pop-out. We wanted to determine whether the responses of cells in the primary visual cortex were correlated with the perceptual salience of an oriented target embedded in a textured background. There was reason to expect such a correlation, given that previous studies in anesthetized cats and monkeys have shown that gratings or textured stimuli containing orientation contrast often elicit greater responses than stimuli consisting of a uniform orientation field (Blakemore and Tobin 1972; DeYoe et al. 1986; Fries et al. 1977; Grinvald et al. 1989; Maffei and Fiorentini 1976; Nelson and Frost 1978; Van Essen et al. 1989). In the present study, our emphasis was on 1) determining the incidence of such cells and the magnitude of the effect in alert animals; 2) assessing spatial factors contributing to this effect; and 3) determining the time course of the

onset of the effect. We found that, at least qualitatively, the results in behaving monkeys were similar to those in anesthetized monkeys (DeYoe et al. 1986; Van Essen et al. 1989). Preliminary reports of some of these results have been published previously (Knierim and Van Essen 1989, 1990; Van Essen et al. 1989).

METHODS

Subjects and training

Two juvenile macaques (*Macaca fascicularis*) were used in these experiments. *Monkey 87A* was a female, ~2–3 yr old at the start of training, weighing ~3 kg. *Monkey 89C* was a male, ~2–3 yr old at the start of training, weighing ~3.5 kg. The monkeys were on a controlled water schedule in which they worked for their daily ration of fluid (apple juice or Tang) in their training or recording sessions. Supplemental water was given when appropriate to keep the monkeys in good health. The monkeys' physical condition was monitored by daily checks on skin condition, appetite, feces, and overall appearance. After the conclusion of these experiments, the animals were used for acute recording sessions in other experiments, after which they were given a lethal injection of pentobarbital sodium and perfused for subsequent histological analysis.

With the use of standard operant conditioning techniques, the monkeys were trained to fixate a spot of light for 4–6 s to obtain a juice reward. *Monkey 87A* was trained to detect a dimming of the fixation spot (Wurtz 1969). When the small fixation spot appeared on the computer screen, the monkey pressed a lever and fixated the spot to begin a trial. Eye position was monitored with the use of an infrared oculometer (Dr. Bouis, Karlsruhe, FRG, Bach et al. 1983). The monkey had to maintain fixation until the spot dimmed slightly, whereupon it had 500–600 ms to release the lever to obtain the reward. *Monkey 89C* was trained merely to fixate the spot of light. When the spot appeared, the monkey had 1500 ms to begin fixation to start a trial. The monkey had to maintain fixation until the spot disappeared, whereupon it was rewarded. Trials were terminated and no data were collected whenever the monkey broke fixation or, in the case of *monkey 87A*, released the lever outside the proper response window. Monkeys had to maintain fixation within a window of 0.5–0.6° radius around the fixation spot. Although this window is large relative to the size of V1 receptive fields, the size was necessary because of artifacts arising from extraocular sources near the eye (e.g., the oculometer's sensitivity to movements of the eyebrows and eyelids). We believe that the monkeys' actual fixation accuracy was much better than this, in part on the basis of the consistently strong responses of V1 neurons from trial to trial.

Surgical procedures

Surgeries were performed with the use of procedures described in detail elsewhere (Felleman and Van Essen 1987; Maunsell and Van Essen 1983), with the following modifications. All major surgeries were performed under anesthesia with halothane (2–4%) or, in one case, pentobarbital sodium (initial dose 8 mg/kg, supplemental doses as necessary), after initial injections of ketamine HCl (10 mg/kg), trifluromazine HCl (0.5 mg/kg), and atropine sulfate (0.01 mg/kg). Initial surgeries entailed the implant of a triangular head-holding post and a recording chamber in a position to enable easy access to opercular V1. Monkeys were given a minimum of 1 wk to recover before any training or recording sessions resumed.

After the monkeys were trained to accept head restraint and to fixate well, an additional operation was performed under ketamine and trifluromazine anesthesia to drill a hole in the skull

inside the recording chamber. This hole was typically 3–4 mm diam. It was at times necessary to perform additional minor operations under ketamine and trifluromazine (or, on one occasion, butorphanol tartrate, one-time dose of 0.1 mg/kg) to strip away the tough, fibrous layers of dura that grow by the exposed recording site, to drill new recording sites, or to perform minor repairs on the dental cement implants. Additional major surgeries were performed on each animal to switch the location of the recording chamber from one hemisphere to the other.

Data collection, visual stimulation, and analysis

Neuronal activity was recorded with glass-coated platinum-iridium wire (Frederick Haer) electrodes (1.5–5 MΩ, Wolbarsht et al. 1960). The electrode was advanced through the dura by means of a stepping motor microdrive (Caltech Central Engineering Services) mounted on a sealed chamber filled with sterile mineral oil. At the end of the recording session, the electrode and microdrive were removed and the chamber was disinfected with 0.05% chlorhexidine diacetate (Nolvasan Solution) or 0.3% hydrogen peroxide and gentamicin sulfate (Garamycin Ophthalmic Solution) before being sealed.

Neural signals were amplified and filtered with a differential amplifier, and single units were isolated and thresholded with a window discriminator (Bak Electronics). Spikes were collected at 1-ms resolution by an AT-compatible computer through a Lab Master interface (Scientific Solutions). Eye position was also digitized at 100 Hz and collected through the Lab Master. The PC monitored the behavior of the animal, determining when the lever was pressed and released, whether the monkey was maintaining good fixation, and whether the monkey performed each trial correctly. The PC controlled delivery of juice for reward through a custom interface with the juicer.

Visual stimuli were presented on a Masscomp Aurora Graphics terminal with a 19 in. noninterlaced 66-Hz color monitor, with the use of customized software initially developed at AT&T Bell Labs (Julesz et al. 1976; Sagi and Julesz 1985) and modified at Caltech. Once a cell was isolated, the borders of its classical receptive field (CRF) were determined by hand with the use of a computer-generated bar-shaped stimulus on a blank background. For the purpose of this study, the CRF was defined as the area of visual field within which a single bar of light could elicit an excitatory neuronal response. The four borders of the CRF were determined subjectively by listening to the electrode activity through the output of an audio monitor while moving a bar of light across the CRF and/or flashing the bar in and around the CRF. The size, shape, color, brightness, and motion of the bar could be varied by the experimenter. Once the borders of the CRF had been mapped, the optimal size and luminance contrast preference (i.e., white bar on black background or vice versa) of the bar were determined qualitatively, again by varying these parameters and listening to the audio monitor. In the majority of cells (87/122), the optimal orientation was determined in a quantitative computer analysis with the use of a single bar of the optimal size presented on a blank background for 500 ms at each of six orientations in pseudorandom order for three to five repetitions.

The basic texture stimulus used in our studies is illustrated in Fig. 1. A single bar was placed in the plotted CRF, and it was surrounded by four rings of bars oriented either orthogonally to the center element (as shown in the figure), identically to the center, or randomly. The cells were also tested with stimuli consisting of the center bar alone (with no surround rings) or the surround rings alone (with no center element in the CRF). The center bar was almost always placed in the center of the plotted CRF; on occasion it was displaced from the center if the most responsive region of the CRF was clearly offset from the CRF center. All of the surround bars were placed outside the borders of

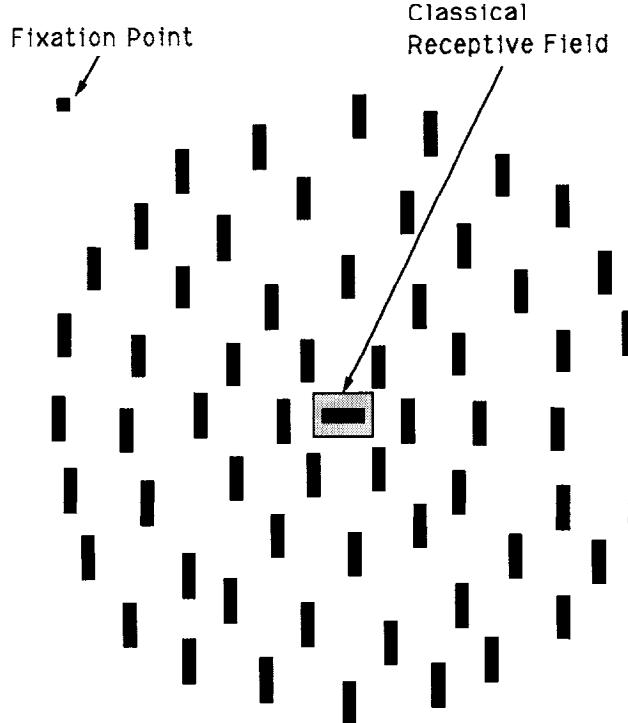


FIG. 1. Orientation contrast stimulus. A center bar is placed within the cell's CRF, and rings of elements are placed outside the CRF. For a uniform orientation stimulus, both center and surround elements have the same orientation.

the CRF. Each cell was tested with three to nine repetitions of the stimulus set. Each stimulus was presented for 500 ms.

Various parameters controlled the exact appearance of the stimulus. For almost all cells tested, stimuli were either white bars on a dark background or dark bars on a white background, depending on the preference of the cell. Bright bars were high contrast ($\sim 95\%$ Michelson contrast) relative to the dark background and were all of the same luminance. Because the relationship between luminance and line orientation on a raster monitor is complex, it was necessary to generate a lookup table that specified the video gun values associated with each element size and orientation to ensure that all elements were of equal luminance. Details of this procedure are given in Olavarria et al. (1992). Because of limitations of our graphics software, however, there were slight differences in the luminance associated with each bar orientation in the random orientation stimulus.

The height and width of the center bar were adjusted to approximately match the previously determined optimal stimulus size. The height was usually close to the size of the long axis of the CRF, whereas the width ranged from very thin "needles" to fat bars. The surround bars were always the same size as the center bar. The spacing between the surround bars was adjusted so that the innermost bars were close to the plotted borders of the CRF without actually encroaching on the borders, without eliciting any discernible neural response on their own (assayed subjectively by audio monitoring of neural activity), and without bars overlapping one another. The actual position of each surround bar was subject to a random positional jitter up to $\pm 10\%$ of the spacing between the centers of the bars to prevent luminance artifacts arising from geometric alignment of the bars.

Response rates were calculated for the 500-ms window starting 40 ms after stimulus onset to adjust for cortical response latencies. In addition, the mean spontaneous firing rate for the 500-ms period preceding the 500-ms response window was subtracted from

the neuronal response rate. We calculated various indexes (described in RESULTS) to quantify the effects of the texture surround. Statistical significance was assessed using *t* tests, which are appropriate because the indexes appear to be distributed fairly normally and because the *t* test is robust to moderate deviations from the normality assumption (Snedecor and Cochran 1967). We also performed nonparametric sign tests on all of the indexes, and all significant differences from the *t* test were confirmed at the $P < 0.05$ level by the nonparametric test (results not shown).

RESULTS

We recorded from a total of 170 cells in V1, most of them located on the operculum (eccentricity 2–6°) but a few in calcarine V1 (eccentricity 12–15°). Of these cells, we analyzed in detail the 122 neurons that gave significant responses to the stimuli, were well isolated, were confidently localized in V1, and were held long enough to collect data from at least three presentations of each texture stimulus. We found that the surrounding texture influenced the response to the center element in the large majority of these cells. The surround influences were almost always suppressive. We drew a distinction between two major types of surround suppression: 1) a general suppression, induced regardless of the orientation of the individual elements, and 2) various types of orientation-dependent suppression.

General suppression

Two examples of the general suppression induced by the texture surround are shown in Fig. 2. The cell illustrated in Fig. 2A was almost completely suppressed by the texture surrounds. Figure 2A, top, shows the cell's mean firing rate (+1 SE) to the different stimuli. Below that are peristimulus time histograms, in which the stimulus presentation time is indicated by the bar beneath the histogram. The icons below the histograms indicate the stimulus configurations. Note that these icons are simplified versions of the real stimuli, one of which was illustrated in Fig. 1. The stimulus set consisted of a single center element at the optimal orientation for that cell (Configuration 1: C) and a center element oriented orthogonally to the optimal orientation (Configuration 5: C'); a uniform orientation texture in which the elements in the center and surround are oriented identically (Configuration 2: C=S and Configuration 6: C'=S'); an orientation contrast texture in which the elements in the surround are oriented orthogonally to the center element (Configuration 3: C≠S and Configuration 7: C'≠S'); and the surround elements alone, with no element encroaching upon the cell's CRF (Configuration 4: S and Configuration 8: S').

This cell had an orientation bias when presented with a single element in its CRF (C vs. C'). The surround elements alone (S and S') did not affect the firing of the cell at all. However, when the surround elements were presented along with the center element, they caused a nearly total suppression of the cell's response (C=S, C≠S, C'=S', C'≠S'). Thus, for this cell, elements outside the CRF that had no effect when presented alone had a strong modulatory effect on the response to an element within the CRF. Both the optimally oriented center bar and the orthogonal bar were suppressed to a comparable degree.

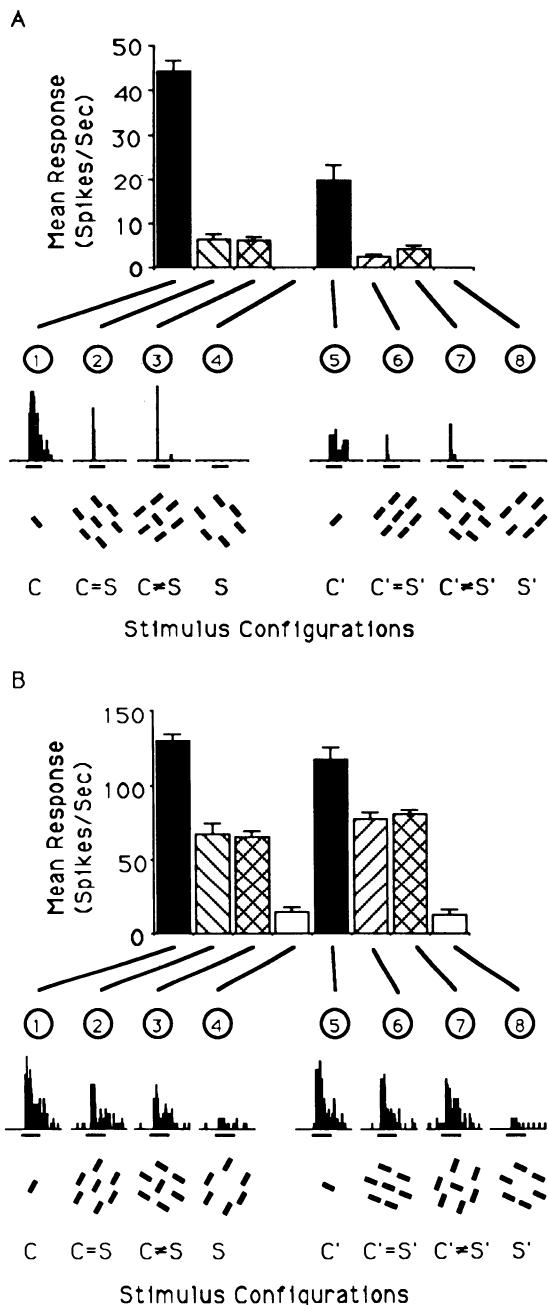


FIG. 2. Examples of cells showing a general suppression effect. *A*: orientation-biased cell with a strong suppressive effect of surround texture. *Cell 89c4A*. *B*: orientation-insensitive cell with a moderate surround suppression. *Cell 87a93B*.

