NEURAL RESPONSES TO TEXTURE PATTERNS IN AREA V1 OF THE ALERT MONKEY

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ABSTRACT

Much of what our visual systems infers about a scene is based on cues derived from the visual texture of objects and surfaces in the scene. Areas of texture contrast are particularly salient and can automatically draw our attention. We recorded responses from cells in area V1 of the alert macaque monkey to texture stimuli in order to study the neurophysiology of texture segregation. A single oriented bar was placed in the center of a cell's classical receptive field (CRF) and we recorded the response to that center bar when it was alone against a blank background and when it was embedded in a texture of orthogonally oriented bars (orientation contrast texture) or identically oriented bars (uniform orientation texture). We found that the addition of the texture background suppressed the response to the center bar by an average of around 35%. In addition, for many cells there was a differential amount of suppression induced by the two texture backgrounds, such that the cell responded more strongly to the orientation contrast texture than to the uniform orientation texture. Such response properties correlate with the perceptual salience of the central bar.

The same pattern of results was obtained when cells were tested with another noncontrast stimulus, a field of randomly oriented bars. The suppression from outside the CRF was shown to originate from areas on all sides of the CRF. A temporal analysis of the population responses to the center bar and the texture stimuli showed that both the general suppression and the orientation contrast effects are evident very early after stimulus onset. However, they both seem to take some small amount of time to develop, with the general suppression effect appearing about 7-10 msec after the onset of the population response and the orientation contrast effect appearing about 10-15 msec later. This short latency is consistent with the short presentation time sufficient in psychophysical studies of the pop-out effect for subjects to detect the presence of a target element differing in orientation from a field of distractors. The physiological response properties discussed here may underlie this perceptual ability.

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1 Introduction

CHAPTER SUMMARY

The visual texture of objects in the world gives our visual systems many important cues in segregating one object from another. Much work has been done on the psychology and psychophysics of texture segregation in an effort to understand why some pairs of textures segregate from each other easily while other pairs do not. Early hypotheses of texture segregation proposed that segregation was based either on the global statistics of the luminance distribution of texture images or on certain local features of texture elements, such as orientation, brightness, or color. By the start of the 1980s, it was widely accepted that the latter view was correct.

Two theories of texture segregation and attention dominated psychophysical research of texture perception in the 1980s: Julesz's texton theory and Treisman's feature-integration theory. Both theories were similar in postulating two distinct modes of visual processing: a preattentive mode, which scans the visual image in parallel and is sensitive to areas of contrast in certain elementary features, and an attentive mode, which scans restricted regions of the visual image serially and is responsible for precise form recognition. The two theories differed in their explanations of why some texture pairs were preattentively discriminable whereas others required focal attention. Feature-integration theory proposed that textures were immediately discriminable if they differed in a single elementary feature, such as color or orientation. If the two textures differed only in the conjunction of elementary features, then focussed attention was required to segregate the two. Texton theory proposed that textures were immediately discriminable if they differed in the number or kind of certain discrete texture elements, called textons. Two textures that had identical numbers and kinds of textons required focal attention to discriminate.

The dichotomy between preattentive and attentive vision was an important element of both theories. The distinction between these two modes of visual processing was studied extensively using the so-called pop-out paradigm, in which a single texture element is embedded in a field of distractor elements, and a subject must detect the presence, location, and/or identity of this target element. In general, pairs of elements that elicit strong texture segregation also elicit a strong pop-out effect, whereby the location of the target can be immediately and effortlessly detected independent of the number of distractors. Using variations of this paradigm, many investigators have tried to characterize exactly what kinds of information each processing mode can analyze. The interpretation of results from these experiments is not always straightforward, though, and there is still much contention over the properties of attentive vs. preattentive processing.

More recent attempts to study texture segregation have been based on computational modelling of human texture segregation. Most models convolve the texture image through a bank of specified filters and then perform some sort of differencing operation to determine whether there is a large enough output difference from one of the filters to signal a texture gradient. Perhaps the most sophisticated and biologically plausible model to date is that of Malik and Perona, who convolved texture images with a bank of 96 filters modelled after oriented and nonoriented V1 receptive fields sensitive to different spatial frequencies. Employing plausible nonlinear operations such as half-wave rectification and local inhibition, their model performs very well in segregating both natural visual textures and classical psychophysical texture patterns. In addition, its ranking of the strength of texture segregation for different texture pairs correlates well with human psychophysical rankings.

Comparatively little is known about how visually responsive neurons respond to texture patterns. Cells have been found to be responsive to different texture patterns in area 17 and in the LGN of cat and in areas V2 and MT of monkey. However, there have been no conclusive demonstrations of cells responding explicitly to static texture borders when the two texture images have equal average luminance. In studies that are potentially relevant to perceptual pop-out and texture segregation, many studies in cat area 17 have demonstrated that neural responses to a standard bar or grating in the receptive field can be modulated by the addition of a surrounding grating outside the receptive field. In many cases, the modulation depends on the orientation of the surround grating, such that the responses are greatest when the center stimulus and surround grating are oriented orthogonally to each other. The present study explores this phenomenon further in the alert monkey by using surround stimuli with discrete oriented texture elements, modelled after stimuli used in psychophysical studies of pop-out.

TEXTURE AS A VISUAL CUE

Few surfaces in the natural visual environment are completely uniform in appearance. Most surfaces are composed of patterns of local nonuniformities, such as in color, luminance, motion, and orientation, to name a few. 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 3-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 in order 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. The main goal of this research is to explain human texture perception in terms of why some texture pairs are effortlessly discriminable from each other while other pairs are not. Our visual system must be sensitive to some difference between the discriminable pair, a difference that is not shared by the indiscriminable pair. Building on the pioneering work of Julesz, Treisman, Beck, and their co-workers, the field has progressed to a point where biologically plausible computer models of texture segmentation have been developed that closely mimic the performance of the human visual system in the ability to segregate different textures.

Related to texture segregation is the so-called pop-out phenomenon, in which a single texture element embedded in a field of distractor elements can be effortlessly detected regardless of the number of distractor elements. In general, single elements that pop out from a field of distractors will also, when grouped together, form a texture that is immediately discriminable from the background texture. The pop-out phenomenon has been studied not only in its own right but also as a simple, more easily controlled (and manipulable) model of texture segregation.

Although much is now known about the psychophysics of texture segregation and pop-out, and we have a good understanding of the probable computational processes involved, there is still little known about the neurophysiological basis of texture perception, especially in primates. The experiments presented in this thesis were designed to start filling in this gap, by looking for neurophysiological correlates of pop-out in the orientation domain. In agreement with previous work in cats (Blakemore and Tobin, 1972) and anesthetized monkeys (DeYoe et al., 1986; Van Essen et al., 1989), we found that a substantial number of cells in area V1 of the alert monkey are sensitive to orientation contrast. Cells in V1 tend to respond more strongly to an oriented bar stimulus if it is surrounded by orthogonally oriented bars rather than identically oriented bars. Before presenting these results, though, I will first review the relevant psychophysical findings on texture segregation and pop-out, the more recent attempts to construct biologically plausible computational models of texture segregation, and the relevant neurophysiological studies related to texture segregation and orientation contrast.

PSYCHOPHYSICS OF TEXTURE SEGREGATION AND POP-OUT

Local vs. Global Processes in Texture Segregation

Early work in texture perception centered on whether the segregation of textures was a global or a local process. Does the visual system compute the global statistics of the luminance distribution of two textures and segregate them if the differences are large enough, or does it instead extract local features from the luminance profiles of the textures and segregate them if the two textures differ in these local features? The early work of Julesz and of Beck illustrate these two approaches. Julesz (1962; Julesz et al., 1973) put forth the notion early on that texture segregation was based on differences between the global statistics of the visual image. This conjecture was based on demonstrations in which statistical methods were used to generate texture pairs differing in either first-, second-, or higher-order statistics. Julesz found that textures were easily discriminable only if they differed in first- or second-order global statistics. He thus conjectured that the visual system was incapable of discriminating two texture regions on the basis of the global distribution of luminance in the image if the two regions differed only in third- or higher-order statistics.

Coming from a different perspective, Beck (1966a, 1966b, 1967, 1983) proposed that texture segmentation was based on a computation of differences of certain local features embedded in the different texture regions. In his studies of perceptual grouping phenomena and texture segmentation, Beck used textures composed of arrays of discrete texture elements, usually letters. He found that texture segregation and similarity grouping in a texture were based on differences in simple local features of the texture elements, such as the orientation of the line segments composing the texture elements. The perceived similarity of individual texture elements had no relation to the ability of subjects to segregate textures composed of those elements. For example, subjects reported that a single upright 'T' was more similar to a tilted 'T' than to an upright 'L'; however, a texture composed of upright 'T's segregated from a texture composed of tilted 'T's and did not segregate from a texture composed of upright 'L's. Beck suggested that the visual system was sensitive to a number of local features of textures, and texture segmentation was based on first-order differences between these local features, not on the global luminance statistics of the image.

Taking these results a step further, Beck linked this "local feature" hypothesis of texture segregation and similarity grouping with a visual processing dichotomy popularized by Neisser (1967), that of preattentive vs. attentive processing. In a series of visual search experiments in which subjects had to detect target elements in a field of distractors, Beck (1972) found that this task was easier when the target differed from the distractors in a feature such as orientation. He suggested that parallel, preattentive processing was sensitive to the differences in orientation, thus allowing the easy discrimination of targets that differed in orientation from the background. Beck and Ambler (1973) tested this idea further by showing that when subjects were precued to the location of the target element, they could detect an upright 'L' in a field of upright 'T's as easily as they could detect a tilted 'T'; however, with no precue, the tilted 'T' was much more easily discriminable than the upright 'L'. Beck and Ambler proposed that in the precued condition, focal attention is able to detect the difference in the arrangement of the line segments that produce the 'T' and 'L' figures, allowing easy detection of the target. However, with no precue, when attention is necessarily distributed over the entire visual display, the differences in line arrangements cannot be easily detected. The orientation difference between the tilted and upright 'T's, on the other hand, is accessible to the preattentive system, and this allows the easy detection of this target.

Although Julesz's work concentrated on the global statistical differences between discriminable textures whereas Beck's work concentrated on the differences between local features of texture elements, it was not clear which model of texture segregation was correct, since both Julesz's discriminable textures also differed in local features, and Beck's discriminable textures also differed in global second-order statistics. This situation remained until Julesz and colleagues published a series of papers in which they generated discriminable texture pairs that had identical 2nd-order (Caelli and Julesz, 1978; Caelli et al., 1978) and even third-order global statistics (Julesz et al., 1978), thus disproving Julesz's earlier conjectures. Julesz proposed that the discriminability of these textures resulted from differences in the first-order statistics of a few local features of the texture elements (quasi-colinearity, corners, closure, and local granularity), thus aligning him with Beck's earlier interpretation that texture segregation was based on differences in the number or density of local features in the texture pairs.

Psychological Theories of Texture Segregation

Beck's "Local Feature" Theory

Beck et al. (1983) published a loose theory of textural segregation based on these notions of local feature differences. In their qualitative model, local feature detectors (e.g., concentric and elliptical receptive fields in striate cortex) extract local features from an image, and these features are linked by some local process to form higher order texture elements. A differencing operation encodes areas in which there are local differences in the elementary features of the texture elements and also in emergent features formed by the texture elements themselves, for example, an oriented "blob" caused by the colinearity of different texture elements. Finally, a decision unit detects a border between texture elements based on the magnitude of the output of the differencing operations. Although this model resembles more quantitative, computational models of texture segregation developed more recently (see below), in general flavor if not in exact details, most psychophysical research in the 1980s was inspired by the feature-integration theory proposed by Treisman and the texton theory proposed by Julesz.

Feature-Integration Theory

The feature-integration theory of attention (Treisman and Gelade, 1980) proposes two stages of visual processing: a preattentive processing stage, which encodes simple local features of the visual image automatically and in parallel across the whole visual scene, and an attentive stage, which identifies individual objects under focussed attention. In this way it resembles Julesz's texton theory, to be discussed in detail below. It differs from texton theory in its explanation of why some targets pop out effortlessly whereas others require focussed attention. According to feature-integration theory, targets that differ from the background only in terms of one elementary feature will pop out immediately, whereas targets that differ from the background in terms of the conjunction of two features require focussed attention to locate.

According to the feature-integration model, early visual processes encode the visual scene onto a set of topographically organized feature maps, such as a map for red, a map for blue, a map for vertical orientation, a map for high spatial frequency, and so forth. Let us take an example of a target that differs from the distractors in only one feature, for example, a red 'T' in a field of blue 'T's and green 'O's. According to feature-integration theory, there will be diffuse activity in the blue feature map and in the green feature map, as well as in any map that might encode aspects of the overall shape of the letters, such as an orientation or spatial frequency map. However, in the red map, there will be a discrete locus of activity corresponding to the position of the red target, and this discrete locus enables the immediate detection of the target element. Now, let us consider the case of a conjunctive target, for example a red 'T' in a field of red 'O's and blue 'T's. In this case, no feature map will contain a discrete locus of activity, for the red and blue maps will both have diffuse activity profiles, as will the appropriate orientation or spatial frequency maps. In order to detect the target, focussed attention must be employed at each spatial location, providing the "glue" necessary to integrate the separable features (color and shape) at the location into a single object, whereupon a decision can be made as to whether it is the proper target.

Texton Theory

Based on his findings that texture pairs with iso-second-order statistics could be discriminated if they differed in the number of certain local features, Julesz put forth a theory of texture segmentation that he called texton theory. Early versions of the theory (Julesz, 1981, 1984a, 1984b; Julesz and Bergen, 1983) took the form of three heuristics of early vision:

> *Heuristic 1.* Human vision operates in two distinct modes: *Preattentive vision* operates in parallel, that is, it is independent of the number of patterns; it is instantaneous, occurring without scrutiny; and covers a large visual field, as in texture discrimination; *attentive vision* is characterized by serial search by focal attention in steps, each lasting 50 msec (four times faster than eye-movement scanning limited to a small aperture), as in form recognition.
>
> *Heuristic 2.* Textons are: *elongated blobs*, for example, rectangles, ellipses, and line segments of specific colors, angular orientations, widths, and lengths; *terminators* or ends-of-lines of line segments; *crossings* of line segments.
>
> *Heuristic 3.* Preattentive vision directs attentive vision to the locations where differences in textons or in the densities (numbers) of textons occur, but ignores the positional relationships between textons. (Julesz, 1984b, p. 590)

The "definition" of textons in Heuristic 2 was derived from the discriminable iso-second-order statistics texture pairs that Julesz and his co-workers generated. They discovered that these texture pairs differed in the density of specific local features of the texture elements, such as orientation and line-segment terminators. Julesz suggested that these local features of the image were the perceptual "atoms" of early, preattentive vision. It is important to note that each texton type was an empirically derived entity, discovered by the examination of many discriminable texture pairs in an effort to determine post hoc what features differ in the two textures to make them segregate. It is also of interest that most textons had an analogue in terms of physiologically defined receptive field properties in the visual cortex, for example, wavelength-tuned cells (color), orientation-tuned cells (blob orientation), and end-stopped cells (terminators). Although a cortical analogue of the crossing texton had not been reported, it was presumed that one would be found if it was looked for.

The role of preattentive vision in the directing of attentive vision to areas of texton contrast in the image was elaborated mostly by experiments in visual pop-out, where subjects must detect a single target element embedded in a field of distractor elements. Julesz's texton theory predicted the ease with which a target could be detected in this paradigm: The target could be immediately and effortlessly detected if it differed from the distractors in texton number or type. For example, Bergen and Julesz (1983a) showed that, with very brief presentation times followed by a masking stimulus, subjects could easily detect a '+' in a field of 'L' distractors independent of the number of distractors; however, subjects' ability to detect a 'T' in a field of 'L' distractors decreased as the number of distractors increased. To explain these results, Bergen and Julesz postulated that the preattentive system acts in parallel across the whole visual field, detecting the location of texton gradients (in this case the presence of a crossing texton) and immediately directing focal attention to the location of the gradient. In the case of the 'T' target, there is no texton gradient between it and the 'L' distractors; although the elements differ in the position of their constituent line segments, the preattentive system is not sensitive to these spatial relationships, and thus cannot direct focal attention to the target location. Instead, the subject must perform a serial, item-by-item search of the display in order to find the target, thus accounting for the effect of distractor number on performance. Based on their subjects' performance, Bergen and Julesz calculated that it takes on average 50 msec to scrutinize each element; they take this number as an indication of the speed with which one can shift the locus of attentive processing.

Preattentive vs. Attentive Processing: A Dichotomy or the Ends of a Continuum?

Using this pop-out paradigm, Julesz and other investigators have attempted to characterize the properties and limitations of the preattentive and attentive systems. Bergen and Julesz (1983b) showed that the quickness with which subjects could detect a target in a field of distractors depended on the magnitude of the texton gradient between the target and the distractors. In their study, subjects were required to detect a target line segment that differed in orientation from the field of distractors. Subjects needed less time to perform the task as the difference in orientation between the target and distractors was made greater. Bergen and Julesz explained this result by postulating a spatial scaling of the preattentive processing window, whereby the spatial extent of the visual field that can be scanned in parallel by the preattentive system varies according to the magnitude of the texton gradients being discriminated. For small or nonexistent texton gradients, each display element must be scanned individually to determine whether it is the target; as the magnitude of the texton gradient increases (in this case, as the orientation contrast increases), larger areas of the visual field can be scanned preattentively, such that a number of texture elements can be scanned in parallel, decreasing the amount of time needed to search for the target; finally, when the texton gradient is large enough, the whole visual field can be scanned in parallel, making the detection of the target almost immediate.

This explanation of their results raises the question of whether there are really two distinct visual processing systems, a parallel preattentive and a serial attentive system, or whether they are really just two extremes of a broad continuum of processing. In this latter model, when visual processing is scaled to a large area of the visual field, it is only sensitive to certain elementary features (textons); if the system must extract more complicated form information (e.g., 'T' vs. 'L'), then the system must scale down in order to extract the fine-scale positional relationships entailed in this, and must thus analyze small pieces of the visual field in turn in order to process the whole image. However, introspection suggests the existence of a processing system working outside this small window of attention. For example, when one is performing a task that requires fine-scale processing, such as reading, one can still be made immediately aware of a moving object out in the visual periphery. Some visual processing must be going on outside the fine-scale processing window.

Braun and Sagi (1990, 1991) tested this notion explicitly by using a dual-task paradigm. Subjects were required to perform a difficult central form discrimination task that was designed to occupy all available attentional resources. Simultaneously, they were asked to perform a peripheral task that was either another fine-scale form discrimination or the localization of a target in a field of distractors differing in orientation. Braun and Sagi found that subjects' performance on the peripheral orientation target detection task was no worse when they were simultaneously performing the central form discrimination task than when they were doing the peripheral task alone; in other words, the presumed lack of attentive resources in the peripheral task did not affect the detection of the target element. However, subjects needed more time to perform the peripheral form discrimination task when they were simultaneously doing the central discrimination task than when they were doing the peripheral task alone; in other words, subjects apparently had to do the two tasks serially, first performing the central task before devoting the necessary attentional resources to do the peripheral task. Braun and Sagi take this result as evidence that there really are two distinct modes of visual processing, an attentive mode and a mode that operates independently outside the window of attention. Moreover, they claim that attentive processing is not necessary for certain kinds of visual information to enter consciousness. Subjects were able to detect and eventually report the location of some target elements even though all attentional resources were presumably occupied in the central discrimination task at the time when the peripheral stimulus was present. If this interpretation is valid, the information extracted by the preattentive processing must also be accessible to consciousness.

Where vs. What in Preattentive Vision

Sagi and Julesz (1985) published results that they interpreted as showing fundamental differences in the types of information processed by the two systems. According to these authors, the preattentive system is very sensitive to the exact location of textons, but it is not sensitive to the exact nature of the texton difference. Attentive processing is required to determine what the texton difference is. Sagi and Julesz likened this difference to a distinction between processing *where* a stimulus is and *what* the stimulus is. In their experiments, subjects had to report the number of targets differing in orientation (either vertical or horizontal line segments) from the distractor elements (all obliquely oriented line segments), and also report whether all target elements shared the same orientation or whether one of them was different. They found that the time required for the subjects to report the number of targets did not change as a function of the number or targets (2, 3, or 4), but that the time required to determine whether they were all the same or different increased as the number of targets increased. In a second experiment, subjects had to report the number of targets (2 or 3), and if there were three targets, the subjects had to report whether the three targets formed a right triangle or not; this second task required the subjects' being able to localize the three targets very precisely. In this case, the time required to perform each task was identical. Sagi and Julesz proposed that preattentive vision is able to determine the location of texture gradients with high precision; however, the exact nature of the texton gradient is not available to the preattentive system. Instead, focal attention is required to analyze the nature of the texton difference, by target-by-target scrutiny. This serial scrutiny explains the dependence of target discrimination on the number or targets.