Another example is shown in Fig. 2*B*. This cell had no orientation preference at all (*C* vs. *C'*). The surround elements presented in conjunction with the center element once again suppressed the firing of the cell, even though the surround elements alone (*S* and *S'*) had a small but significant excitatory influence on the cell. All of the surround elements were located outside the plotted CRF. Such small excitatory influences from the surround textures presented alone were seen on occasion (see also Fig. 15); however, when they had any influence on the response to the center element, it was almost always suppressive.

We quantified the amount of general suppression in-

duced by the texture background by computing a general suppression index (GSI) for each cell. We first calculated an average suppression index (ASI) for the optimal center orientation based on the responses (above background activity) to the center element alone (R_C) and to the contrast and uniform textures ($R_{C=S}$, $R_{C=S'}$)

$$ASI = 1 - \frac{\text{Average}(R_{C=S}, R_{C=S'})}{R_C}$$

An analogous index (ASI') was calculated for the orthogonal center element (*C'*). The GSI was then calculated from the two ASIs after weighting by the response to the center element alone:

$$GSI = -\frac{R_C(ASI) + R_{C'}(ASI')}{R_C + R_{C'}}$$

Thus the GSI for a cell represents the average fractional suppression induced by the texture backgrounds relative to the responses to the center elements alone, reversed in sign so that suppression is negative and enhancement is positive. A high positive GSI indicates that the cell's response was highly enhanced by the texture background (1.0 indicating a 100% increase); a high negative GSI indicates that the cell's response was highly suppressed by the texture surround (-1.0 indicating 100% suppression); and a value of 0 indicates no net effect of the texture surrounds. The GSIs for the cells illustrated in Fig. 2 are -0.85 (*A*) and -0.42 (*B*).

Figure 3 shows the distribution of GSIs for the sample of 122 cells. The mean GSI was -0.34, which is highly statistically different from 0 (2-tailed *t* test, *t* = 11.33, *P* < 0.001). Thus, on average, the presence of a texture background suppressed V1 cells by 34%.

Orientation-dependent suppression

For 41% of the cells, there was a significant difference in the amount of suppression induced by the two different texture backgrounds. Importantly, the great majority of these cells fired more strongly in response to the orientation contrast texture than in response to the uniform orientation texture. Examples of these cells are shown in Fig. 4. The cell in Fig. 4*A* showed no orientation selectivity for the center

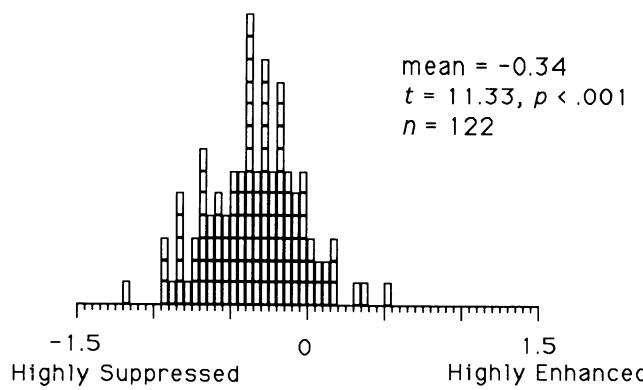


FIG. 3. Distribution of general suppression index (GSI). -1.0 indicates 100% suppression; +1.0 indicates 100% enhancement. A value surpassing -1.0 can result from response suppression below the baseline activity for that cell. The average amount of suppression is 34%.

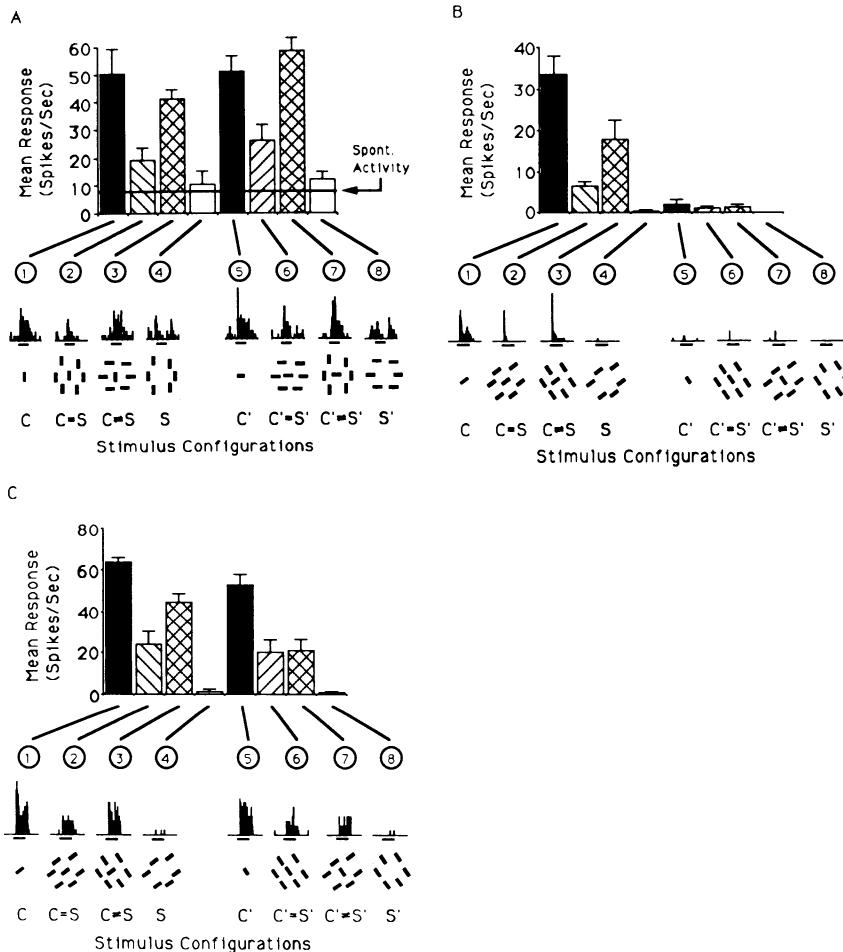


FIG. 4. Examples of cells showing an orientation contrast effect, where the response to the orientation contrast stimulus is greater than the response to the uniform orientation stimulus. *A*: orientation-insensitive cell showing a strong orientation contrast effect for both center orientations. For this cell, there is no suppression induced by the orientation contrast stimulus. *Cell 87a30A*. *B*: strongly orientation-selective cell showing a fairly strong orientation contrast effect for the responsive center orientation. Both contrast and uniform stimuli suppress the response, but suppression is greater for the uniform stimulus. *Cell 89c8A*. *C*: orientation-insensitive cell showing a moderate orientation contrast effect for one center orientation and a general suppression effect for the other. This pattern was typical for those cells classified as orientation contrast. *Cell 89c37A*.

element alone (C vs. C'). When the center element was surrounded by identically oriented elements ($C=S$, $C'=S'$), the cell's response was strongly suppressed. However, when the surround elements were oriented orthogonally to the center element ($C \neq S$, $C' \neq S'$), there was no significant suppression. For both center orientations, the cell fired more strongly to the orientation contrast texture than to the uniform orientation texture. Note that the amount of suppression did not depend on the absolute orientation of the surround elements: vertical surround elements suppressed the response to a vertical center bar, whereas horizontal surround elements suppressed the response to a horizontal center bar. Thus this cell's firing rate was dependent on orientation contrast, regardless of the absolute orientations of the individual elements.

Another example is shown in Fig. 4*B*. This cell was highly orientation selective for the center element alone (C vs. C'). Both the uniform orientation texture and the orientation contrast texture elicited weaker responses than the center element alone. However, the suppression induced by the uniform texture ($C=S$) was significantly greater than that induced by the contrast texture ($C \neq S$). Figure 4*C* shows a third example of orientation-dependent suppression. Like the cell in Fig. 4*A*, this cell was not selective for the orientation of the center element alone. It showed an orientation-dependent surround suppression for one of the center orientations ($C=S$ vs. $C \neq S$) but showed a general

suppression for the orthogonal center orientation ($C'=S'$ vs. $C' \neq S'$). This was a common result. The three cells in this figure show what we call an orientation contrast effect; that is, for at least one center orientation, they fire more strongly to an orientation contrast texture than to a uniform orientation texture. Of the 39 cells that showed an orientation contrast effect, 31 (80%) showed the effect for only one of the center orientations, either because the cell was highly orientation selective for the center element alone (as in Fig. 4*B*) or because it just did not show the effect for one of the two center orientations (as in Fig. 4*C*). The remaining eight cells (20%) had an orientation contrast effect for both center orientations (as in Fig. 4*A*).

To quantify the orientation-dependent suppression between the two different texture backgrounds, we calculated for each cell a differential suppression index (DSI). We first calculated a differential firing rate (DF) between the responses (above background activity) to the orientation contrast and uniform orientation textures ($R_{C \neq S}$, $R_{C=S}$) relative to the response (above background) to the optimally oriented center element alone (R_C):

$$DF = \frac{R_{C \neq S} - R_{C=S}}{R_C}$$

An analogous differential firing rate (DF') was calculated for the orthogonally oriented center element (C'). The dif-

ferential suppression index was calculated as the weighted average of the DFs for each center element orientation:

$$DSI = \frac{R_C(DF) + R_{C'}(DF')}{R_C + R_{C'}}$$

Thus the DSI indicates the difference in the response rates to each texture stimulus as a fraction of the response to the center elements alone. A high positive DSI indicates that the response to the orientation contrast texture was much stronger than the response to the uniform orientation texture (a value of 1.0 indicates the difference in responses was equal to the response to the center element alone); a high negative value indicates that the response to the uniform orientation texture was much greater than the response to the orientation contrast texture; a value of 0 indicates no difference in the responses between the two textures. The DSIs for the examples in Fig. 4 are 0.62 (*A*), 0.33 (*B*), and 0.18 (*C*).

Figure 5*A* shows the distribution of DSIs for the sample. The mean DSI for the sample was 0.09, which shows that, on average, cells in V1 responded more strongly to the orientation contrast texture than to the uniform orientation texture, by an average of 9% of the responses to the center elements alone. This average is highly statistically different from 0 (2-tailed *t* test, $t = 4.50$, $P < 0.001$). Figure 5, *B* and *C*, breaks the sample down into two populations: cells like those in Fig. 4 that showed a statistically significant orientation contrast effect (Fig. 5*B*; see next section) and the remaining cells in the sample (Fig. 5*C*). The mean DSI for the orientation contrast cells was 0.28 (2-tailed *t* test, $t = 7.00$, $P < 0.001$); for all other cells, the mean DSI was 0.

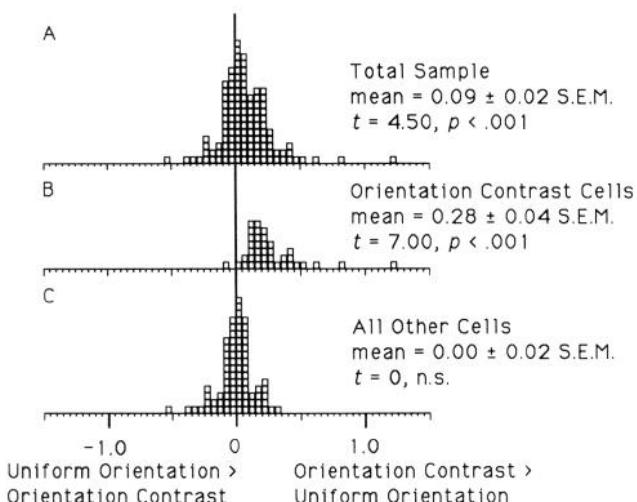


FIG. 5. Distribution of differential suppression index (DSI). *A*: distribution for the entire sample of 122 cells. Overall, the average suppression induced by the uniform surround was ~10% greater than the suppression induced by the contrast surround. *B*: distribution for the 39 cells classified as orientation contrast. For these cells, the average difference in suppression was almost 30%. The 1 negative value for this group resulted from a cell that had a small but statistically significant orientation contrast effect for 1 center orientation and a large but statistically insignificant uniform orientation effect for the other orientation. *C*: distribution for all cells except the 39 orientation contrast cells. For these cells, on average, there was no difference in suppression between the uniform and contrast surrounds.

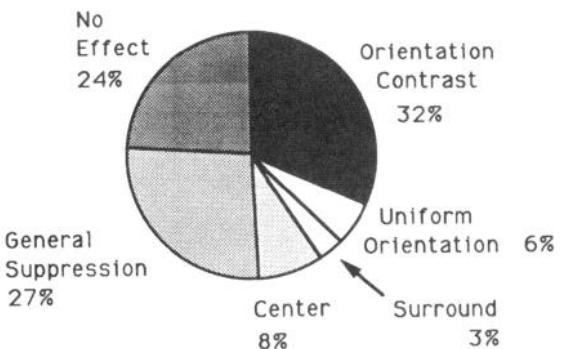


FIG. 6. Breakdown of sample into 6 cell classes. The detailed rules for classifying cells are as follows: a cell was regarded as responding differently to 2 stimuli if the mean + 1 SE for the less effective stimulus was smaller than the mean - 1 SE for the more effective stimulus. If a cell had an orientation selectivity index (1 - orthogonal/preferred) for the center elements alone >0.7, then the cell was classified according to the pattern of responses for the preferred center orientation only. If the orientation selectivity index was <0.7, the response patterns for both center orientations were considered. 1) Cells were classified as *orientation contrast* if the response to the orientation contrast pattern was larger than the response to the uniform orientation pattern for at least 1 center orientation. The 1 exception is when the response to the uniform orientation pattern was stronger than the response to the orientation contrast pattern for the orthogonal center orientation; in this case, the cell would be classified as *surround-dependent*, for the magnitude of the surround effect depends on the absolute orientation of the surround, rather than on orientation contrast per se. 2) Cells were classified as *uniform orientation* if the response to the uniform orientation texture was larger than the response to the orientation contrast texture for at least 1 center orientation. The same exception applies with regard to a surround-dependent effect. 3) Cells were classified as *general suppression* if the responses to both texture patterns were smaller (or, in very rare cases, larger) than the response to the center element alone but did not differ from one another. This pattern had to hold true for both center orientations. If the responses to the texture patterns were the same as the response to the center bar alone for the orthogonal center orientation, then the cell was classified as *center-dependent*. If the cell was orientation selective (index >0.7), it was classified as general suppression rather than center-dependent. 4) Cells were classified as *no effect* if responses to texture patterns were the same as the response to the center element alone for both center orientations.