However, Folk and Egeth (1989) performed a number of experiments that shed some doubt on Sagi and Julesz's interpretation. Folk and Egeth replicated the Sagi and Julesz result of localization being parallel and discrimination being serial when they had their subjects report whether the targets were the same or one different, as in the Sagi and Julesz paper. However, when they changed the nature of the task such that subjects had to report, not whether all targets were the same or different, but whether one of the targets was vertical (or horizontal), they found that subjects' reaction times were independent of the number of target elements, reflecting a parallel discrimination effect. Thus, they claim that the nature of the texton difference is indeed available to the preattentive system, but that the serial effect seen by Sagi and Julesz and by themselves in the same-different task reflected different decision processes of the subjects under the two tasks, rather than any inherent limitation on the nature of the information available to the preattentive system.

Problems with Texton Theory

In the mid and late 1980s, a number of studies appeared that cast some doubt on the validity of parts of the texton theory and on its explanatory power in understanding the neural mechanisms behind texture segregation. Enns (1986) showed that by changing the aspect ratio of the texture elements in a display, he could make a previously indiscriminable texture pair discriminable, and vice-versa. Changing the aspect ratio did not alter the numbers of such textons as line terminators, which texton theory proposed were the basis of the segregation. However, this procedure did change the probable population of "blob" detectors responding to each texture pair, perhaps making the population the same or similar for both texture pairs. Enns concluded that texture segregation had to be more complicated than just counting the absolute number and kind of textons in the texture pairs; instead, segregation depended on the degree to which the two textures shared common features as well as the degree to which there were differences in the unique features of each texture.

Gurnsey and Browse (1987) and Nothdurft (1990a) each presented data casting doubt on the claim that line terminators and crossing were textons at all. Gurnsey and Browse suggested that the texture segregation induced by texture pairs differing in the number of crossings or line terminators was more likely due to the overall size differences of the texture elements. They performed a number of experiments to test the discriminability of texture pairs that differed either in the number of crossings or line terminators but kept the overall size of the texture elements the same. They found that many texture pairs differing in crossings or terminators did not segregate well if the sizes of the elements were similar, whereas textures sharing the same number of crossings or terminators did segregate easily if the overall size or blob shape of the elements differed. In addition, Gurnsey and Browse showed that there was often an asymmetry in the discriminability of a texture pair depending on which texture elements formed the background and which formed the foreground. The original texton theory does not account for this result (see Gurnsey and Browse, 1989, for their model of texture segregation asymmetry).

Along these lines, Nothdurft (1990a) showed that the discriminability of texture pairs differing in line crossings or terminators was extremely sensitive to manipulations that changed the local luminance distribution in the pattern without changing the relative number of line crossings or terminators in the textures, such as randomly varying the contrast of texture elements or randomly jittering the element positions to eliminate regular gaps between texture elements. Textures based on orientation differences were not nearly as sensitive to these manipulations. Nothdurft concluded that terminators and crossings were not textons, but that the segregation observed in these textures was likely due to local luminance cues in the textures.

SPATIAL FREQUENCY CHANNEL MODELS OF TEXTURE SEGREGATION

The aforementioned experiments showing various inconsistencies between predictions of the texton theory and empirical results, along with an increased interest in the potential of physiologically-motivated neural filter models to explain texture segregation, have shifted much recent work on texture to computational models of texture segregation. Most of these models have a bank of filters with which the texture image is convolved, and then some sort of differencing operation determines whether there is a large enough output difference from one of the filters to signal a texture gradient.

Caelli (1985) published one of the first attempts to construct a computational model capable of texture segregation. His model had three stages: (1) a nonlinear convolution of the image with a selected group of filters; (2) perceptual impletion, whereby the detectors with strong responses spread activity nearby and detectors with weak activity inhibit activity nearby; and (3) grouping, where the outputs of detectors at different spatial locations are compared to result in perceptual grouping. Although Caelli's model performs well on many texture pairs, it does not have an a priori bank of filters to be used on any image; instead, the filters were chosen specifically for each texture pair, depending on whether a crossing or a terminator was to be detected, on the probable assumption based on texton theory that such filters were likely to be found in the cortex. Interestingly enough, when the model segregated a field of '+'s from a field of 'L's, the texture difference was signalled more strongly by the vertical and horizontal filter outputs, rather than by the terminator or crossing detector filters.

Bergen and Adelson (1988) built a model using simple size-tuned, center-surround linear filters, followed by nonlinear half-wave rectification, to see how much of texture segregation could be explained by such a simple mechanism. They found that differential outputs of some of these filters worked very well in detecting texture differences between fields of '+'s and 'L's. Moreover, if they increased the size of the 'L's, making the textures even more discriminable, or decreased the size of the 'L's, making the textures less discriminable, the output of the model increased or decreased accordingly. The results on this one set of textures led Bergen and Adelson to propose that texture segregation might be explained by mechanisms not requiring more complex texton detectors.

Voorhees and Poggio (1988) published a paper accompanying that of Bergen and Adelson, in which they detail a more elaborate model of texture perception. Fine-scale center-surround filters were used to detect "texton blobs," and these blobs were segmented into "small compact and thin elongated" components. Five attributes of these blob components were computed: contrast, orientation, width, length, and "area and area density." Constructing histograms of the distributions of each of these attributes in two adjacent restricted neighborhoods of the image, they computed a "maximum frequency difference" score for each attribute histogram by finding the largest difference between corresponding bins of the histograms. A texture border was signalled if the maximum frequency difference score was high enough for one of the attributes. This model performed well both on natural texture images as well as on the typical '+'s and 'L's textures.

The Voorhees and Poggio model explicitly constructed "texton blobs" from the outputs of their center-surround filters, and detected texture borders based on the differences in attributes of these blobs. In contrast, Sutter et al. (1989) proposed a model of texture segregation that did not extract any textons explicitly, but instead relied on the output of oriented spatial frequency channels to detect texture borders. In this model, the outputs of

39 channels (13 spatial frequencies x 3 orientations) are computed for each of the two texture regions, and weighted differences of channel output for each texture region are pooled to give a texture discriminability score. Assuming this score to be a monotonic function of human observers' ratings of segregation strength, Sutter et al. test the model's predictions of texture segregation with results from psychophysical experiments. Varying the size, contrasts, spacing, positions, and types of texture elements, they found that the model predicted human observers' ratings of texture segregation at least to a first-order approximation. Various inconsistencies led them to suggest that an additional nonlinear operation might account more exactly for the psychophysical results. They propose a more complex model employing two stages of linear filtering--the first tuned for high spatial frequencies, the second tuned for low spatial frequencies--separated by a nonlinear operation such as half-wave or full-wave rectification. Although they do not test this more complex model, their initial simple model suggests that simple oriented spatial-frequency-tuned filters can go a long way in explaining texture segregation.

Similarly, Turner (1986) and Fogel and Sagi (1989) used banks of Gabor filters to extract texture borders from a variety of images. Turner showed that some texture pairs could elicit differential outputs from some of the filters. Fogel and Sagi's model went somewhat further and added a stage to the model that took the differential outputs of the Gabor filters and generated a representation of the borders between the texture regions. Although their model worked well on many of the classical psychophysical textures, it failed to discriminate textures based on differences in "terminators."

Perhaps the most complete model to date that performs very close to human observers and that is biologically plausible is that of Malik and Perona (1990). Their model employs three stages of processing. The first stage convolves the image with a set of 96 filters. The filters are of eight types: two radially symmetric filters designed to model cortical nonoriented simple cells and six elongated filters at different orientations, designed to model orientation tuned simple cells. Each type of filter comes in twelve different spatial frequencies, thus generating the 96 filters. The output of each filter is half-wave rectified, giving a total of 192 neural responses: 96 for the positive portion of the response and 96 for the negative portion. The second stage involves a localized inhibition, whereby weak responses in some filters are suppressed by stronger responses of filters in the same or nearby locations. Finally, the third stage convolves the postinhibition responses of each channel with a wide radially symmetric Gaussian filter to find peaks in the postinhibition responses, corresponding to areas of high texture gradients. Malik and Perona tested their model on natural visual images and on classical psychophysical texture images, and found that the model was able to pick out the texture borders quite well. Moreover, the model's "ratings" of the strength of the texture border corresponded quite well with human observer's ratings, for a large number of texture pairs. Thus, their model is not only able to detect texture borders but reliably predicts the perceptual strength of these borders based on human psychophysical data.

The success of these models in discriminating texture pairs suggests that texture segregation depends on the filtering properties of cortical receptive fields, tuned for size, orientation, and spatial frequency; differences in the outputs of these filters can signal a texture border. However, as the Malik and Perona model shows, certain nonlinear operations must be applied to these filters to make the model output mimic human perceptual performance. Although the operations applied by Malik and Perona are biologically plausible, at least to a first approximation, they need rigorous experimental testing to confirm.

NEUROPHYSIOLOGY OF TEXTURE SEGREGATION

Taking their cues from both psychophysical and physiological evidence, the model of Malik and Perona can mimic human performance in the detection of texture borders. The filters employed in the model were themselves modeled on receptive field properties of cells in primary visual cortex. The receptive field models were based on cell responses to simple, bar-shaped stimuli and oriented gratings, and they account well for the visual system's ability to discriminate texture borders. However, at the present, comparatively little is known about the responses of neurons to these textured stimuli. This section will review the physiological studies that are relevant to this question.

Neural Responses to Texture Figures

Hammond and MacKay (1975, 1977) recorded from cells in area 17 of the cat while stimulating with textured patterns of visual noise (e.g., snow on a TV screen). The patterns were either moved as a whole across the cell's receptive field, or a small bar-shaped region of static noise moved across a stationary background of noise; in the latter case, the texture bar was invisible in any single frame but was clearly visible when the bar was set in motion against the background. Hammond and MacKay found that complex cells were responsive to these textured stimuli, whereas simple cells were not. However, the responses of some simple cells to standard luminance bars were modulated by the addition of a textured background. Albright (1987) found that cells in monkey area MT and area V1 (Albright and Chaudhuri, 1989) were also responsive to stimuli similar to those used by Hammond and MacKay. He found that cells in MT were also responsive to moving bars that differed from the background in their static texture profiles. Similarly, Olavarria et al. (1988; Van Essen et al., 1989) found that cells in MT were responsive to moving texture bars that differed from the background in the orientation of their constituent texture elements and in the differential motion between the bar and the background texture elements.