Because the comparisons were based on a range of values for each stimulus (mean ± 1 SE), transitivity of the response relationships did not always hold. In some cases, for example, the response to the uniform texture would be smaller than that to the center bar alone, but the response to the orientation contrast texture would be statistically the same as that to the uniform orientation texture and the center bar alone. To classify these cells, we took the average of the mean + 1 SE for the 2 texture stimuli and compared that to the mean - 1 SE for the center bar alone. If the mean texture value was smaller than the center bar alone, the cell was classified as general suppression; otherwise, it was classified as no effect.

Categorization of response patterns

To illustrate the distribution of response patterns elicited by the overall population of cells, we grouped the cells into six response categories. We do not presume that this classification represents a natural functional division of cell types in the cortex; it may well be that the range of responses to these stimuli forms a continuum. Nonetheless, this scheme is a useful way of describing the main effects encountered and the relative frequency of the different effects in the population. Figure 6 shows the incidence of cells in the six groups, on the basis of the relationship of the responses to the two texture patterns and the center bar alone.

1) General suppression: for 33 cells (27%), the response to each texture pattern was significantly less than the re-

sponse to the center bar alone, but the texture responses were not significantly different from each other (cf. Fig. 2).

2) Orientation contrast: For 39 cells (32%), the response to the orientation contrast texture was significantly greater than the response to the uniform texture for at least one of the center bar orientations (cf. Fig. 4). In most cases, both texture backgrounds suppressed the firing rate somewhat, but the magnitude of the suppression was different. In other cases, only the uniform orientation texture surround elicited a significant suppression, whereas the orientation contrast texture surround produced no effect.

3) No effect: For 29 cells (24%), the responses to both texture conditions were statistically indistinguishable from the response to the center element alone.

These were the three main types of responses found, accounting for 83% of the cells studied. The other cells were classified as follows:

4) Center-dependent suppression: For 10 cells (8%), both texture surrounds suppressed the response to one of the center bar orientations equally, but did not affect the other center bar orientation.

5) Surround-dependent suppression: For four cells (3%), the cell showed a differential suppression for each center orientation, but for one center orientation the orientation contrast texture was the stronger response, whereas for the orthogonal center orientation the uniform texture response was the stronger. Thus, for these cells, the surround suppression depended on the absolute orientation of the surround, rather than on the presence or lack of orientation contrast.

6) Uniform orientation: For seven cells (6%), the response to the uniform orientation texture was significantly greater than the response to the orientation contrast texture for at least one of the center orientations. Only one of these cells showed more than a modest effect, though.

Thus, of the cells showing an orientation-dependent suppression (orientation contrast, uniform orientation, and surround-dependent suppression), the great majority (39/50) were orientation contrast cells. The responses of these cells to different texture patterns correlate with the perceptual salience of the center element; that is, they fired more strongly when there was a contrast in orientation between the center and surround.

Random orientation surround

As a whole, cells in V1 respond more strongly to an orientation contrast texture than to a uniform orientation texture. We tested 50 cells in monkey 89C with an additional texture pattern in which each background element was oriented randomly at one of six orientations (Fig. 7). This stimulus was similar to the uniform orientation texture in that there was no systematic difference in orientation between the center element and the surround elements. In the uniform orientation texture, the center element was merely one of many identically oriented elements; in the random orientation texture, the center element was merely one of many randomly oriented elements. Because in both cases there was no systematic contrast between the center element and the pattern of orientation in the surround, we refer to both of these stimuli as noncontrast textures. We

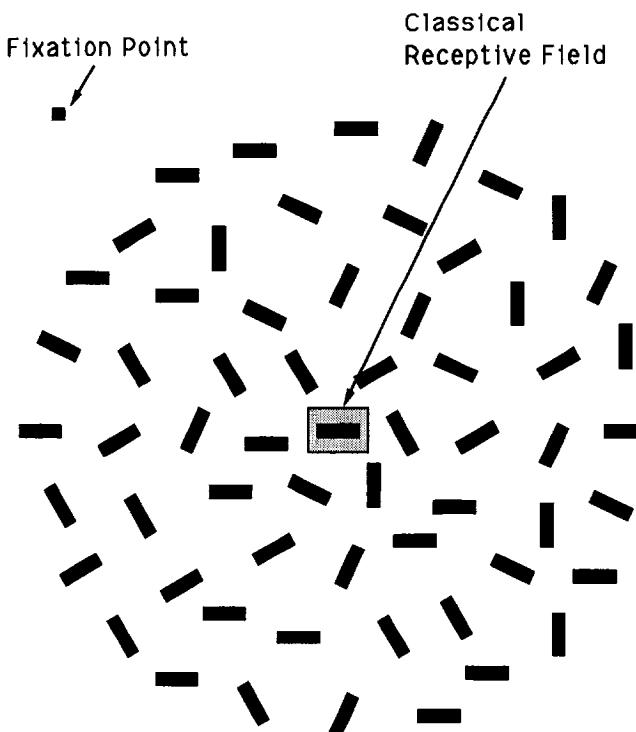


FIG. 7. Random orientation texture stimulus.

wondered how much the random orientation surround would suppress responses to a center element, and whether a comparison between responses to the orientation contrast pattern and the random orientation pattern would show an orientation contrast effect similar to that shown in the comparison between the orientation contrast texture and the uniform orientation texture (that is, greater responses to the contrast texture than to either noncontrast texture).

To quantify the difference in responses elicited by the orientation contrast and random orientation textures, we calculated an index analogous to the DSI by the use of the values from the random orientation texture in place of the uniform orientation texture in the DSI formula (see Fig. 8 legend). The distribution of this random orientation differential suppression index (RODSI) is shown in Fig. 8A. The distribution of DSIs for the same 50 cells is shown in Fig. 8B. Although the mean DSI for this subset of cells was smaller than that for the whole sample, the difference is not statistically significant (2-tailed t test, 50 cells in Fig. 8B vs. 72 remaining cells in sample, $t = 0.68$, NS). A comparison of Fig. 8A with Fig. 8B shows that the distributions of DSI and RODSI are statistically indistinguishable. The mean RODSI value was 0.06, which was significantly larger than 0 (2-tailed t test, $t = 3.00$, $P < 0.05$). Thus, on average, cells were suppressed more strongly by the random orientation texture than by the orientation contrast texture. The average difference in suppression was 6% of the firing to the center element alone. For these cells, there was no average difference in responses to the uniform or the random textures.

When one compares the values of DSI and of RODSI for those cells that showed a statistically significant orientation contrast effect (these cells are shaded dark in Fig. 12), there was no statistically significant difference in the means

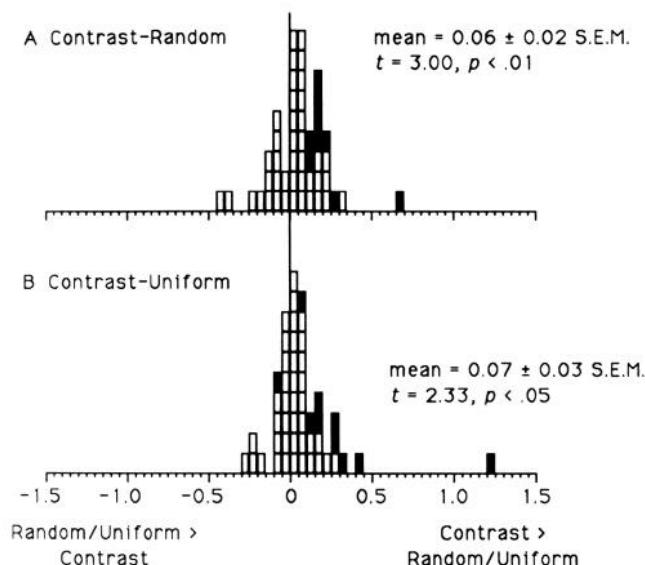


FIG. 8. Distributions of random orientation differential suppression index (*A*) and differential suppression index (*B*) for 50 cells tested with the random orientation texture. RODSI was calculated with the use of the following equations: $DF = (R_{C+S} - R_R)/R_C$ and $RODSI = [R_C(DF) + R_C(DF')]/(R_C + R_C')$. See text description of DSI for details. The distributions for both RODSI and DSI are statistically >0 . The dark shading indicates those cells classified as orientation contrast (*A*: C > R; *B*: C > U). The 1 negative orientation contrast cell in *B* resulted from a cell that had a small but statistically significant orientation contrast effect for 1 center orientation and a large but statistically insignificant uniform orientation effect for the other orientation.

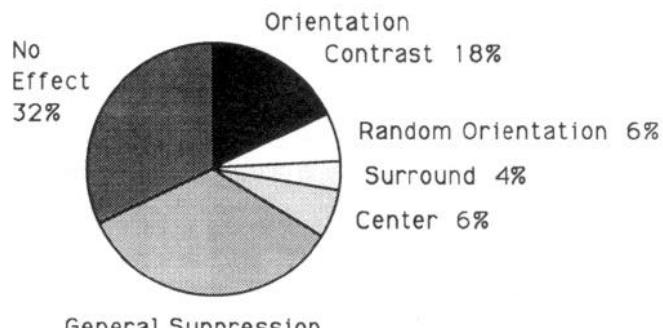
(mean DSI = 0.30 ± 0.11 SE; mean RODSI = 0.24 ± 0.06 SE; 2-tailed *t* test, *t* = 0.54, NS). Thus the random orientation texture did not differ from the uniform orientation texture in suppressing the responses of these cells; each non-contrast texture suppressed the response more strongly than the orientation contrast texture.

We classified these cells into groups analogous to those described above for the comparison between the orientation contrast and uniform orientation textures. These results are shown in Fig. 9*A*. Of the 50 cells tested, 9 (18%) responded more strongly to the orientation contrast texture than to the random orientation texture. Only three (6%) responded more strongly to the random orientation texture. Roughly equal numbers of cells were generally suppressed by both textures (17/50, 34%) or were not affected by either texture (16/50, 32%). Figure 9*B* shows the cell groups on the basis of the comparison with the uniform orientation texture. A comparison of the two pie charts shows that there are nearly equal numbers of cells in each category. These results show that a surround of randomly oriented elements is just as effective as a surround of elements oriented identically to the center in suppressing the response to the center element, even though in the random stimulus only $\frac{1}{6}$ of the elements are oriented identically to the center element and the other $\frac{5}{6}$ are oriented differently. The important attribute of the stimuli appears to be the overall lack of a systematic contrast in orientation between the center and the surround elements.

CELL-BY-CELL COMPARISONS. One question that arises from these results is whether there might be a population of cells specialized for signaling orientation contrast in general, or

whether some cells show an orientation contrast effect under certain stimulus conditions and not under others. Of the 50 cells tested with all three texture patterns, 16 showed an orientation contrast effect for at least one pair of surrounds. Of these, seven showed the effect only with the uniform texture, six showed it only with the random orientation texture, and only three showed a significant orientation contrast effect when the orientation contrast texture was compared with both of the noncontrast textures. Overall, only about half of the cells studied (28/50, 56%) were classified identically when the contrast texture was compared with either noncontrast texture. Of these 28 cells, 23 were classified as general suppression or no effect. Thus cells that were suppressed equally by any texture background and cells unaffected by textures tended to maintain these properties under different stimulus conditions. Cells showing any kind of orientation-dependent suppression induced by the texture backgrounds had variable response properties that depended on the exact stimulus conditions. These cells jumped categories from one comparison (contrast vs. uniform) to the other (contrast vs. random) in no orderly fashion. This was especially true for the orientation contrast cells. Thus cells do not appear to act as general orientation contrast detectors in their responses to these stimuli. There is a great deal of heterogeneity at the individual cell level in the responses to the contrast and noncon-

A Orientation Contrast vs. Random Orientation



B Orientation Contrast vs. Uniform Orientation

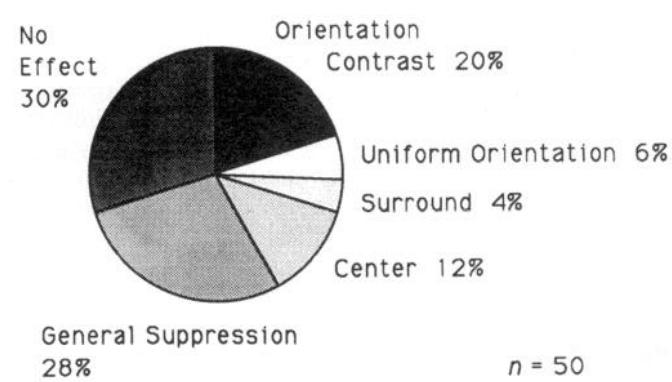


FIG. 9. Breakdown of sample of 50 cells tested with random orientation texture into cell classes on the basis of orientation contrast vs. random orientation response comparison (*A*) and orientation contrast vs. uniform orientation response comparison (*B*).

trast patterns. However, at the population level, the individual cell responses add up to form a picture that is consistent with perceptual salience (i.e., overall stronger responses to patterns with orientation contrast than to patterns lacking such contrast). How much of the individual cellular variability is due to real functional differences between cells and how much merely reflects inherently noisy neuronal responses is unclear.

Normalized population responses

To provide a picture of how the population responded as a whole to the different texture configurations, we first normalized each cell's responses to that obtained for the optimally oriented center bar alone. Thus the response to the center bar alone (Configuration 1) always had a value of 1, and the responses to all other configurations were a fraction of that. We then calculated the mean normalized response rate for each configuration over the sample, and the results are shown in Fig. 10. The right side of the figure shows the normalized responses for the whole sample of 122 cells. The responses to Configurations 2 and 3 (uniform orientation and orientation contrast) were clearly suppressed in relation to Configuration 1 (center bar alone), by an average of about 30%. In addition, the response to the orientation contrast texture was significantly greater than the response to the uniform orientation texture, by about 10% of the response to the center element alone. The two graphs on the left break the sample down into the 39 cells showing a significant orientation contrast effect and the remainder of the sample. The orientation contrast cells showed a larger difference between the uniform texture and the contrast texture (~30%) than did the total sample. The other cells

showed an overall general suppression of ~30% but no significant difference between the two texture patterns. Overall, V1 was suppressed by the presence of surround textures, and because of the presence of some cells that showed a large orientation contrast effect, the response of V1 as a whole to an orientation contrast texture was significantly larger than its response to a uniform orientation texture (paired t test, $t = 5.32, P < 0.001$).

Figure 11 shows a similar analysis for the 50 cells tested with the random orientation texture. The format of these graphs is similar to Fig. 10, except that the random orientation responses (Configurations 3 and 8) have been inserted between the responses to the uniform and contrast textures. The right side of the figure shows the mean normalized responses to all texture patterns for the whole subsample. The overall general suppression induced by all three texture surrounds was ~25–30%. The difference in responses between the uniform texture (Configuration 2) and the contrast texture (Configuration 4) was statistically significant (paired t test, $t = 3.00, P < 0.01$) and did not differ statistically from the response difference for the whole sample (Fig. 10). The difference between the random orientation texture (Configuration 3) and the contrast texture (Configuration 4) was somewhat smaller, and it barely missed statistical significance at the .05 level (paired t test, $t = 2.00, P < 0.10$). There is no significant difference between the uniform texture and the random orientation texture. The orientation contrast effects are more apparent when the sample is broken down on the *left* of the figure. The *top* graph illustrates the nine cells that showed a significantly greater response to the contrast texture than to the random orientation texture (the orientation contrast cells of Fig. 9A). The

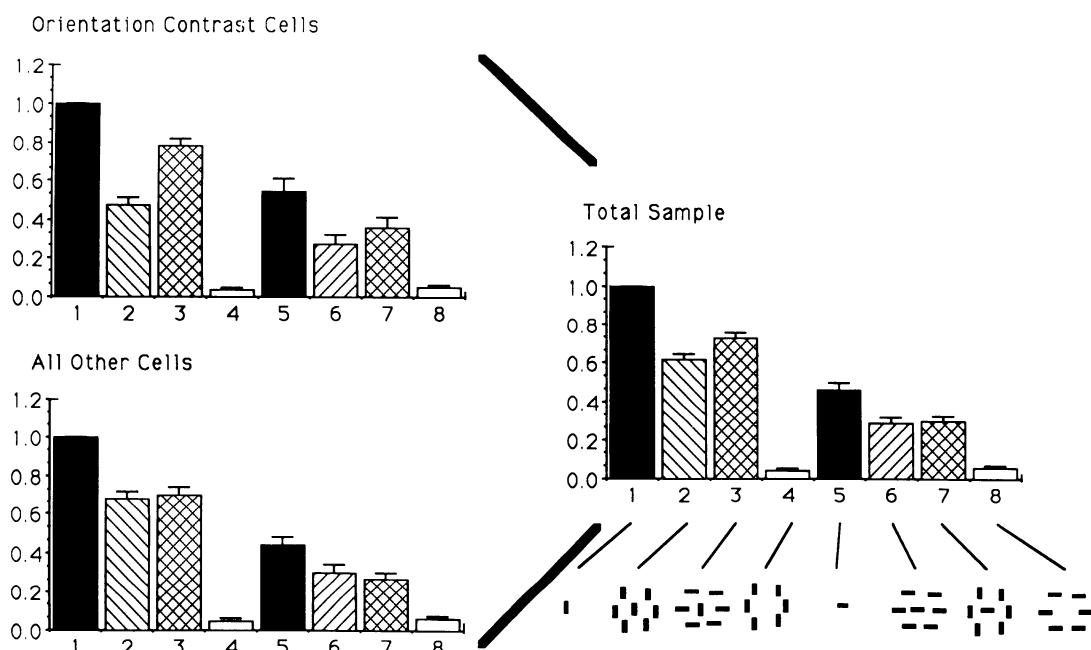


FIG. 10. Normalized population responses. Each cell's response pattern was normalized to the cell's response to the optimally oriented center bar alone. The *right* of this figure shows the mean normalized responses for the whole sample of 122 cells. A large general suppression and modest but significant orientation contrast effect are evident for the population when comparing Configurations 1, 2, and 3. The left side of the figure breaks the sample down into the 39 cells classified as orientation contrast and the remainder of the sample. The former cells show a much more pronounced orientation contrast effect than does the population as a whole.

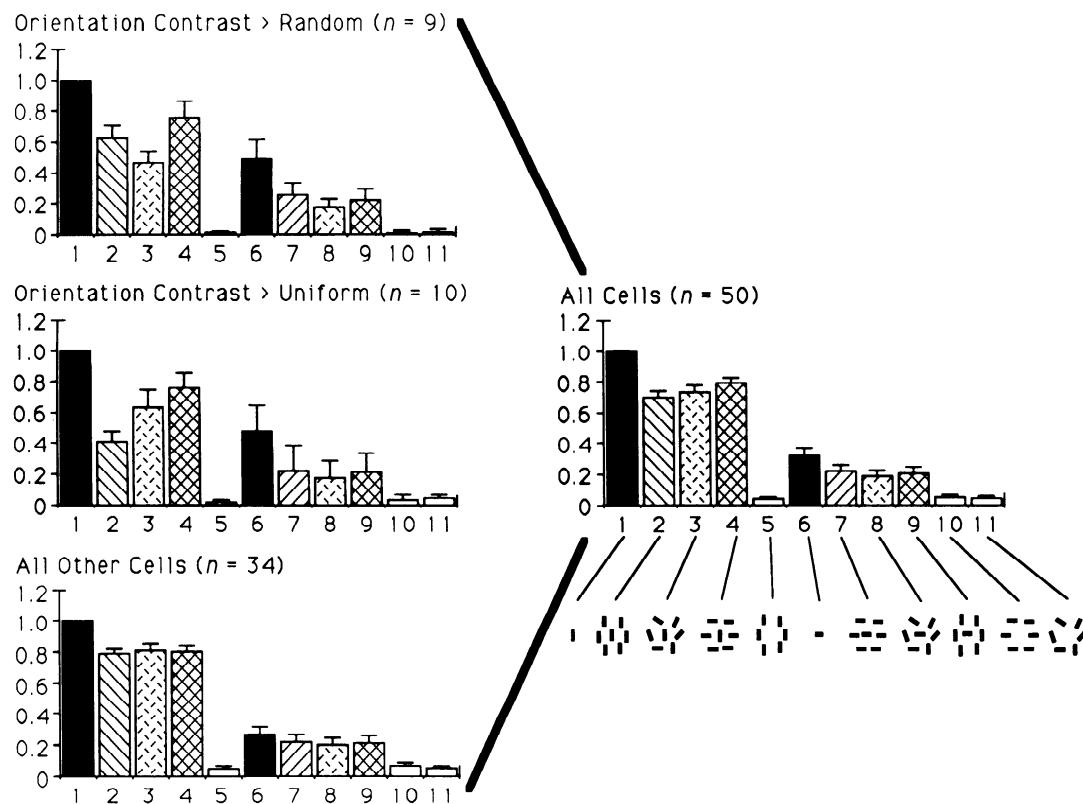


FIG. 11. Normalized population responses for the 50 cells tested with the random orientation stimulus. The responses for the whole sample of 50 cells is shown on the right. A small but statistically significant orientation contrast effect is evident between the orientation contrast pattern (Configuration 4) and the uniform orientation pattern (Configuration 2); the comparison between the orientation contrast pattern and the random orientation pattern (Configuration 3) barely missed significance. The left of the figure breaks the sample down into those cells that show a contrast vs. random orientation contrast effect (top), those cells that show a contrast vs. uniform orientation contrast effect (middle—includes 3 cells that are also represented in top), and the remainder of the sample (bottom).

middle graph illustrates the 10 cells that showed a significantly larger response to the orientation contrast texture than to the uniform orientation texture (the orientation contrast cells of Fig. 9B). Three cells are shared by both groups. The bottom graph illustrates the 34 remaining cells. These graphs illustrate that V1 as a whole responded more strongly to an orientation contrast pattern than to either noncontrast pattern. This population effect is due to the presence of two moderately overlapping populations of cells that showed a much stronger suppression to either the random orientation texture or the uniform orientation texture than to the orientation contrast texture.

Spatial organization of surround effects

We tested all 122 cells with texture patterns covering only a portion of the surround to ascertain whether the suppressive effects originated from surround regions at the ends of the center bars (by a mechanism similar or identical to end-stopping), from surround regions along the flanks of the center bars (by a mechanism similar or identical to side-band suppression), or from both sets of surround regions. Examples of the stimuli are shown in Fig. 12. To test the contribution of the flanking regions, we placed the surround elements only in the two quadrants at the sides of the center bar, leaving the end-zone quadrants blank (Fig. 12A); to test the contribution of the end-zone regions, we

placed the surround elements only in the quadrants at the ends of the center bar, leaving the flanking regions blank (Fig. 12B). Figure 13 shows the normalized population responses to the full-field texture and the two sets of surround quadrants. The whole population is shown in A and the subpopulation of orientation contrast cells is shown in B. For simplicity, we have only illustrated the results for the optimally oriented center element. To quantify the surround effects, we calculated a GSI and a DSI for each set of surround quadrants with the use of the response rates for both the optimally oriented and orthogonally oriented center elements; these indexes are analogous to those computed previously for the full texture surround.

Figure 13A shows that both the flanking quadrants (Configurations 5 and 6) and the end quadrants (Configurations 7 and 8) suppressed the response to the center element by an average of $\sim 25\%$ (flank GSI = -0.24 , $t = 8.00$, $P < 0.001$; end GSI = -0.26 , $t = 13.00$, $P < 0.001$). The amount of general suppression did not differ between the two sets of quadrants, but each was significantly smaller than the general suppression induced by the full-field texture, which was $\sim 35\%$ [paired t tests; t (flank, end) = 1.50 , NS; t (full, flank) = 5.00 , $P < 0.001$; t (full, end) = 7.00 , $P < 0.001$]. Thus each set of quadrants contributed substantially and equally to the overall general suppression induced by the texture surround, but each individual contribution was less than the effect of the full-field surround.

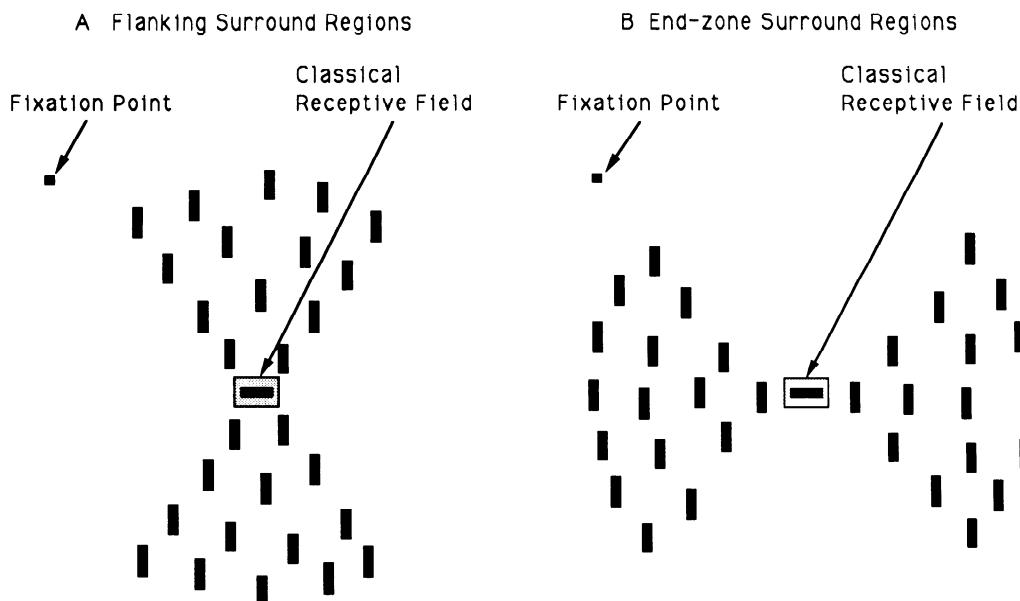


FIG. 12. Surround quadrant stimuli. *A*: stimulus in which the surround texture elements are restricted to quadrants along the flanks of the center bar. *B*: stimulus in which the surround texture elements are restricted to quadrants at the ends of the center bar.

Just as with the general suppression effect, the size of the orientation contrast effect was also equal for the two sets of quadrants, ~8–9% (Configurations 5 vs. 6, 7 vs. 8). The mean DSI for each set was significantly greater than 0 [$t(\text{flank}) = 4.00, P < 0.001$; $t(\text{end}) = 4.50, P < 0.001$], but there was no significant difference between the two. However, unlike the general suppression effect, the full-field orientation contrast effect (Configurations 2 vs. 3) was no stronger than that for either set of quadrants. For the subset of 39 cells that were classified as orientation contrast cells, though, the picture is rather different (Fig. 13*B*). Although both sets of quadrants again showed a significant degree of orientation-dependent suppression for these cells, the size of the orientation contrast effect induced by the end-zone quadrants (end DSI = 0.17, $t = 5.67, P < 0.001$) was roughly twice that induced by the flanking quadrants (flank DSI = 0.09, $t = 3.00, P < 0.01$); this difference was statistically significant (paired t test, $t = 2.67, P < .02$). Moreover, the size of the orientation contrast effect for the full-field texture (full-field DSI = 0.28, $t = 8.00, P < 0.001$) was roughly an additive combination of the two sets of quadrants. The population responded identically to all contrast patterns (Configurations 3, 6, and 8), at ~80% of the response to the center element alone (Configuration 1). However, the response to the end surround uniform pattern (Configuration 7) was smaller than that to the flank surround uniform pattern (Configuration 5) and the response to the full-field uniform pattern (Configuration 2) was smaller than the responses to either subregion uniform pattern (Configurations 5 and 7). Thus the increased orientation contrast effect of the full-field surround over either set of quadrants was due to an increased suppression of the uniform pattern, whereas the suppression to each contrast texture did not change. It appears that, on average, the orientation contrast effect originated significantly from both sets of quadrants, but more strongly from the end-zones. In

addition, the orientation contrast effect was stronger for the full-field texture than for either set of quadrants alone.