Nothdurft and Li (1984, 1985) recorded from cells in cat area 17 while slowly scanning texture displays of oriented line segments across the cell's receptive field. The stimuli consisted of arrays of line segments in which a circle-shaped region was defined by either a contrast in orientation between the foreground and background or a difference in luminance of the line segments. By varying the size of the texture elements and the spacing between them, Nothdurft and Li found that simple cells responded to each appropriately oriented line segment individually at large-scale textures but lost responsiveness when the texture became too fine-scale. Complex cells, on the other hand, would maintain their responsiveness to the central region even when the texture had become so fine-scale that the responses to each line segment could not be resolved. For the stimuli in which the circle was defined by a difference in luminance, at large scales the simple cells once again responded only to the individual elements, whereas at small scales, they responded to the luminance contrast between the foreground and background; these cells did not respond at all to intermediate scales. Complex cells showed a similar trend, but the transition from large- to fine-scale texture responses was much smoother. These results showed that changing the scale of the textures can influence whether the cell will respond to the individual texture elements or will integrate its response over the full texture region. These results did not show evidence that the cells were capable of responding selectively to a texture border when the two textures have equal mean luminances.

Similar results were reported by Nothdurft (1990b) in the cat LGN. Stimulating the cells with a number of textured stimuli in which a circle-shaped central figure was defined by different cues ("texton differences"), Nothdurft found that LGN cells respond strongly to a texture border if there is a luminance difference between the figure and the background, but not if the two regions are equiluminant. However, many LGN cells did respond preferentially to one of the two texture regions, at certain texture element densities. Thus, LGN cells can respond differently to regions of different texture, as do striate cells, but it appears that, at least in the cat, they do not represent explicitly the borders of texture pairs having equal average luminance.

Using a different experimental paradigm, Schiller et al. (1990) showed results that suggest that equiluminant texture segregation is mediated by the parvicellular visual pathway. They trained monkeys to detect and saccade to targets in the peripheral field that could be defined by a number of visual cues, one being a difference in the orientation of texture elements. Schiller et al. found that small ibotenic acid lesions of the parvicellular layers of the LGN severely impaired the monkeys ability to detect the texture-defined target, whereas magnocellular lesions had no effect.

Orientation Contrast

A number of studies, mostly in the cat, have addressed the effects on neural responses of adding an oriented surround pattern to a central oriented pattern. The results of such studies may hold significance for the neural basis of perceptual pop-out of oriented texture elements as well as for the segregation of texture borders based on orientation differences. Blakemore and Tobin (1972) published a research note describing a complex cell they found in cat that showed such an effect. They recorded responses to an optimally oriented bar moving in the receptive field alone or surrounded by a moving grating pattern outside the cell's receptive field. If the surround grating was oriented identically to the center bar, the cell's response was shut down to spontaneous level. This suppression was gradually reduced as the orientation of the grating changed, such that when the grating was oriented orthogonally to the central bar, the response was actually slightly enhanced over the response to the bar alone.

A number of investigators subsequently studied this phenomenon in detail. Maffei and Fiorentini (1976) stimulated cells with optimally oriented grating patterns in the receptive field and varied the orientation and spatial frequency of gratings outside the receptive field. These authors found both facilitatory (32/80 cells) and inhibitory (48/80 cells) effects of the surround gratings. In both cases, for some cells the effect was strongest when the orientation and spatial frequency of the surround grating matched those of the center grating. Fries et al. (1977) used stimuli similar to that used by Blakemore and Tobin and found that the effect of the surround grating fell into 3 classes. The responses of some cells were suppressed by the addition of a surround grating at any orientation; other cells were suppressed more strongly if the orientation of the surround grating was similar to that of the center bar; finally, other cells were not affected by the addition of the surround grating. All cells that showed an effect of the surround grating were simple cells, whereas all cells that showed no effect were complex. In addition, the cells that showed an orientation-tuned surround effect had inhibitory sidebands (Bishop et al., 1973), whereas the cells that showed no effect had no sideband regions. Unlike Maffei and Fiorentini, Fries et al. saw no facilitatory effects of the surround grating. By masking off the sideband regions, these authors showed that the suppression induced by the surround grating was reduced around 60%. They suggested that this result shows that the surround suppression can be explained by classical receptive field mechanisms, such as side-band suppression or end-stopping.

However, Nelson and Frost (1978) showed that a large part of the orientation-specific surround suppression came from nonclassical receptive field mechanisms. Using the "jiggle" technique to map out both excitatory and inhibitory regions of a cell's receptive field, these authors were able to ensure that their surround gratings did not encroach upon any "classical" receptive field responsive area. Nevertheless, they reported that 17/22 cells, both simple and hypercomplex, displayed orientation-specific surround modulation of the response to a center bar. Most effects were inhibitory, but a few cells showed facilitatory effects. This study shows that, in the cat, at least some of the suppression induced by a surround grating comes from mechanisms outside the classical receptive field. (For a review of other effects from stimuli outside the classical receptive field, see Allman et al., 1985a).

These studies, all in cat striate cortex, show that many cells respond more strongly to a bar or grating if it is surrounded by a grating that has a different orientation. Such response properties may be involved in the perception of orientation pop-out. Similar effects were seen by Grinvald et al. (1989), using voltage-sensitive dyes to record activity in striate cortex of anesthetized monkeys. They saw that cortical activity in a region stimulated by a central grating was suppressed by the addition of surround gratings, and that this suppression was greater when the surround grating was at the same orientation as the center. Thus, striate cells in monkey appear to show the same effect of surround gratings as do striate cells in cats.

Similar surround effects have been reported with other stimulus modalities. Allman et al. (1985b, 1990) reported motion-specific surround effects in MT, V1, and V2 of owl monkeys. Desimone et al. (1985) reported that cells in V4 of macaques showed color- and spatial-frequency-specific surrounds. In all cases, cellular responses were suppressed more strongly when there was no contrast between the center and surround stimuli.

PRESENT STUDY

With the exception of the Grinvald et al. (1989) study, all demonstrations of orientation-specific surround effects were done in cats, using gratings as the surround stimulus. As a part of a series of investigations into neuronal responses to texture and pop-out patterns, DeYoe et al. (1986) tested for orientation-specific surround effects in the anesthetized macaque monkey using stimuli modelled after those used in human psychophysical experiments on pop-out. Those results showed effects qualitatively similar to the surround effects demonstrated in cats. However, as one uses more complicated visual stimuli and asks more sophisticated questions about the neuronal basis of visual perception, the effects of anesthesia on neuronal response properties become even more worrisome. With this in mind, we set out to replicate the DeYoe et al. findings in an alert behaving monkey. We found that, at least qualitatively, the results in behaving monkeys were similar to those in anesthetized monkeys. This thesis presents the results of these studies, along with new results not previously reported by DeYoe et al.

2 Methods

SUBJECTS

Two juvenile macaques (*M. fascicularis*) were used in these experiments. Monkey 87A was a female, approximately 2-3 years old at the start of training, weighing around 3 kg. Monkey 89C was a male, approximately 2-3 years old at the start of training, weighing around 3.5 kg. The monkeys were housed in separate cages in the same room with other monkeys. They were fed regularly with the other monkeys, but were put on a controlled water schedule, in which they worked for their daily ration of water (apple juice or Tang) in their training or recording sessions. Supplemental water was given when necessary 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 Nembutal and perfused.

TRAINING

The monkeys were fitted with special collars, and using the pole and collar technique of Anderson and Houghton (1983) were trained to allow capture in their cages and to accept restraint in the primate chair. Using standard operant conditioning techniques, the monkeys were trained to fixate a spot of light for 4-6 seconds in order to obtain a reward of a few drops of juice. Monkey 87A was trained to detect a subtle 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. The monkey had to maintain fixation until the spot dimmed slightly, whereupon it had 500-600 msec to release the lever to obtain the reward. Monkey 89C was trained to merely fixate the spot of light. When the spot appeared, the monkey had 1500 msec to begin fixation in order to start a trial. The monkey had to maintain fixation until the spot disappeared, whereupon it was rewarded. Trials were terminated and no data collected whenever the monkey broke fixation or, in the case of 87A, released the lever outside the proper response window. Monkeys worked on average around 1200 correct trials a day, drinking between 150-200 ml juice.

EYE POSITION MONITORING

Eye position was monitored using an infrared oculometer from *Dr. Bouis* (Karlsruhe, Germany). The oculometer was positioned in front of the monkey's right eye and was calibrated at the beginning of each training and recording session. The monkey looked through a coated piece of glass, which served as an IR mirror, oriented at 45°. Two arrays of IR-emitting diodes illuminated the eye by reflecting off the IR mirror. The image of the eye was then reflected back toward the detector tube, where it was focussed on the detector. The output voltages corresponding to the horizontal and vertical components of eye position were digitized at 100 Hz by the A/D converter on a Lab Master interface with the personal computer (Scientific Solutions, Solon, OH). Monkeys had to maintain fixation within a window of 0.5°-0.6° degrees radius around the fixation spot. Although this is a large window relative to the size of V1 receptive fields, the size was necessary due to artifacts arising from extraocular sources near the eye. We believe that the monkeys' actual fixation accuracy was much better than this, based on the consistent strong responses of V1 neurons from trial to trial and a subjective viewing of the eye tracker output during each trial.

SURGICAL PROCEDURES

Surgeries were performed using procedures described in detail elsewhere (Maunsell and Van Essen, 1983; Felleman and Van Essen, 1987), with the following modifications. All major surgeries on Monkey 87A were performed under halothane (2.5%-3%) or Nembutal (initial dose 25 mg/kg, supplemental doses as necessary) anesthesia; all major surgeries on Monkey 89C were performed under halothane (2%-4%) anesthesia. In all cases animals were initially knocked down with ketamine (10 mg/kg), supplemented with Vesprin (0.5 mg/kg) and atropine (0.01mg/kg). Initial surgeries entailed the implant of a triangular head-holding post on the skull just behind the brow ridge. In the same surgical procedure, a recording chamber was also implanted posterior to the head post, in a position to enable easy access to opercular V1. After surgery the animals were transported back to their home cages once they showed signs of recovery, and were monitored afterward. Monkeys were given a minimum of 1 week 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 Vesprin anesthesia to drill a hole in the skull inside the recording chamber. This hole was typically 3-4 mm diameter, although over a number of weeks bone erosion tended to increase the diameter substantially.