To test further the relationship between end-stopping and the texture surround effects reported here, we tested 10 cells with a conventional end-stopping test, in which we recorded responses to an optimally oriented bar of different lengths centered in the cell's CRF. The length of the bar was varied in six equal steps ranging from less than the length of the CRF to 5–15 times the CRF length. We calculated an end-stopping index (ESI) for each cell, defined as $1 - (\text{response to the longest bar} / \text{response to the optimal length bar})$. A high value indicates a large end-stopping effect; a small value indicates little end-stopping. There was a significant correlation between a cell's ESI and its GSI ($r = .65, P < 0.05$), but no significant relationship between its ESI and its DSI ($r = -.14, \text{NS}$). This analysis supports the probable contribution of end-stopping to the general suppression effect of the texture surround. Informal observations on an additional 13 cells reinforced the lack of a correlation between the orientation contrast effect and the strength of conventional end-stopping, indicating that although end-stopping may make an important contribution to the orientation contrast effect in some cells, it is not sufficient to explain the results in all cells.

CELL-BY-CELL VARIABILITY. Although the preceding analysis of the population mean GSIs and DSIs shows a clear and consistent picture of the separate contributions of the two surround subregions and their effects relative to the full-field surround, there was considerable cell-by-cell variability in the relative contribution of each set of quadrants to the texture surround effects. Only 53/122 cells (43%) had consistent response patterns for all three surround textures with the optimally oriented center bar in the CRF. For the remaining cells, only the response pattern for the flank or neither, or neither, was consistent with the full-field

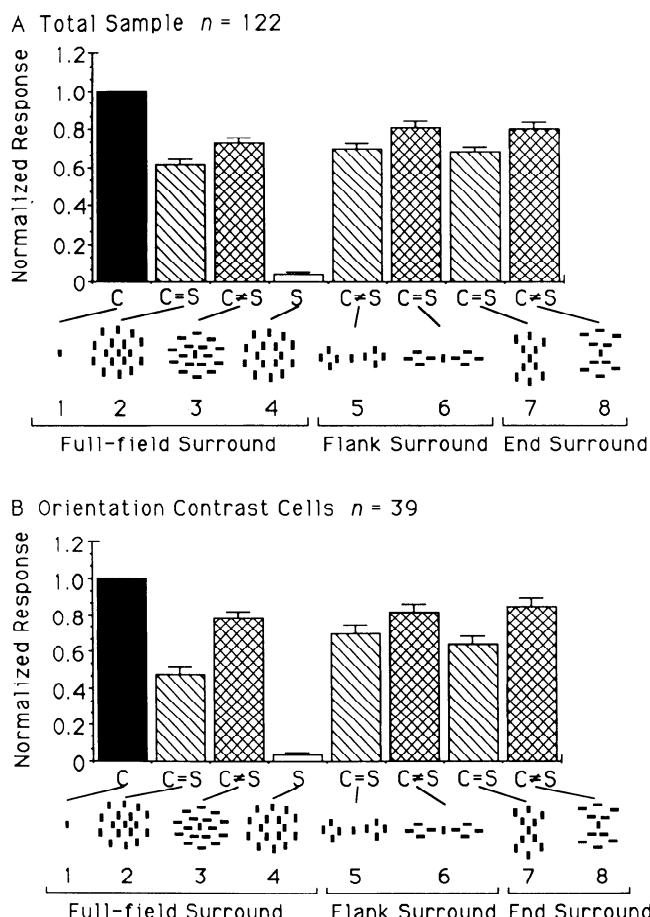


FIG. 13. *A*: normalized population responses for the full-field surround and the 2 sets of surround quadrants. On the population response level, both sets of quadrants contribute equally to both the general suppression effect and the orientation contrast effect. *B*: normalized population responses for the 39 cells classified as orientation contrast. For this subset of cells, the orientation contrast effect is stronger in the end-zones than in the flanks. It is also apparent that the increased differential effect in the full-field surround is due to a greater suppression to the uniform texture (Configuration 2 vs. Configurations 5 and 7), whereas responses to the contrast textures remain about the same (Configurations 3, 6, and 8).

response pattern. Thus for any given cell (other than cells classified as no effect), the pattern of responses to the surround subregions was a poor predictor of the response to the full-field texture.

To test the significance of this inconsistency, we performed an analysis of variance on six of the texture configurations, each with the optimally oriented center element: the full-field contrast and uniform textures, the flanking contrast and uniform textures, and the end-zone contrast and uniform textures. There was a significant ($P < 0.05$) main effect of the spatial organization (full, flank, and end) for 25 of the cells (20%); this reflects the overall greater general suppression induced by the full-field surround than by either set of quadrants alone. In addition, 25 cells (20%) showed a significant main effect of the presence of orientation contrast. However, only five cells (4%) showed a significant interaction between the two factors, a number no larger than that expected by chance. Thus we cannot rule out the possibility that the apparent inconsistencies between the different surround quadrants are due merely to

noisy responses and do not necessarily reflect different spatial organizations of the receptive field surrounds. This analysis does point out, though, that due to the inherent unreliability of individual cell responses to these texture stimuli, it is necessary to look at the responses of the whole population of neurons to determine that V1 as a whole responds reliably to these texture patterns in a manner consistent with perceptual salience.

Texture density

Psychophysical experiments have shown that the magnitudes of texture segregation and pop-out effects are reduced as the density of texture elements decreases (Nothdurft 1985; Sagi and Julesz 1987). To see how the present neurophysiological surround effects were related to the density of the texture elements, we tested the responses of 23 cells from monkey 89C to a series of texture patterns in which the average distance between the texture elements was made increasingly larger. Five different spacings were tested; the largest spacing was usually 3–4 times greater than the smallest spacing. In general, the second smallest spacing was that used in the original test, where the elements were close to the CRF but not encroaching upon it. The smallest spacing, therefore, often (but not always) caused the surround elements to encroach on the CRF. The three largest spacings were all well outside the CRF.

The pattern of responses of individual cells to the different texture densities was quite variable. For example, one cell showed a significant orientation contrast effect at all densities tested, whereas another cell showed an orientation contrast effect only at the tightest spacing, with a general suppression at higher spacing. (For this cell, the surround elements even at the smallest spacing did not encroach upon the CRF.) Another cell showed no effect of the texture surround at small spacings, but a general suppression at larger spacings. Finally, a fourth cell showed a general suppression at smaller spacings that became weaker as the spacing increased.

Normalized population responses for the density test are shown in Fig. 14. The general suppression effect was largest at the smallest spacings, and it became increasingly weaker as the spacing increased. For these 23 cells, on average there was no significant orientation-dependent suppression at any of the five spacings tested. Although four of the cells were classified as orientation contrast cells, only one of them showed a strong effect. However, one cell showed a moderate orientation contrast effect over a wide range of texture densities, whereas other cells lost the contrast effect as the spacing became too large. This latter effect is consistent with psychophysical pop-out experiments (Nothdurft 1985; Sagi and Julesz 1987).

To quantify the suppressive effects at the different densities, we calculated GSIs and DSIs for each cell at each density, analogous to the indexes calculated for the earlier tests. For these cells, the average amount of general suppression ranged from 0.35 at the smallest spacing to 0.1 at the largest. The decrease in GSI as the spacing increased was significant [1-factor repeated-measures ANOVA, $F(4,88) = 2.75$, $P < 0.05$]. There was no significant orientation-dependent suppression at any density for these cells.

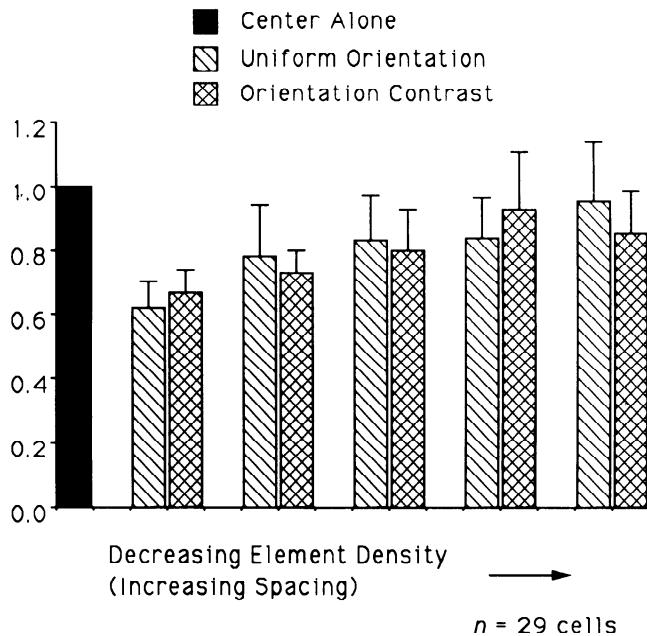


FIG. 14. Normalized population responses for the texture density test. Overall, as the texture element density decreases, the general suppression effect for the population response also decreases. There is no evidence of an orientation-dependent suppression at any texture density for these cells. Because the size of the individual elements and the number of surround rings remained constant, patterns with larger spacing were larger overall than those with smaller spacing.

Thus, overall, a decrease in texture density tended to decrease the amount of general suppression induced by the texture surround. However, because the sample of 23 cells that we tested did not show a strong orientation-dependent suppression effect overall, we cannot make any statements about the effect of texture density on orientation-dependent suppression at the population level.

Temporal analysis

Because human observers are able to detect the presence of a pop-out target in very brief, masked stimulus presentations (with time between onset of stimulus and mask as little as 50–100 ms; Bergen and Julesz 1983a,b), we reasoned that the surround effects reported here should be evident early in a cell's response to a stimulus, if these responses are indeed related to the perception of pop-out. To address this question, we calculated peristimulus time histograms for each cell and each stimulus configuration, added these histograms together for the whole sample of cells, and then divided each bin by the total number of cells. The resulting average histograms for the center bar alone, the uniform orientation texture, and the orientation contrast texture, as well as both surround alone textures, are shown superimposed on each other in Fig. 15A. It is clear that by the time the population reached its peak response (~60 ms after stimulus onset and ~20 ms after response onset), both the uniform orientation and the orientation contrast textures evoked a smaller response than did the center bar alone. Moreover, the response to the orientation contrast texture was already larger than that to the uniform orientation texture. Thus, at peak response, both the gen-

eral suppression effect and the orientation contrast effect were evident in the population response.

To analyze more closely the time period leading up to the peak response, we expanded the time scale and plotted the data with less temporal smoothing (Fig. 15B). The response started ~40 ms after stimulus onset. The histograms for the center bar alone, the orientation contrast tex-

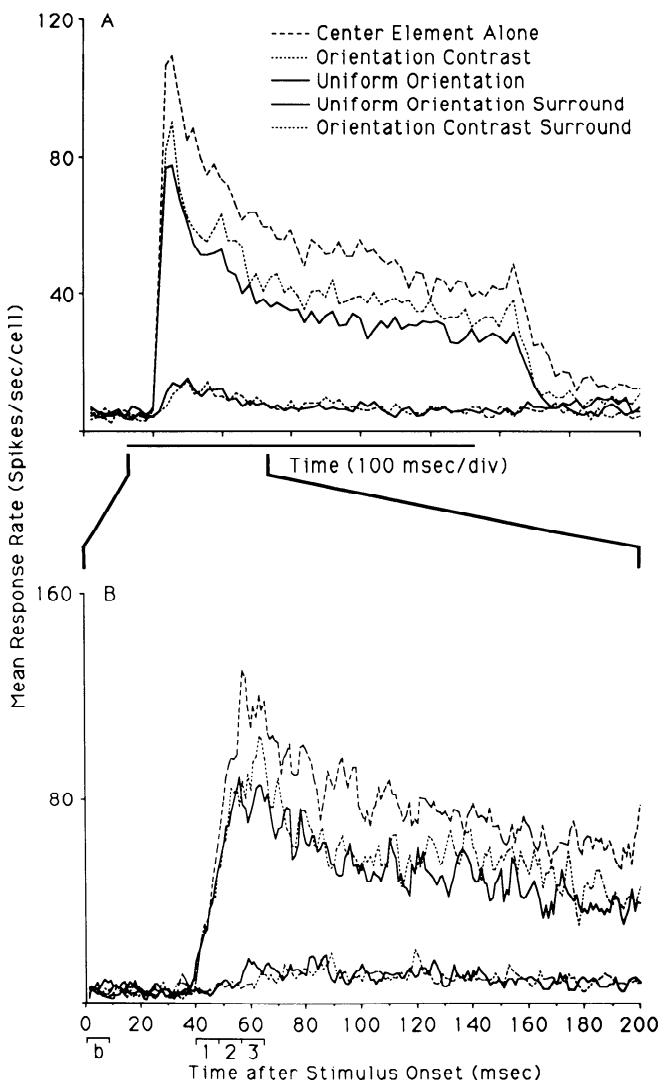


FIG. 15. A: average response histograms for the optimally oriented center element alone (---), the orientation contrast texture (----), the uniform orientation texture (—), the uniform orientation surround elements alone (—), and the orientation contrast surround elements alone (---). The bar underneath the histograms represents the stimulus on time (500 ms). Histograms for individual cells were initially constructed by adding all spikes in each 10-ms bin over all presentations of a particular stimulus, and then dividing by the number of presentations. The individual histograms were then summed over all cells and divided by the total number of cells in the sample to produce a population average response histogram. B: expanded version of histograms in A. For these histograms, bin size is 1 ms. The histograms were smoothed with the use of a boxcar algorithm (with a boxcar width of 3 ms). The hint of oscillatory responses in the center element alone histogram is a reflection of the neuronal sensitivity to the 66-Hz refresh rate of the graphics monitor. The 8-ms time epochs used in the statistical analysis of Table 1 are shown by the small scale numbered 1–3 below the abscissa between 40 and 64 ms. The 8 ms before period used in the analysis of the surround only response latencies is marked b.

ture, and the uniform orientation texture are all superimposed until $\sim 45\text{--}47$ ms after stimulus presentation, whereupon the two texture conditions evoked smaller responses than did the center bar alone. It was not until $\sim 58\text{--}60$ ms after stimulus onset that the uniform orientation texture response became smaller than the orientation contrast texture. To analyze the statistical significance of these differences, we calculated the mean response rate for each neuron during three consecutive 8-ms intervals starting 40 ms after stimulus onset. Although the *a posteriori* selection of the 8-ms time intervals increases the chances of falsely rejecting the null hypothesis, Table 1 shows 1) that during the first 8-ms interval there were no significant differences between the responses to all three stimuli; 2) that during the second 8-ms interval both texture stimuli elicited weaker responses than the center element alone stimulus but were no different from each other; and 3) that during the third 8-ms interval all three stimuli elicited different responses. Thus the surround effects were not present from the onset of the population response to the texture patterns, but they became evident very quickly. The general suppression effect appeared earlier than the orientation contrast effect, and both of them were present by the time the population reached its peak response.