It was at times necessary to perform additional minor operations under ketamine and Vesprin (or on one occasion Torbutrol, 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. Also, additional major surgeries were performed on each animal to switch the location of the recording chamber from one hemisphere to the other.

VISUAL STIMULI

Visual stimuli were presented on a Masscomp Aurora Graphics terminal, using customized software initially developed at AT&T Bell Labs (Julesz et al., 1976; Sagi and Julesz, 1985) and modified at Caltech to run on a Masscomp Graphics workstation. The graphics workstation used a 19" noninterlaced 60 Hz color monitor.

Receptive Field Plotting

Once a cell was isolated, the borders of its classical receptive field (CRF) were determined using a computer-generated bar-shaped stimulus on a blank background. The size, shape, color, brightness, and motion of the bar could all be varied by the experimenter. Once the borders of the CRF had been mapped, the optimal size and color of the bar were determined qualitatively. Most cells responded to either a black on white or white on black stimulus. Due to the problems associated with ensuring that all elements in the more complex texture stimuli had equal luminances, most cells that were completely unresponsive to black or white stimuli were passed by; these cells were rare.

Orientation Tuning

For most cells in our detailed analysis (87/122), the optimal orientation of the cell was determined quantitatively under computer control. A single bar of the optimal size for the particular cell under study was presented on a blank background at each of 6 orientations in pseudorandom order (0°-150° in steps of 30°). Usually 3 sets of data were taken to determine the optimal orientation for the cell. The remaining tests were performed with the central bar at the cell's preferred and orthogonal orientation. For the 35 cells not tested quantitatively for orientation tuning, the preferred orientation was determined qualitatively by the experimenter.

Texture Stimuli

The basic stimulus used in our studies is illustrated in Figure 1. A single bar was placed in the plotted CRF, and it was surrounded by 4 rings of bars, oriented either orthogonally to the center element (as shown in the figure), identically to the center, or randomly. The

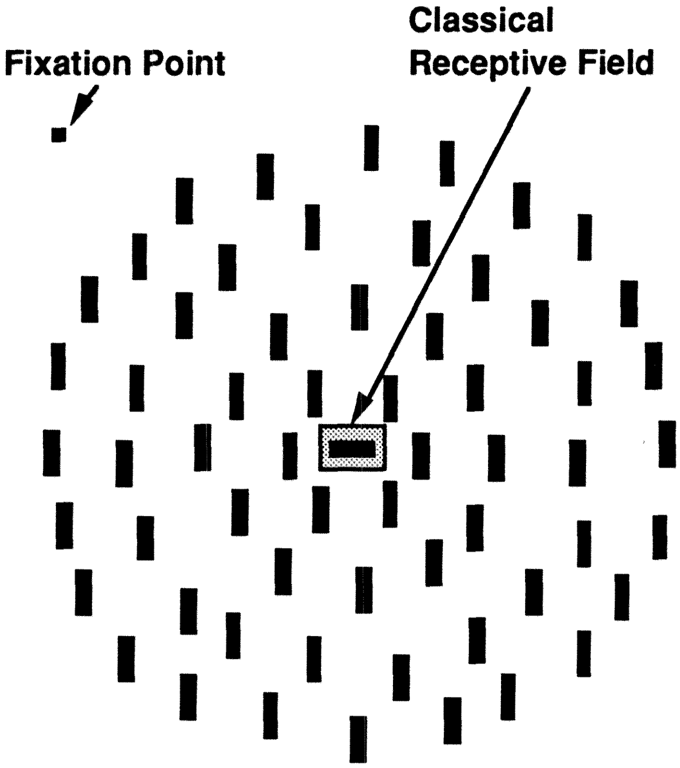


Figure 1. Orientation contrast stimulus. A center bar is placed within the cell's CRF, and rings of elements are placed outside the CRF. For a uniform orientation stimulus, both center and surround elements have the same orientation.

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). All of the surround bars were placed outside the borders of the CRF.

Various parameters controlled the exact appearance of the stimulus. The luminance of all the bars was kept equal. The height and width of the center bar was 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 elements were always the same size as the center element. 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. The spacing between elements was adjusted using one or two parameters: A spacing parameter changed the interelement distance while leaving the size of the elements the same, and a scaling parameter changed both the interelement distance as well as the size of both center and surround bars. The spacing of the surround was adjusted so that the innermost bars were as close to the plotted borders of the CRF as possible without actually encroaching within 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 positions of the surround bars were subject to a random positional jitter up to ±10% of the spacing between the centers of the elements, in order to eliminate higher order percepts arising from colinearity of the bars.

DATA COLLECTION

Neuronal activity was recorded with etched platinum-iridium wire (Frederick Haer Co.) electrodes insulated with a glass coating (Corning) (Wolbarsst, MacNichol, and Wagner, 1960). Electrode impedance ranged from around 1.5-5 MΩ. The electrode was passed through the dura each day by means of a stepping motor microdrive (Caltech Central

Engineering Services) mounted on a sealed chamber filled with mineral oil. At the end of the recording session, the electrode was removed and the chamber was disinfected with 0.05% Nolvasan solution or 0.3% hydrogen peroxide, and Garamycin Ophthalmic Solution (gentamicin sulfate), before being sealed.

Neural signals were amplified and filtered with a differential amplifier and single units were isolated with a time-amplitude window discriminator (Bak Electronics). Spikes were collected at 1 msec resolution by an AT compatible computer through the Lab Master interface. Eye position was also digitized and collected by the PC at 100 Hz. 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.

The presentation of stimuli, the initial plotting of receptive fields and testing of stimulus parameters, and the actual control of test runs were performed using custom software on the Masscomp workstation. Online bar graphs showed the results of each test run. Response histograms, dot rasters, and other analyses were performed offline on the Masscomp workstation.

STATISTICAL ANALYSIS OF SUPPRESSION INDICES

We calculated various indices (described in the Results chapter) to quantify some of the effects of the texture surround and performed t tests to statistically analyze the results. Although the indices were not known to be distributed normally *a priori*, t tests are still appropriate for two reasons: The data appear to be distributed fairly normally and the t test is known to be quite robust to deviations from the normality assumption. To be safe, we also performed nonparametric sign tests on all of the indices, and all significant differences from the t test were confirmed at the $p < .05$ level by the nonparametric test.

3 Results

Experimental log, April 10, 1989, Recording site A: "Unit, green selective, crummy response to white -- plotted RF with green bar, couldn't get good response to white -- lost cell when monkey sneezed"

CHAPTER SUMMARY

We recorded single unit responses to a set of textured stimuli: a center bar placed alone in the receptive field; a uniform orientation texture, in which the center bar was surrounded by rings of identically oriented elements, all outside the receptive field; an orientation contrast texture, in which the center bar was surrounded by rings of elements oriented orthogonally to the center bar; and the surround rings alone, with no bar in the receptive field. The addition of the surround elements modulated the response to the center element alone in the majority of cells tested. This modulation was almost always suppressive: On average, the surround textures reduced the response by about 35%. In addition, for a significant number of cells, the amount of suppression induced by the surround texture was dependent on the orientation of the surround elements. These cells responded more strongly to the orientation contrast texture than to the uniform orientation texture. Thus, the response properties of these neurons correlate with the perceptual salience of the center element.

We also tested responses to a texture pattern in which the surround elements were all oriented randomly. This stimulus is similar to the uniform orientation texture, in that there is no contrast in orientation between the center and surround. Overall, cells responded similarly to the random orientation texture and to the uniform orientation texture; the responses to both of these stimuli were smaller than the responses to the orientation contrast stimulus. This shows that the greater suppression induced by a noncontrast surround is not limited to the case in which all elements are oriented identically, but is instead a more general phenomenon.

In order to see whether the suppressive effects originated from regions at the ends of the center bars or along the flanks of the center bar, or from both regions, we tested cells with modified versions of the previous stimulus set, in which we restricted the surround elements to sets of quadrants at the ends of the bar or along the flanks. We found that both sets of quadrants contributed equally to the general suppression effect, but neither one suppressed the response as much as the full-field surround did. In addition, both sets of quadrants also contributed to the orientation-dependent differential suppression effect, but the contribution of the end regions was somewhat larger than that of the flank regions. These results indicate that the surround suppression is not limited to restricted regions at the ends or sides of the receptive field, but instead arises from all around the receptive field.

We tested the effect of increasing the spacing between the surround texture elements, since this is a critical parameter in the psychophysical perception of pop-out. As the spacing between elements increased, in general the suppression induced by the surround decreased. It is unclear whether this effect is due to the increased distance between the center element and the innermost ring of elements or whether it is due to the overall decreasing density of surround elements.

We analyzed the time course of the population response to the different texture patterns. Both the general suppression effect and the differential suppression effect were evident very early in the population response, both appearing by the time the population reaches its peak response shortly after stimulus onset. However, it takes about 7 msec for the general suppression effect to become evident and about 20 msec for the differential effect to become evident. Thus, these effects do not appear instantaneously; some degree of processing goes on at the population level before the suppressive effects are generated.

Overall, these results are consistent with the psychophysics of pop-out, in that cells respond more strongly to an orientation contrast pattern than to a noncontrast pattern. In addition, the quickness with which the population responses show the suppressive effects is consistent with the short exposure times sufficient for human observers to perceive pop-out targets.

OVERVIEW

We recorded from a total of 170 cells in V1, most of them located on the operculum but a few in calcarine V1. 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 3 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. Moreover, there were two major types of surround suppression revealed: (1) a general suppression induced regardless of the orientation of the individual elements and (2) various types of orientation-dependent suppression. The most prevalent type of orientation-dependent suppression was a differential suppression based on whether the surround elements were identical in orientation to the center element (uniform orientation texture) or were orthogonal in orientation to the center element (orientation contrast texture). For the great majority of cells showing differential suppression, the responses were significantly larger to the orientation contrast texture than to the uniform orientation texture.

GENERAL SUPPRESSION

The most common effect of adding a texture background to a single bar in the CRF was to suppress the firing of the cell. For the majority of cells (93/122, 76%), the response to the center bar was significantly suppressed by at least one of the texture backgrounds. Slight enhancement was seen on occasion, but infrequently.

Some examples of the general suppression induced by the texture surround are shown in Figure 2. The cell illustrated in Figure 2A was almost completely suppressed by the texture surrounds. The upper part of the figure shows the cell's mean firing rate (+ 1 S.E.M.) to the different stimuli. Below that are post-stimulus 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 Figure 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 Configfuration 7: C'≠S'); and the *surround elements alone,* with no element encroaching upon the cell's classical receptive field (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

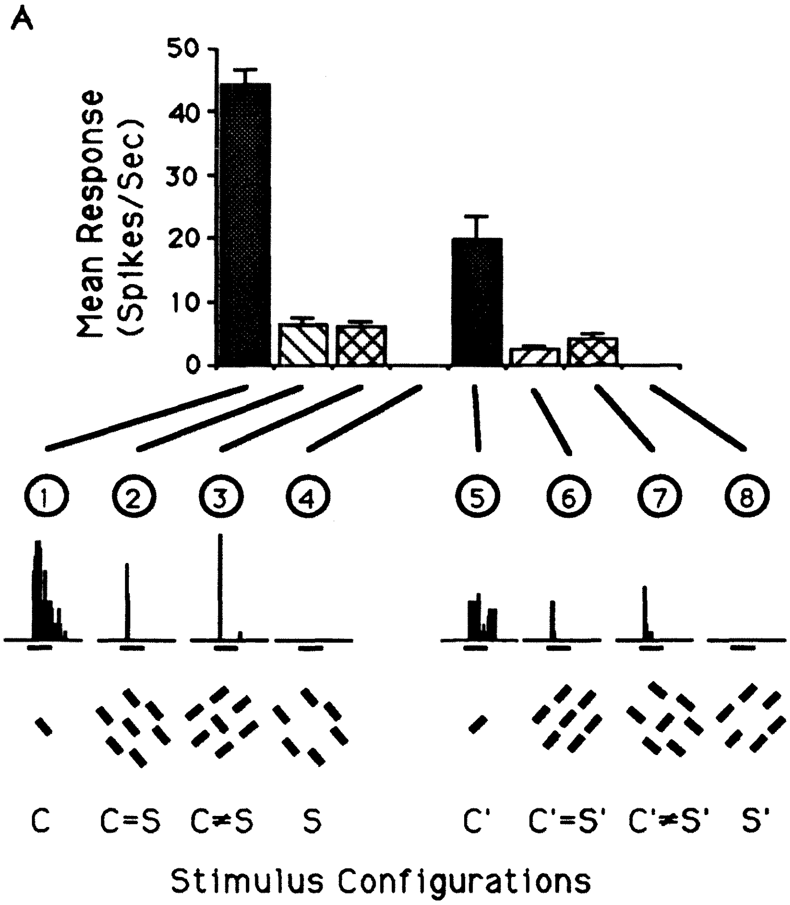


Figure 2. Examples of cells showing a general suppression effect. (A) Orientation biased cell with a strong suppressive effect of surround texture. Cell 89c4A. (B) Strongly orientation selective cell with a strong suppressive effect of the surround texture. Cell 89c11A. (C) Orientation insensitive cell with a moderate surround suppression. Cell 87a93B.

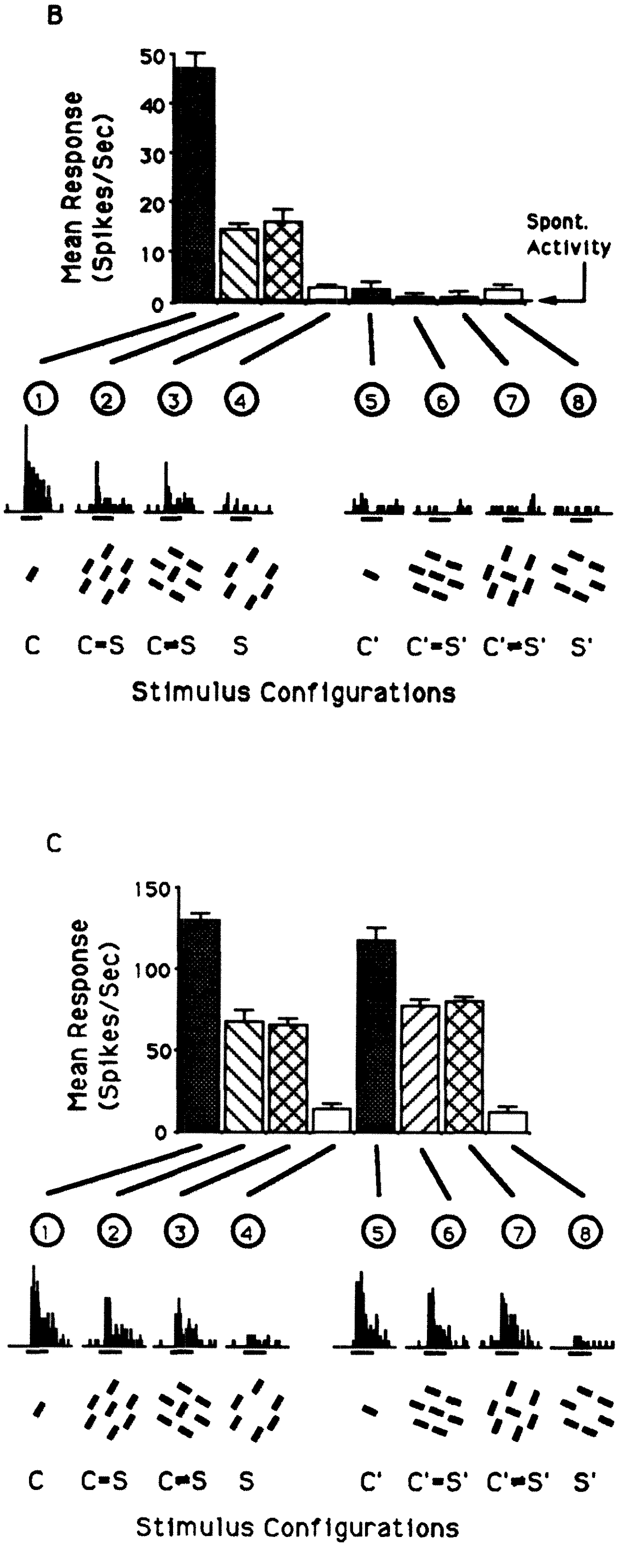


Figure 2 (cont.)

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 elements within the CRF. Both the optimally oriented center bar and the orthogonal bar were suppressed by similar amounts.

Another example is shown in Figure 2B. This cell was strongly orientation selective (C vs. C'). When the optimally oriented center bar was surrounded by the texture elements, there was a similar strong suppression of the cell's response. A final example is shown in Figure 2C. 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; however, when they had any influence on the response to the center elements, it was almost always suppressive. (See Discussion for further comments on this result.)

General Suppression Index

We quantified the amount of general suppression induced by the texture background by computing a general suppression index (GSI) for each cell. This index calculated the average amount of suppression induced by both the orientation contrast texture and the uniform orientation texture, weighted by the response to the center element alone, according to the following formulae:

1) Calculate Average Suppression Index (ASI) for each center element:

$$\mathrm{ASI} = 1 - \frac{\text{Average}\,(C \neq S,\ C = S)}{C}$$

2) General Suppression Index is the weighted average of the ASIs for each center orientation, reversed in sign so that suppression is negative, enhancement is positive:

$$\mathrm{GSI} = -\ \frac{(C * \mathrm{ASI} + C' * \mathrm{ASI}')}{(C + C')}$$

Thus, the GSI for a cell represents the average percent suppression induced by the texture backgrounds relative to the responses to the center elements alone. 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 Figure 2 are -0.85 (A), -0.71 (B), and -0.42 (C).

Figure 3 shows the distribution of GSIs for the sample of 122 cells. The mean GSI is -0.34, which is highly statistically different from 0 (2-tailed t test, $t = 11.33$, $p < .001$). Thus, on average, the presence of a texture background suppresses V1 cells by 34%.

DIFFERENTIAL SUPPRESSION

For 41% of the cells, there was a significant difference in the amount of suppression induced by the two different texture backgrounds. Importantly, for the great majority of these cells, the response was greater to the orientation contrast texture than to the uniform orientation texture. For the few cells responding better to the uniform texture, only one of them showed a strong difference. Examples of these cells are shown in Figure 4.

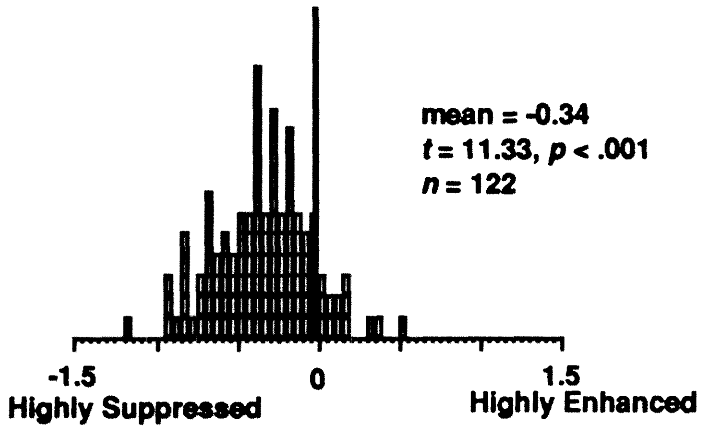


Figure 3. Distribution of General Suppression Index (GSI). -1.0 indicates 100% suppression; +1.0 indicate 100% enhancement. A value surpassing -1.0 can result from the surround suppressing the response below the baseline activity for that cell. The average amount of suppression is around 35%.

The cell in Figure 4A showed no orientation selectivity for the center element alone (C vs. C'). When the center element was surrounded by identically oriented elements (C=S, C'=S'), the cell was strongly suppressed. However, when the surround elements were oriented orthogonally to the center element (C≠S, C'≠S'), there was no significant suppression. For both center orientations, the cell responded 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 is sensitive to orientation contrast regardless of the absolute orientations of the individual elements.