The histograms for the two surround alone conditions demonstrate the small but significant excitatory responses sometimes elicited by the elements outside the CRF. It is noteworthy that the apparent onset of these population responses (45–48 ms after stimulus onset; Fig. 15B) was delayed by $\sim 5\text{--}8$ ms relative to the onset of the population responses for the three conditions in which a center element was within the CRF. This population latency corresponds to the latency for the onset of the general suppression effect shown above. Moreover, at ~ 55 ms after stimulus onset, the response evoked by the uniform orientation surround alone suddenly rose sharply, unlike the response to the orientation contrast surround alone. This rise corresponds roughly with the onset of the orientation contrast effect. To address the statistical significance of these effects, we compared the responses of the two surround alone textures in the same 8-ms time intervals used in the previous analysis

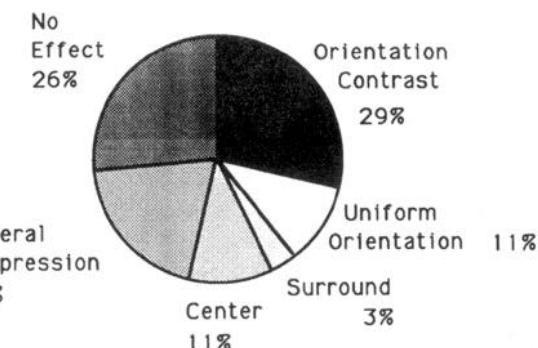


FIG. 16. Breakdown of sample into 6 cell classes based on the first 100 ms of each cell's response. This distribution resembles closely that of Figure 6, where the cells were classified on the basis of their full 500-ms responses.

to the firing rate in the 8-ms time interval immediately after the stimulus onset (marked *b* in Fig. 15B) for all 122 cells. Neither surround alone texture evoked a significant response above background during the first 8-ms interval; the uniform orientation surround alone elicited a significant response above background during the second 8-ms interval (paired *t* test, $t = 2.02, P < 0.05$) but the response to the orientation contrast surround alone was still statistically insignificant; and during the third 8-ms interval, both surround textures elicited statistically significant responses (uniform orientation surround: $t = 4.80, P < 0.0001$; orientation contrast surround: $t = 2.17, P < 0.05$). This analysis suggests an interesting interaction between the center alone and surround alone conditions. Whereas, on average, both center and surround elements alone caused an excitatory response, when they were presented together, the effect of the surround was to suppress rather than enhance the neuronal response to the center element.

CELL-BY-CELL VARIABILITY. To again address the question of individual cellular variability, we grouped the sample of cells into the classification scheme described earlier, this time on the basis of the first 100 ms of response for each cell. The results of this classification are shown in Fig. 16. A comparison of this figure with Fig. 6 (the classification based on the full 500-ms response) shows that the two pie charts are very similar. However, only about half of the cells (17/36, 47%) classified as orientation contrast cells on the basis of the first 100 ms maintained the orientation contrast effect when their responses were looked at over the full 500 ms. Likewise, only about half of the cells (17/39, 44%) that were classified as orientation contrast cells on the basis of the full 500 ms were also classified as such based on the first 100 ms; the other 22 cells (56%) did not show the orientation contrast effect early on, but over time acquired it. This might be due to either a genuine latency before the onset of the orientation-dependent suppression in these cells or the result of an improved signal-to-noise ratio when the response is integrated over a larger time period. The same pattern of results holds true for the other response classes. Thus this type of analysis once again reveals substantial individual cellular heterogeneity in response properties, this time in the temporal domain, which nonetheless gives rise to a consistent picture when analyzed at the population level (e.g., Fig. 16 vs. Fig. 6).

TABLE 1. Latency of general suppression and orientation contrast effects: results of paired *t* test comparisons

Time interval	n*	Configuration Comparison	Difference, spikes/s	t	P
1–8 ms	58	3–2	-0.59 ± 7.53	-.08	NS
		1–3	13.60 ± 8.49	1.60	NS
		1–2	13.01 ± 7.12	1.83	NS
9–16 ms	96	3–2	2.38 ± 7.06	0.34	NS
		1–3	22.99 ± 8.67	2.65	<0.01
		1–2	25.38 ± 8.51	2.98	<0.01
17–24 ms	107	3–2	21.66 ± 6.74	3.21	<0.01
		1–3	21.63 ± 7.22	3.00	<0.01
		1–2	43.29 ± 7.30	5.95	<0.01

Values for difference are means \pm SE. Configuration 1, Center bar alone; Configuration 2, Uniform orientation texture; Configuration 3, Orientation contrast texture; NS, not significant. *If a cell did not respond to any of the 3 stimuli during a particular time interval, then it was not included in the analysis for that interval.

RESPONSE LATENCIES. We were interested in determining whether there was any relationship between the response latency of a cell and its responses to the texture patterns. We calculated the mean response latency for each cell on the basis of its responses to the optimally oriented center element alone with the method of Seal et al. (1983). The mean latency for all cells was 58 ms (range 36–121 ms, excluding 2 outliers; Fig. 17). When broken down into the six response classes, there were no significant differences in latency among the classes. To investigate this further, we divided the sample into three groups on the basis of latency: early (<50 ms), middle (50–65 ms), and late (>65 ms). We then classified the cells in the early and late groups according to their full 500-ms responses to the texture patterns. The distribution of response types was very similar in both latency groups: there were nearly equal numbers of all response types ($\chi^2 = 1.5$, NS). If one looks at the response classification on the basis of the first 100 ms of response, though, the classification schemes are significantly different ($\chi^2 = 15.0$, $P < 0.05$). In particular, the ratio of orientation contrast cells to uniform orientation cells for the early latency cells (13:3) is larger than the ratio for the late latency cells (7:5). Thus, in the early part of their responses, cells that have a shorter latency may be more likely to show an orientation contrast effect than cells with a longer response latency. These results may explain why the orientation contrast effect is evident at the peak of the population response (see Fig. 15), disappears for ~50 ms, and then reappears for the remainder of the response. Interesting temporal dynamics apparently occur, such that late responding cells that initially are less likely to show an orientation contrast effect develop the effect as the response is integrated over a longer time course.

Relationships to other CRF characteristics

We examined whether the two suppression indexes (GSI and DSI) were correlated with other characteristics of the cells, including the CRF size scaled to its eccentricity in the visual field; the estimated depth of penetration; the orienta-

tion selectivity for the center bar alone [orientation index = $1 - (\text{orthogonal response}/\text{optimal response})$]; and the transiency of the response (transiency index = response during third 100-ms interval after stimulus onset/response during the first 100-ms interval). There were no strong relationships between the GSI or the DSI and any of these properties. The fact that both general suppression and orientation contrast effects occurred for a wide range of recording depths suggests that these characteristics are present in both supragranular and infragranular layers, but our data lacked adequate resolution to test for differences among the numerous sublaminae of V1.

Time course of orientation selectivity

Some authors (e.g., Dinse et al. 1990) have presented evidence for a delay in the onset of orientation selectivity in some striate cells. We looked at this issue at the population level by comparing the population average histograms for the response to an optimally oriented center bar alone to the response to the orthogonally oriented center bar alone (an analysis similar to that shown in Fig. 15). We included in the analysis only those 61 cells that showed a significant response difference between the two stimuli, showed a significant response above background for the orthogonal stimulus, and had an orientation selectivity index ≥ 0.3 . (Significance was defined as the mean -1 SE of the larger response being greater than the mean $+1 \text{ SE}$ of the smaller response.) This analysis showed no evidence of a delay in the onset of orientation selectivity at the population level; the orthogonal orientation histogram was smaller than the optimal orientation histogram from the outset of the response. An informal inspection of the individual cell responses suggests that some cells may have a delay before the onset of an orientation bias, but the majority of cells showed a response difference from the beginning. The results of this analysis place some constraints on any population-level model of orientation selectivity.

DISCUSSION

Modulatory effects from outside the CRF

The present results add to a growing list of modulatory effects from visual stimuli outside the classical receptive field (see Allman et al. 1985a, for review). Previous reports have demonstrated similar modulatory effects induced by such diverse stimuli as random noise surrounding the CRF in V1 (Gulyás et al. 1987; Hammond and MacKay 1975, 1977; Squatrito et al. 1990), oriented gratings in V1 (Blakemore and Tobin 1972; Fries et al. 1977; Maffei and Fiorentini 1976; Nelson and Frost 1978), color and spatial frequency in V4 (Desimone et al. 1985), and moving random dot patterns in MT (Allman et al. 1985b) as well as in V1 and V2 (Allman et al. 1990). Our results show that textured surround stimuli composed of oriented line segments tend to suppress neuronal responses to line segments within the CRF for the majority of cells in monkey primary visual cortex; moreover, these suppressive surround effects are often orientation dependent, such that the response tends to be stronger when there is a contrast in orientation between the center element and the texture surround compared with

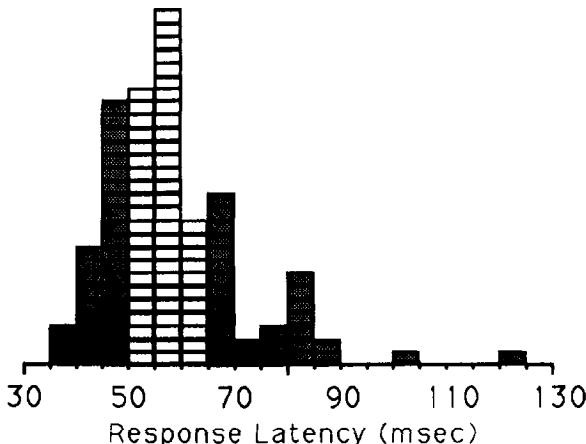


FIG. 17. Histogram of response latencies for 120 cells, divided into 3 groups for analysis of surround effects: early responding cells (<50 ms); middle responding cells (50–65 ms); and late responding cells (>65 ms). Two outliers (189 and 192 ms) were excluded because the responses were noisy and the latencies were erratic.

when there is no such contrast. Such responses correlate with the perceptual salience of the center element. The prevalence of modulatory effects arising from outside the CRF suggests that center-surround interactions are a critical feature of visual information processing and neuronal function. Many cells in primate visual cortex are sensitive not only to simple visual features (e.g., orientation, motion, and color) but also to the context in which the features are present. Specifically, they tend to respond more strongly when there is a contrast between the stimulus within the CRF and that outside. The possible functional significance of this is apparent when one considers that such areas of contrast in the visual world tend to occur along borders between objects, surfaces, or other behaviorally relevant features of the visual world.

Psychophysical pop-out

These results also point to a possible physiological basis for the psychophysical pop-out effect. In very brief presentation times followed quickly (50–100 ms) by a masking stimulus, human observers can effortlessly detect the presence and location of a target element in a field of distractors if the target differs in certain elementary features (such as orientation, color, motion, etc.) from the distractors (Bergen and Julesz 1983a,b; Treisman and Gelade 1980). If the target and distractors differ only in more complicated ways (e.g., conjunctions of simple features), but not in these elementary ways, then subjects must perform a serial search of the pattern to locate the target. The presence of contrast in one of these elementary features in the display tends to automatically direct the subject's attention to the location of the contrast.

The response properties of cells in V1 reported here are well-suited for signaling the presence of orientation contrast and are appropriate for the process that produces the involuntary, "reflexive" shift of attention to regions of potential interest. The population response to the particular orientation contrast textures used in this study is 15% larger than the response to the uniform orientation textures. In addition, our temporal analysis indicates that the orientation contrast effect is evident very early in the population response to the texture stimuli, providing good agreement with the brief exposure times sufficient to produce the psychophysical effect. However, the link between these physiological response properties and visual perception must remain tentative until different types of evidence are obtained. One thing that should be examined is whether the cells that project to the attentional control system display the orientation contrast effect. This will not be an easy task, however, for the brain mechanisms mediating attentional control are not well understood, and indeed may not occupy a single anatomic locus (for review, see Desimone et al. 1990). Thus at best all we can do now is demonstrate a correlation between the response properties of these neurons and psychophysical results, to see whether the neuronal responses reasonably match predictions expected from the psychophysics. All of the population data presented in this paper are consistent with psychophysical predictions.

If these response properties do indeed underlie the perception of pop-out, they suggest a simple model for the automatic directing of attention to areas of texture contrast, in which a hypothetical attention control mechanism

(ACM) is sensitive simply to "hot spots" of overall activity in the cortex. According to this scenario, the ACM monitors the whole visual field and directs attention to that region where activity is greatest. For the orientation pop-out patterns, this hot spot would occur at the portion of V1 corresponding to the topographic location of the target element, where overall neural activity would be slightly (~15%) higher than in surrounding regions. Thus a mechanism that set a threshold level for the input to the ACM could ensure that only the most active region of V1 could drive the ACM, drawing attentional processing to it. This idea is similar to the proposal of Koch and Ullman (1985) that a winner-take-all mechanism can control the directing of attention. This notion is attractive because it does not require separate sets of connections from specific cells to direct attention to an area of orientation contrast as opposed to an area of color or motion contrast. Presumably, if one were to look for results analogous to those reported here for the domains of color, motion, spatial frequency, etc., one might see similar contrast effects. Thus any of these types of contrast would produce a hot spot in cortical activity, allowing a common set of projections to drive the ACM and drawing attentional processing to the location of the hot spot for detailed analysis of the scene there.

Relationship to texture segregation

The relationship between pop-out and texture segregation has been noted by several authors (e.g., Beck 1972; Bergen and Julesz 1983a,b; Treisman and Gelade 1980). A question that naturally follows is whether the response properties of V1 neurons reported here are involved in the perceptual segregation of texture borders. If V1 cells were stimulated with a texture pattern in which a border was defined by orientation differences, one might expect, in view of our results, that a subset of cells would respond more strongly at the boundaries between the two texture regions (where there is orientation contrast) than at the regions within the middle of the texture regions (where there is no orientation contrast). Tests of this type have not been reported in monkeys. Some cells in cat striate cortex (Nothdurft and Li 1984, 1985) and lateral geniculate nucleus (LGN, Nothdurft 1990) are sensitive to orientation-based texture differences, even when the texture density is so fine that the neuronal responses to individual texture elements cannot be discerned in the spike train; some of these cells also respond selectively to the borders between texture regions, but only if the two textures have different average luminances. Other studies have shown that cells in monkey cortex are responsive to texture-defined bars (Albright 1987; Albright and Chaudhuri 1989; Hammond and MacKay 1975, 1977; Olavarria et al. 1992). However, we are not aware of any studies that provide convincing evidence of cells that are explicitly tuned for the shape of a texture-defined bar or that show enhanced responses at the borders between two textures of equal average luminance. The present results suggest that it might be profitable to look for such response properties with the use of texture stimuli based on orientation differences.

Possible mechanisms mediating surround suppression

We can envision four possible anatomic substrates for the suppressive surround effects reported in this study: 1)

subcortical origin; 2) interlaminar connections within striate cortex; 3) long-range horizontal connections within striate cortex; and 4) feedback connections from V2. Although our results do not distinguish among these possibilities, we will discuss the plausibility of each one.

SUBCORTICAL ORIGIN. Modulatory effects from stimuli well outside the classical receptive field have been demonstrated as early in the visual pathway as the retina and LGN of cats (McIlwain 1964) and monkeys (Krüger 1977; Krüger et al. 1975; Marrocco et al. 1982). There is also a massive feedback projection from V1 to the LGN, the function of which is poorly understood (Holländer 1974; Lund et al. 1975) and which might contribute to suppressive effects. It is therefore possible that some of the surround effects reported here, particularly the general (nonoriented) suppression, have a subcortical origin, perhaps arising from the increase in mean luminance of the surround as a result of the addition of the texture elements. This might partially explain the decrease in general suppression observed in the surround quadrant stimuli in comparison with the full-field texture stimuli and the decrease in suppression observed as the density of texture elements decreased. In both cases, the amount of suppression decreased as the mean luminance of the surround decreased. Further experiments are required to test the effects of mean luminance of the surround on these results.

INTERLAMINAR CONNECTIONS: END-STANDING AND SIDE-BAND SUPPRESSION. Another possible anatomic substrate is the set of interlaminar connections in striate cortex, which have been proposed as the mechanism underlying end-stopping in cat striate cortex (Bolz and Gilbert 1986). Both end-stopping and side-band suppression are well-known properties of visual neurons that are relevant to the textural suppression reported here. The side-band regions studied in the cat by Bishop et al. (1973) were not markedly orientation dependent, but they might contribute to the general suppression induced by the texture surround. The end-stopped regions of cells in both striate cortex (Orban et al. 1979) and area 18 (Hubel and Wiesel 1965) of cats have been shown to be orientation dependent, such that the suppressive effects of these regions are greater if the orientation of the stimulus in the end-zone matches the orientation of the stimulus in the excitatory receptive field center. Our results show that there is a correlation between the degree of end-stopping exhibited by a cell and the amount of general suppression induced by a texture background, but we found no clear relationship between end-stopping and the orientation-dependent suppression. This latter result may appear surprising, given the evidence that end-stopping is also orientation dependent. However, the lack of a correlation indicates only that end-stopping cannot be the sole explanation for the orientation-dependent suppression in our population of cells. Many differences between our texture stimuli and the standard simple bar stimuli conventionally used to test end-stopping may account for the lack of a strong correlation. For example, the large size of the texture stimuli and the large number of elements may cause regions outside the CRF to interact in different ways with the conventional end-stopped regions. In addition, the surround elements in the texture stimuli were often not aligned with the element within the CRF. In some cells, though, end-

stopping may indeed play an important role in the generation of the orientation contrast effect. If so, then orientation pop-out should be added to the growing list of suggested tasks in which end-stopping may be involved, including the detection of corners or borders (Hubel and Wiesel 1965), the representation of curvature (Dobbins et al. 1987; Hubel and Wiesel 1965), and the perception of subjective (illusory) contours (Peterhans and von der Heydt 1989; von der Heydt and Peterhans 1989). There is no reason why end-stopping cannot contribute to all of these tasks, but more definitive tests are needed to establish convincingly its contribution to any of them.

LONG-RANGE HORIZONTAL CONNECTIONS. Anatomic studies in both the monkey (Blasdel et al. 1985; Fitzpatrick et al. 1985; McGuire et al. 1991; Rockland and Lund 1983) and the cat (Gilbert and Wiesel 1983) have revealed the existence of long-range horizontal connections within striate cortex. These connections vary in length, depending on the cortical layer of the cells of origin, but can reach distances ≥ 4 mm (e.g., layer 4B of monkey; Blasdel et al. 1985). However, in most layers of monkey striate cortex, the lateral extent of connections ranges from <0.5 to 1.5 mm. Evidence in the cat suggests that $\sim 95\%$ of these long-range connections are excitatory onto pyramidal cells (Gabbott et al. 1987; Kisvarday et al. 1986) and that they connect areas of cortex with similar orientation preferences (Gilbert and Wiesel 1989; T'so et al. 1986). In the monkey, however, these issues are not as clear. T'so and Gilbert (1988), with the use of a cross-correlation analysis, show evidence only for excitatory interactions between cells of like orientation preferences in monkey striate cortex, similar to results they see in cat. However, McGuire et al. (1991) showed that $\sim 20\%$ of synapses made by two long-ranging axons in monkey striate cortex were onto smooth, presumably inhibitory, interneurons. Lund and colleagues (Lund 1987; Lund et al. 1988) have shown that smooth interneurons in monkey striate cortex can extend laterally for distances >1 mm. It is not known whether these neurons connect areas of similar or different orientation preferences. These pieces of evidence indicate that the long-range connections are suitable to produce suppressive effects from outside a cell's CRF.

Based on the evidence in the cat that the long-range horizontal connections appear to be mostly excitatory and connect similar orientation columns, Gilbert and Wiesel (1989) suggested that these connections may not be strong enough to bring a cell to firing threshold, but may instead play a modulatory role analogous to the one proposed here. In support of this idea, Hirsch and Gilbert (1991) showed that the size of an excitatory postsynaptic potential (EPSP) evoked by electrical stimulation of distant horizontal fibers in slices of cat visual cortex can depend on the voltage of the postsynaptic cell. Specifically, the evoked EPSP was stronger when the postsynaptic cell was depolarized than when it was at its resting potential. Although the sign of the effect is opposite to that which would explain the surround suppression in the present study, voltage-dependent response properties such as these may account for the ability of lateral connections to strongly modulate responses to stimuli within the CRF while having little influence on the cell's firing when the CRF is not directly stimulated. Hori-

zontal connections may also explain a phenomenon reported by Marrocco et al. (1986), and also noticed in the present results, in which a large field of stimuli placed outside the CRF can elicit a small but significant excitatory response from the cell (for example, see Configurations 4 and 8 in Figs. 2B and 15). A typical single-bar stimulus used to plot a CRF may not drive the cell alone in these outer regions because the excitatory connections are so weak. However, when there are many such stimuli present outside the CRF, then enough activity may be generated to bring the cell to threshold, albeit weakly. A related finding was presented by Fiorani et al. (1990), who showed neuronal responses from a single stimulus located well outside the CRF, but only in certain restricted locations relative to the CRF. They interpreted these results as a possible mechanism for certain perceptual completion phenomena. Our results add another twist to this picture: even though the surround elements sometimes have an excitatory effect on their own, their modulatory influence on the response to the center element in the CRF is almost always suppressive. This finding may turn out to be useful in understanding the mechanism of these suppressive surround effects once more information about the spatial structure of the surround is obtained.

FEEDBACK FROM HIGHER CORTICAL AREAS. A final set of possible anatomic substrates for these suppressive surround effects are the connections to V1 arising from other cortical areas. The most likely candidate would be feedback projections from area V2 to V1. We have shown previously that cells in V2 of anesthetized monkeys show similar surround effects to those reported here (DeYoe et al. 1986). One possibility is that the feedback connections from V2 generate the surround effects in V1, which then pass the effect back up to V2. This mechanism is attractive, for it provides a plausible functional role for the ubiquitous feedback pathways in visual cortex, that of providing a broader context for the firing of cells in lower areas. To test this notion, one would need to selectively eliminate the feedback projections to see whether or not V1 cells still display the surround effects without the input from V2. It is noteworthy that interareal response latencies differ by 5–10 ms (Maunsell 1986; Raiguel et al. 1989). This fits roughly with the 5- to 7-ms delay before the general suppression effect becomes evident and the 18- to 20-ms delay before the onset of the orientation contrast effect in our study.

Individual cellular unreliability/variability in response to texture

One of the striking results of this study is the degree of heterogeneity of responses at the single-cell level, contrasted with the consistency of responses at the population level. For example, at the population level, the full-field surround, the flanking quadrants, and the end-zone quadrants all showed both the general suppression and orientation contrast effects (see Fig. 13A); however, at the individual cell level, there was no strong consistency of responses across these different stimulus types. At the population level, cells responded more strongly to the contrast pattern than to either noncontrast (uniform and random) pattern; at the single-cell level, most cells showing an orientation contrast effect for one noncontrast pattern did not show it

for the other. At the population level, at both early and late time periods after response onset, both effects were present; at the single cell level, some cells showed the effect when looked at over the whole stimulation period, whereas others showed it only during the first 100 ms. This variability in single-cell responses is probably due to the small size of the surround effects (on average, 35% general suppression, 10% orientation contrast) compared with the inherent variability in neuronal responses to any textured stimulus. When the responses are added up over the whole population, a clearer, more consistent picture emerges as to how neurons respond to the texture patterns, a picture that is consistent with the perceptual salience of the visual patterns. Thus, because of this inherent single-cell variability in responses, the amount of information transmitted by single neurons about the presence of orientation contrast in a single trial would, in general, appear to be quite small, suggesting that consistent, reliable decisions about orientation contrast can be made only from a population of many neurons. This is in apparent contrast to the ability of some single neurons in V1 to signal accurately the orientation of a single oriented grating. Vogels and Orban (1990), with the use of signal-detection theory techniques, showed that some of these neurons can reliably signal small orientation differences that are near the limit of human and nonhuman primate perceptual performance (which does not imply, though, that perceptual judgments are based on the output of any single neuron). How reliably the responses of single V1 neurons can signal the presence of orientation contrast awaits such an analysis where appropriate stimuli are used.

Relationship to other studies of orientation contrast effects

The results from this study in the alert monkey are quite consistent with the results of similar experiments in both anesthetized monkeys and cats. The effects of the surround texture are somewhat more robust and more prevalent in the alert monkey than in the anesthetized monkey (DeYoe et al. 1986), but they are qualitatively the same. It is also impressive how well our results compare with the results of Grinvald et al. (1989), considering the different recording techniques employed in both studies (microelectrode recording of single-units vs. optical dye recording of widespread electrical activity) and the different stimuli used (discrete oriented texture elements vs. moving oriented gratings).

Our results also agree with most studies of orientation-dependent surround effects in anesthetized cat visual cortex (Blakemore and Tobin 1972; Fries et al. 1977; Maffei and Fiorentini 1976; Nelson and Frost 1978). Although these investigations used an oriented grating pattern in the surround, rather than discrete texture elements, as in the present study, and either a bar or a grating in the center, the effects of the surround were quite similar: in general, surround suppression was greater when the orientation of the surround stimulus matched the orientation of the center stimulus. In addition to suppression, Maffei and Fiorentini (1976) also reported significant enhancement effects of their surround stimuli, an effect not seen in our data in the monkey nor in the results of Fries et al. (1977) in the cat. The center-alone gratings of Maffei and Fiorentini usually encompassed not only the CRF but also extended

along the long axis of the grating into the end-zone regions. This difference in the stimulus conditions may account for their enhancement effects, perhaps revealing some interesting interactions between end-zone and side-band regions around the CRF. It is informative that in the Fries et al. (1977) study, the three classes of responses correspond identically to the three major classes of results reported here (orientation contrast, general suppression, and no effect).

Gilbert and Wiesel (1990) recorded activity from cells in cat striate cortex in response to contextual stimuli similar to the flanking surround quadrant stimuli of the present study (Fig. 12A). They measured the tuning curve for the orientation of the center element while systematically changing the orientation of the surround elements and reported that, for 9/27 cells studied, the peak of the tuning curve shifted by an average of 11° when the surround elements were close (within 30°) to the optimal center orientation. Gilbert and Wiesel suggested that this orientation tuning shift may be related to the perceptual tilt illusion. It would require a much finer examination of the orientation tuning of both the CRF and the surround than that performed in the present study to determine whether cells in monkey striate cortex show the same result. More relevant to the present study, though, is the finding of Gilbert and Wiesel that although the surround elements tended to suppress the response to the center element, the suppression tended to be greater when the surround elements were nearly orthogonal to the center element than when the surround elements were similar in orientation to the center element. The reason for this apparent difference in results between the Gilbert and Wiesel study and our study in the monkey and other studies in the cat is unclear, although a more fine-grained analysis of the orientation tuning of the surround than that performed here might again be informative.

Concluding remarks

These results provide a possible physiological basis for the perceptual pop-out effect, and by the relationship between pop-out and texture segregation, for the effortless perception of texture borders. Both of these suggestions need further experimental testing. With respect to pop-out, other questions remain, such as the spatial extent of the surround effects, the orientation tuning of the surround, extension of these results to other stimulus modalities, the effect of texture density on the orientation contrast effect, and possible attentional effects on the surround suppression. More generally, these results support and extend previous studies demonstrating the importance of the spatial context in which a visual stimulus is presented. The early visual system appears to be particularly sensitive not only to areas of luminance contrast in the visual field, but also to areas of orientation, motion, and other types of contrast. These contextual effects on the CRF must be addressed in any complete biological model of early visual processing, and experiments such as the present study can provide the quantitative data that is necessary for biologically relevant models.

We thank D. Bilitch, D. Chan, and U. Wehmeier for computer programming; K. Hasselblatt, C. Draeger, and M. Lazzaro for assistance in animal training; Drs. J. Maunsell, R. Siegel, and W. Newsome for help and advice on recording from alert animals; J. Fox and Dr. G. Carman for assistance

in various parts of the experiment; Dr. J. Olavarria for helpful comments on the manuscript; and Dr. J. Gallant for help with the data analyses. We also acknowledge the contributions of Drs. E. DeYoe, D. Sagi, B. Julesz, and H. C. Nothdurft to the original ideas behind some of these experiments.

This work was supported in part by a National Research Service Award (T32 GM 07737) from the National Institute of General Medical Sciences and from an Office of Naval Research grant (N00014-89-1192) to D. Van Essen.

Address for reprint requests: J. J. Knierim, University of Arizona, Arizona Research Laboratories, Division of Neural Systems, Memory, and Aging, Life Sciences North Building, Tucson, AZ 85724.

Received 6 August 1991; accepted in final form 10 December 1991.