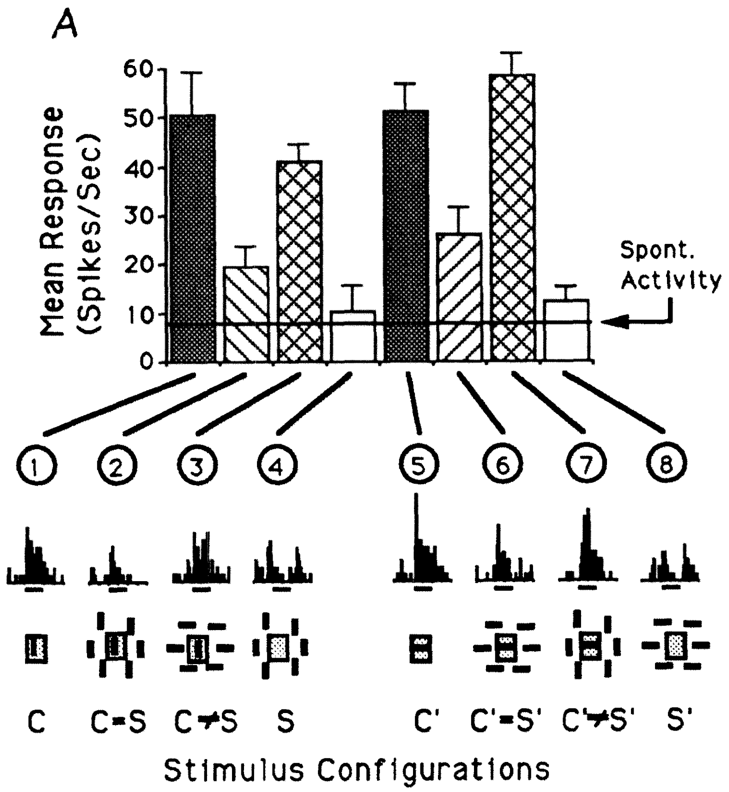


Figure 4. Examples of cells showing a differential supppression effect, where the response to the orientation contrast stimulus is greater than the response to the uniform orientation stimulus. (A) Orientation insensitive cell showing a strong differential suppression effect for both center orientations. For this cell, there is no suppression induced by the orientation contrast stimulus. Cell 87a30A. (B) Strongly orientation selective cell showing a fairly strong differential suppression effect for the responsive center orientation. Both contrast and uniform stimuli suppress the response, but the suppression is greater for the uniform stimulus. Cell 89c8A. (C) Orientation insensitive cell showing a moderate differential suppression 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.

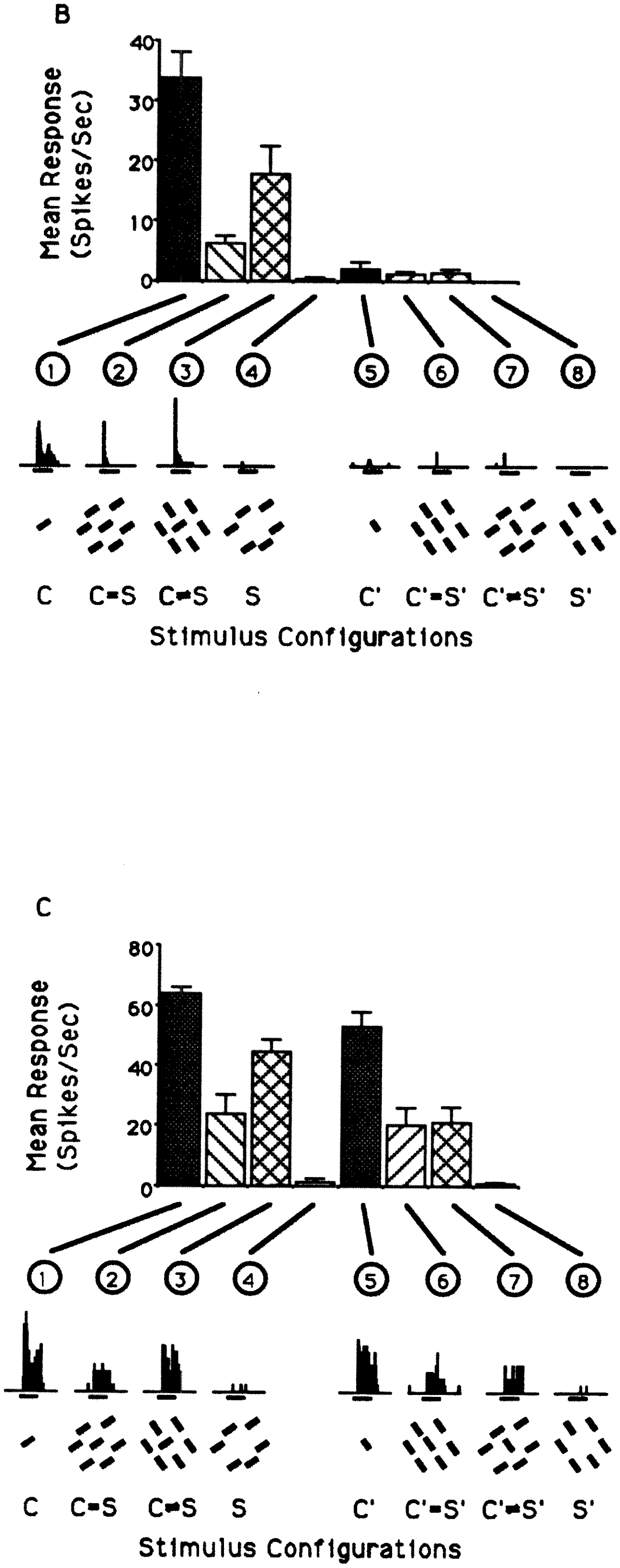


Figure 4 (cont.)

Another example is shown in Figure 4B. 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≠S). This was a typical pattern of results for such cells. In general, both surround textures tended to suppress the cell's response; however, in cells like this example, the suppression was greater for a uniform texture than for an orientation contrast texture.

Figure 4C shows a third example of differential suppression. Like the cell in Figure 4A, this cell was not selective for the orientation of the center element alone. It showed a differential suppression for one of the center orientations (C=S vs. C≠S) but showed a general suppression for the orthogonal center orientation (C'=S' vs. C'≠S'). This was also a common result. 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 Figure 4B) or just did not show the effect for one of the two center orientations (as in Figure 4C). The remaining 8 cells (20%) had an orientation contrast effect for both center orientations (as in Figure 4A).

Differential Suppression Index

In order to quantify the differential suppression between the two different texture backgrounds, we calculated for each cell a differential suppression index (DSI), according to the following formulae:

1) Calculate the difference in firing rates (DF) between the orientation contrast and uniform texture fields relative to the firing rate to the center element alone:

$$DF = \frac{(C \neq S) - (C = S)}{C}$$

2) Differential Suppression Index is the weighted average of the DFs for each center orientation:

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

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

Figure 5A shows the distribution of DSIs for the sample. The mean DSI for the sample is 0.09, which shows that on average cells in V1 respond 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, $t = 4.50$, $p < .001$). Figures 5B and 5C break the sample down into two populations: cells like those in Figure 4 that show a statistically significant orientation

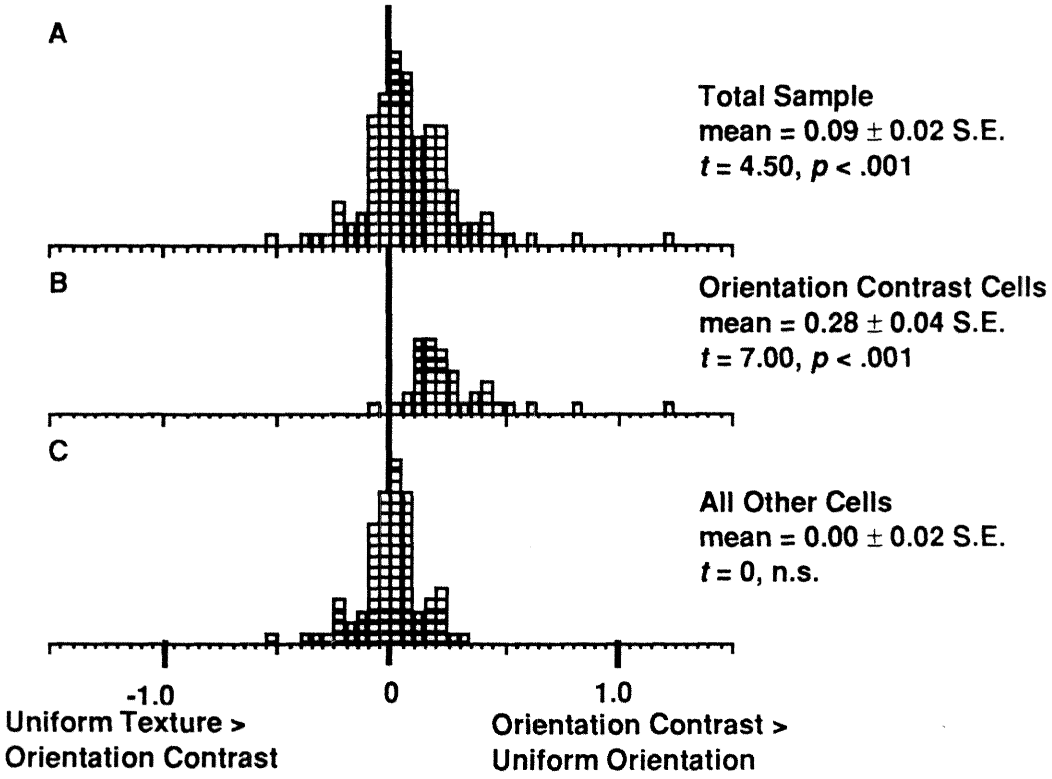


Figure 5. Distribution of Differential Suppression Index. (A) Distribution for the entire sample of 122 cells. Overall, the average suppression induced by the uniform surround was about 10% greater than the supression induced by the contrast surround. (B) Distribution for cells classified as Orientation Contrast. For these cells, the average difference in suppression was almost 30%. The one negative value for this group resulted from a cell that had a small but statistically significant orientation contrast effect for one 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.

contrast effect (Figure 5B; see next section) and the remaining cells in the sample (Figure 5C). The mean DSI for the Orientation Contrast cells was 0.28 ($t = 7.00, p < .001$); for all other cells, the mean DSI was 0.

CELL CLASSES

In order to convey an idea of the types of responses elicited by individual cells, we grouped the cells into six response classes. It should be emphasized that this classification is somewhat artificial and may not reflect a natural functional division of cell types in the brain. The range of responses to these stimuli probably forms a continuum. Still, such a classification scheme is a useful way of describing the main effects encountered and the relative frequency of the different effects in the population.