REFERENCES

- ALBRIGHT, T. D. Isoluminant motion processing in macaque visual area MT. *Soc. Neurosci. Abstr.* 13: 1626, 1987.
- ALBRIGHT, T. D. AND CHAUDHURI, A. Orientation selective responses to motion contrast boundaries in macaque V1. *Soc. Neurosci. Abstr.* 15: 323, 1989.
- ALLMAN, J., MIEZIN, F., AND MCGUINNESS, E. Stimulus specific responses from beyond the classical receptive field: neurophysiological mechanisms for local-global comparisons in visual neurons. *Annu. Rev. Neurosci.* 8: 407–430, 1985a.
- ALLMAN, J., MIEZIN, F., AND MCGUINNESS, E. Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). *Perception* 14: 105–126, 1985b.
- ALLMAN, J., MIEZIN, F., AND MCGUINNESS, E. Effects of background motion on the responses of neurons in the first and second cortical visual areas. In: *Signal and Sense: Local and Global Order in Perceptual Maps*, edited by G. M. Edelman, W. E. Gall, and M. W. Cowan. New York: Wiley, 1990, p. 131–142.
- BACH, M., BOUIS, D., AND FISCHER, B. An accurate and linear infrared oculometer. *J. Neurosci. Methods* 9: 9–14, 1983.
- BECK, J. Similarity grouping and peripheral discriminability under uncertainty. *Am. J. Psychol.* 85: 1–19, 1972.
- BECK, J. AND AMBLER, B. The effects of concentrated and distributed attention on peripheral acuity. *Percept. Psychophys.* 14: 225–230, 1973.
- BERGEN, J. R. AND JULESZ, B. Parallel versus serial processing in rapid pattern discrimination. *Nature Lond.* 303: 696–698, 1983a.
- BERGEN, J. R. AND JULESZ, B. Rapid discrimination of visual patterns. *IEEE Trans. Syst. M.* 13: 857–863, 1983b.
- BISHOP, P. O., COOMBS, J. S., AND HENRY, G. H. Receptive fields of simple cells in the cat striate cortex. *J. Physiol. Lond.* 231: 31–60, 1973.
- BLAKEMORE, C. AND TOBIN, E. A. Lateral inhibition between orientation detectors in the cat's visual cortex. *Exp. Brain Res.* 15: 439–440, 1972.
- BLASDEL, G. G., LUND, J. S., AND FITZPATRICK, D. Intrinsic connections of macaque striate cortex: axonal projections of cells outside lamina 4C. *J. Neurosci.* 5: 3350–3369, 1985.
- BOLZ, J. AND GILBERT, C. D. Generation of end-inhibition in the visual cortex via interlaminar connections. *Nature Lond.* 320: 362–365, 1986.
- DESIMONE, R., SCHEIN, S. J., MORAN, J., AND UNGERLEIDER, L. G. Contour, color and shape analysis beyond the striate cortex. *Vision Res.* 25: 441–452, 1985.
- DESIMONE, R., WESSINGER, M., THOMAS, L., AND SCHNEIDER, W. Attentional control of visual perception: cortical and subcortical mechanisms. *Cold Spring Harbor Symp. Quant. Biol.* 55: 963–971, 1990.
- DEYOE, E., KNIERIM, J., SAGI, D., JULESZ, B., AND VAN ESSEN, D. Single unit responses to static and dynamic texture patterns in macaque V2 and V1 cortex (Abstract). *Invest. Ophthalmol. Vis. Sci.* 27 Suppl.: 18, 1986.
- DINSE, H. R., KRÜGER, K., AND BEST, J. A temporal structure of cortical information processing. *Concepts Neurosci.* 1(2): 199–238, 1990.
- DOBBINS, A., ZUCKER, S. W., AND CYNADER, M. S. Endstopped neurons in the visual cortex as a substrate for calculating curvature. *Nature Lond.* 329: 438–441, 1987.
- FELLEMAN, D. J. AND VAN ESSEN, D. C. Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex. *J. Neurophysiol.* 57: 889–920, 1987.
- FIORANI, M., JR., GATTASS, R., ROSA, M. G. P., AND ROCHA-MIRANDA, C. E. G. Changes in receptive field (RF) size of single cells in primate V1 as a correlate of perceptual completion. *Soc. Neurosci. Abstr.* 16: 1219, 1990.
- FITZPATRICK, D., LUND, J. S., AND BLASDEL, G. G. Intrinsic connections

- of macaque striate cortex: afferent and efferent connections of lamina 4C. *J. Neurosci.* 5: 3329–3349, 1985.
- FRIES, W., ALBUS, K., AND CREUTZFELDT, O. D. Effects of interacting visual patterns on single cell responses in cat's striate cortex. *Vision Res.* 17: 1001–1008, 1977.
- GABBOTT, P. L. A., MARTIN, K. A. C., AND WHITTERIDGE, D. Connections between pyramidal neurons in layer 5 of cat visual cortex (area 17). *J. Comp. Neurol.* 259: 364–381, 1987.
- GILBERT, C. D. AND WIESEL, T. N. Clustered intrinsic connections in cat visual cortex. *J. Neurosci.* 3: 1116–1133, 1983.
- GILBERT, C. D. AND WIESEL, T. N. Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. *J. Neurosci.* 9: 2432–2442, 1989.
- GILBERT, C. D. AND WIESEL, T. N. The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. *Vision Res.* 30: 1689–1701, 1990.
- GRINVALD, A., TS'O, D. Y., FROSTIG, R. D., LIEKE, E., ARIELI, A., AND HILDESHIM, R. Optical imaging of neuronal activity in the visual cortex. In: *Neural Mechanisms of Visual Perception*, edited by D. M.-K. Lam and C. Gilbert. Woodlands, TX: Portfolio, 1989, p. 117–136.
- GUILYÁS, B., ORBAN, G. A., DUYSENS, J., AND MAES, H. The suppressive influence of moving textured backgrounds on responses of cat striate neurons to moving bars. *J. Neurophysiol.* 57: 1767–1791, 1987.
- HAMMOND, P. AND MACKAY, D. M. Differential responses of cat visual cortical cells to textured stimuli. *Exp. Brain Res.* 22: 427–430, 1975.
- HAMMOND, P. AND MACKAY, D. M. Differential responsiveness of simple and complex cells in cat striate cortex to visual texture. *Exp. Brain Res.* 30: 275–296, 1977.
- HIRSCH, J. A. AND GILBERT, C. D. Synaptic physiology of horizontal connections in the cat's visual cortex. *J. Neurosci.* 11: 1800–1809, 1991.
- HÖLLÄNDER, H. Projections from the striate cortex to the diencephalon in the squirrel monkey (*Saimiri sciureus*): a light microscopic radioautographic study following intracortical injection of H^3 leucine. *J. Comp. Neurol.* 155: 425–440, 1974.
- HUBEL, D. H. AND WIESEL, T. N. Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *J. Neurophysiol.* 28: 229–289, 1965.
- JULESZ, B., BREITMEYER, B., AND KROPFL, W. Binocular-disparity-dependent upper-lower hemifield anisotropy and left-right hemifield isotropy as revealed by dynamic random-dot stereograms. *Perception* 5: 129–141, 1976.
- KISVARDAY, Z. F., MARTIN, K. A. C., FREUND, T. F., MAGLOCZKY, Z., WHITTERIDGE, D., AND SOMOGYI, P. Synaptic targets of HRP-filled layer III pyramidal cells in the cat striate cortex. *Exp. Brain. Res.* 64: 541–552, 1986.
- KNIERIM, J. J. AND VAN ESSEN, D. C. Single-unit responses to texture patterns in area V1 of the alert monkey. *Soc. Neurosci. Abstr.* 15: 323, 1989.
- KNIERIM, J. J. AND VAN ESSEN, D. C. Spatial organization of suppressive surround effects in neurons of area V1 in alert macaques. *Soc. Neurosci. Abstr.* 16: 1270, 1990.
- KOCH, C. AND ULLMAN, S. Shifts in selective visual attention: towards the underlying neural circuitry. *Hum. Neurobiol.* 4: 219–227, 1985.
- KRÜGER, J. The shift-effect in the lateral geniculate body of the rhesus monkey. *Exp. Brain Res.* 29: 387–392, 1977.
- KRÜGER, J., FISCHER, B., AND BARTH, R. The shift-effect in retinal ganglion cells of the rhesus monkey. *Exp. Brain Res.* 23: 443–446, 1975.
- LUND, J. S. Local circuit neurons of macaque monkey striate cortex. I. Neurons of lamina 4C and 5A. *J. Comp. Neurol.* 257: 60–92, 1987.
- LUND, J. S., HAWKEN, M. J., AND PARKER, A. J. Local circuit neurons of macaque monkey striate cortex. II. Neurons of lamina 5B and 6. *J. Comp. Neurol.* 276: 1–29, 1988.
- LUND, J. S., LUND, R. D., HENDRICKSON, A. E., BUNT, A. H., AND FUCHS, A. F. The origin of efferent pathways from the primary visual cortex, area 17, of the macaque monkey as shown by retrograde transport of horseradish peroxidase. *J. Comp. Neurol.* 164: 287–304, 1975.
- MAFFEI, L. AND FIORENTINI, A. The unresponsive regions of visual cortical receptive fields. *Vision Res.* 16: 1131–1139, 1976.
- MARROCCO, R. T., MCCLURKIN, J. W., AND ALKIRE, M. The not-so-silent peripheries of receptive fields in macaque striate cortex. *Soc. Neurosci. Abstr.* 12: 127, 1986.
- MARROCCO, R. T., MCCLURKIN, J. W., AND YOUNG, R. A. Spatial summation and conduction latency classification of cells of the lateral geniculate nucleus of macaques. *J. Neurosci.* 2: 1275–1291, 1982.
- MAUNSELL, J. H. R. Physiological evidence for two visual subsystems. In: *Matters of Intelligence*, edited by L. Vaina. New York: Academic, 1986, p. 59–87.
- MAUNSELL, J. H. R. AND VAN ESSEN, D. C. Functional properties of neurons in the middle temporal visual area (MT) of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *J. Neurophysiol.* 49: 1127–1147, 1983.
- MCGUIRE, B. A., GILBERT, C. D., RIVLIN, P. K., AND WIESEL, T. N. Targets of horizontal connections in macaque primary visual cortex. *J. Comp. Neurol.* 305: 370–392, 1991.
- MCILWAIN, J. T. Receptive fields of optic tract axons and lateral geniculate cells: peripheral extent and barbiturate sensitivity. *J. Neurophysiol.* 27: 1154–1173, 1964.
- NELSON, J. I. AND FROST, B. J. Orientation-selective inhibition from beyond the classic visual receptive field. *Brain Res.* 139: 359–365, 1978.
- NOTHDURFT, H. C. Sensitivity for structure gradient in texture discrimination tasks. *Vision Res.* 25: 1957–1968, 1985.
- NOTHDURFT, H. C. Texture discrimination by cells in the cat lateral geniculate nucleus. *Exp. Brain Res.* 82: 48–66, 1990.
- NOTHDURFT, H. C. AND LI, C. Y. Representation of spatial details in textured patterns by cells of the cat striate cortex. *Exp. Brain Res.* 57: 9–21, 1984.
- NOTHDURFT, H. C. AND LI, C. Y. Texture discrimination: representation of orientation and luminance differences in cells of the cat striate cortex. *Vision Res.* 25: 99–113, 1985.
- OLAVARRIA, J. E., DE YOE, E. A., KNIERIM, J. J., FOX, J. M., AND VAN ESSEN, D. C. Neural responses to visual texture patterns in the middle temporal area (MT) of the macaque monkey. *J. Neurophysiol.* In press.
- ORBAN, G. A., KATO, H., AND BISHOP, P. O. Dimensions and properties of end-zone inhibitory areas in receptive fields of hypercomplex cells in cat striate cortex. *J. Neurophysiol.* 42: 833–849, 1979.
- PETERHANS, E. AND VON DER HEYDT, R. Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps. *J. Neurosci.* 9: 1749–1763, 1989.
- RAIGUEL, S. E., LAGAE, L., GUILYÁS, B., AND ORBAN, G. A. Response latencies of visual cells in macaque areas V1, V2, and V5. *Brain Res.* 493: 155–159, 1989.
- ROCKLAND, K. S. AND LUND, J. S. Intrinsic laminar lattice connections in primate visual cortex. *J. Comp. Neurol.* 216: 303–318, 1983.
- SAGI, D. AND JULESZ, B. "Where" and "what" in vision. *Science Wash. DC* 228: 1217–1219, 1985.
- SAGI, D. AND JULESZ, B. Short-range limitation on detection of feature differences. *Spat. Vision* 2: 39–49, 1987.
- SEAL, J., COMMENGES, D., SALAMON, R., AND BIOLAC, B. A statistical method for the estimation of neuronal response latency and its functional interpretation. *Brain Res.* 278: 382–386, 1983.
- SNEDECOR, G. W. AND COCHRAN, W. G. *Statistical Methods*. Ames, IA: Iowa State Univ. Press, 1967.
- SQUATRITO, S., TROTTER, Y., AND POGGIO, G. F. Influences of uniform and textured backgrounds on the impulse activity of neurons in area V1 of the alert macaque. *Brain Res.* 536: 261–270, 1990.
- TREISMAN, A. M. AND GELADE, G. A feature-integration theory of attention. *Cognit. Psychol.* 12: 97–136, 1980.
- TS'O, D. Y. AND GILBERT, C. D. The organization of chromatic and spatial interactions in the primate striate cortex. *J. Neurosci.* 8: 1712–1727, 1988.
- TS'O, D. Y., GILBERT, C. D., AND WIESEL, T. N. Relationships between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlation analysis. *J. Neurosci.* 6: 1160–1170, 1986.
- VAN ESSEN, D. C., DE YOE, E. A., OLAVARRIA, J. F., KNIERIM, J. J., FOX, J. M., SAGI, D., AND JULESZ, B. Neural responses to static and moving texture patterns in visual cortex of the macaque monkey. In: *Neural Mechanisms of Visual Perception*, edited by D. M.-K. Lam and C. Gilbert. Woodlands, TX: Portfolio, 1989, p. 137–154.
- VOGELS, R. AND ORBAN, G. A. How well do response changes of striate neurons signal differences in orientation: a study in the discriminating monkey. *J. Neurosci.* 10: 3543–3558, 1990.
- VON DER HEYDT, R. AND PETERHANS, E. Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity. *J. Neurosci.* 9: 1731–1748, 1989.
- WOLBARSHT, M. L., MACNICHOL, E. F., JR., AND WAGNER, H. G. Glass insulated platinum microelectrode. *Science Wash. DC* 132: 1309–1310, 1960.
- WURTZ, R. H. Visual receptive fields of striate cortex neurons in awake monkeys. *J. Neurophysiol.* 32: 727–742, 1969.