The cells were placed into the following groups based on the relationship of the responses to the two texture patterns and the center bar alone:

> *General Suppression:* Response to each texture pattern was significantly less than the response to the center bar alone, but the texture responses were not significantly different from each other. Examples are shown in Figure 2.
>
> *Orientation Contrast:* 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. In most cases both texture backgrounds suppressed the firing rate somewhat, but the magnitude of the effect was different. In other cases, only the uniform orientation texture surround elicited a significant suppression, whereas the orientation contrast texture surround produced no effect. Examples of this group are shown in Figure 4.

No Effect: Responses to both texture conditions were statistically identical to the response to the center element alone. An example is shown in Figure 6. For this cell, the responses to the center element alone (C) are indistinguishable from the responses to either texture surround (C=S, C≠S).

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

Center-Dependent Suppression: Both texture surrounds suppressed the response to one of the center bar orientations equally, but did not affect the other center bar orientation. Figure 7 shows an example of one such cell. Both texture surrounds suppress the response to the first center orientation (C) but neither have any effect on the orthogonal center orientation (C').

Surround-Dependent Suppression: The cell shows a differential suppression for each center orientation, but for one center orientation the orientation contrast texture is the stronger response, whereas for the orthogonal orientation the uniform texture response is the stronger. Thus, for these cells, the surround suppression depends on the absolute orientation of the surround, rather than on the presence or lack of orientation contrast. An example is shown in Figure 8.

Uniform Orientation: 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. The only moderately

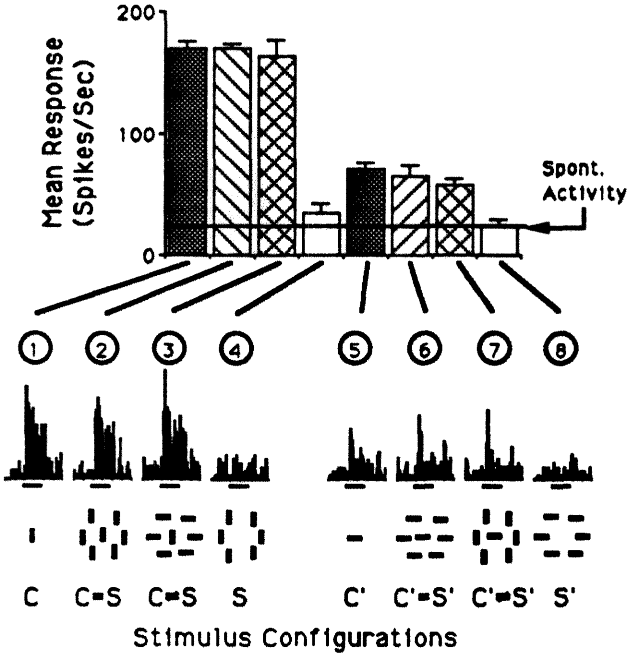


Figure 6. Example of a cell that was not affected by the surround. Cell 87a91A.

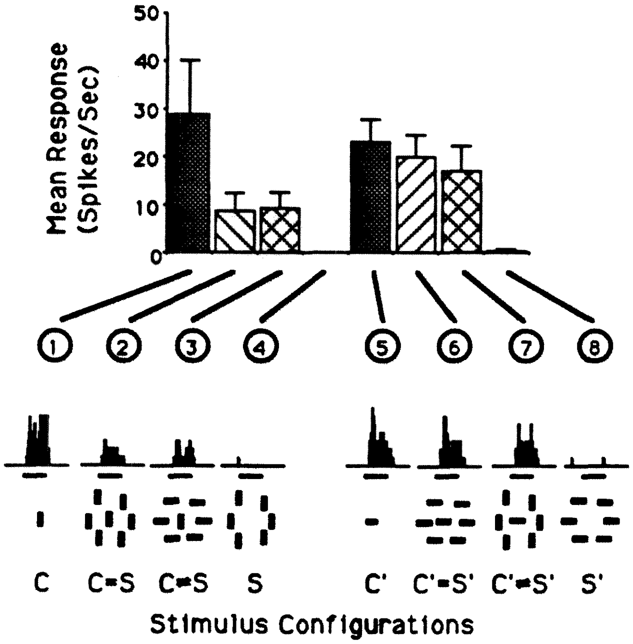


Figure 7. Example of a cell that had a center-dependent suppression: for one center orientation, the surround textures suppressed the response generally, but for the other center orientation, they had no effect. Cell 87a49B.

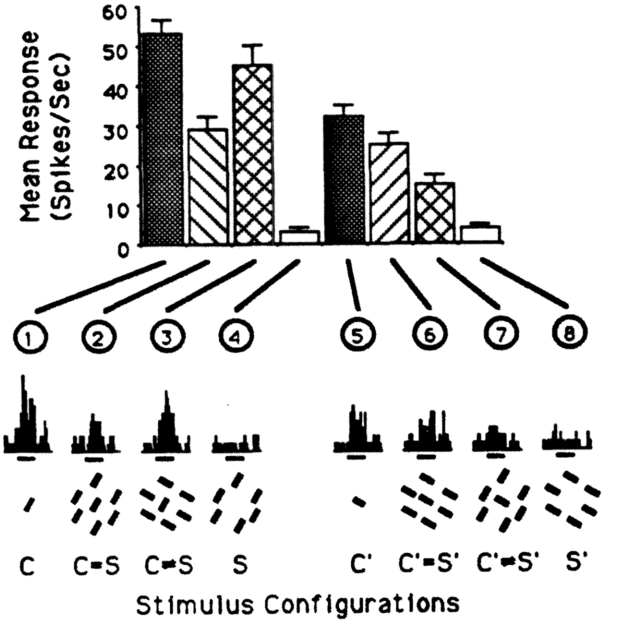


Figure 8. Example of a cell that had a surround-dependent suppression. For both center orientations, a particular surround orientation suppressed the response greater than the orthogonal surround orientation. Cell 89c31a.

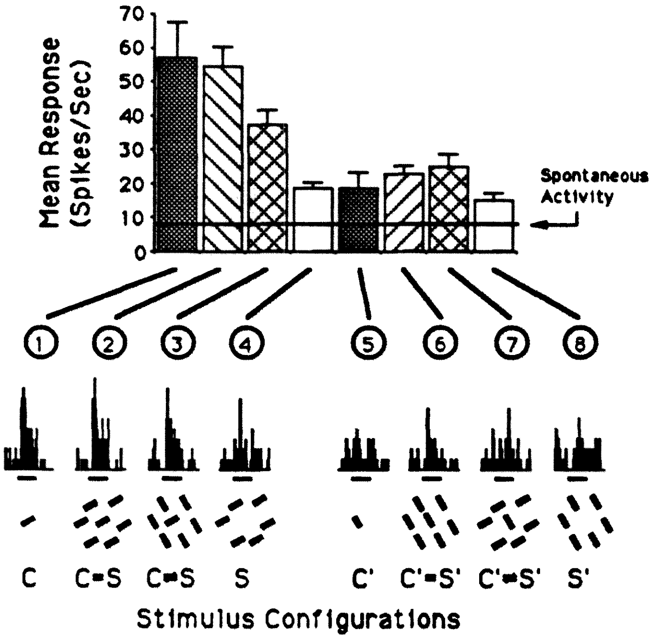


Figure 9. Example of a cell that had a uniform orientation effect. For the optimal center orientation, the response to the uniform orientation stimulus was greater than the response to the orientation contrast stimulus. This cell is the only fairly strong example of this effect in our sample. Cell 89c45A.

strong example of this effect is shown in Figure 9. For the optimally oriented bar in the center, there is no suppression induced by the uniform surround, whereas the orientation contrast surround induces a moderate suppression. There is no effect of either surround for the orthogonal center element.

Figure 10 shows the relative frequency of the different cell groups within the sample of cells studied. About 30% of the cells showed a significant orientation contrast effect, whereas only about 6% showed a uniform orientation effect. Thus, of the cells showing a differential suppression effect, the great majority have response properties that correlate with the perceptual salience of the center element; that is, they fire more strongly when there is a contrast in orientation between the center and surround. About 25% of the cells were generally suppressed by both texture backgrounds, and 25% showed no significant effect for any of the texure backgrounds. The remaining cells fall into the center- and surround-dependent groups.

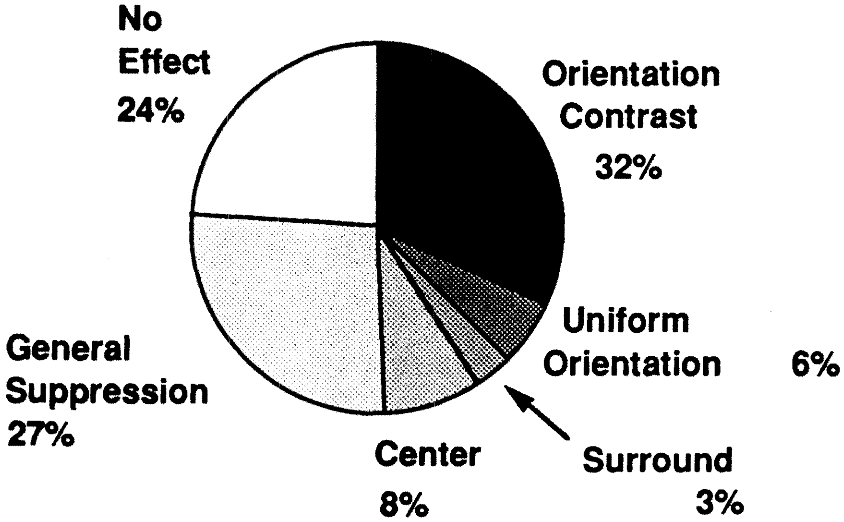


Figure 10. Caption on next page.

Figure 10. (cont.) Breakdown of sample into 6 cell classes. The detailed rules for classifying cells are as follows: A cell was regarded as responding differently to two stimuli if the mean + 1 S.E.M. for one stimulus was smaller than the mean - 1 S.E.M for the other. If a cell had an orientation selectivity index (1 - Orthogonal/Preferred) for the center elements alone greater than 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 less than 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 one center orientation. The one 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 one center orientation. The same exception applies in regards 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 classed as General Suppression rather than Center-dependent. (4) Cells were classified as *No Effect* if the responses to

(cont. next page)

RANDOM ORIENTATION SURROUND

As a whole, cells in V1 respond more strongly to an orientation contrast texture than to a uniform orientation texture. We wondered whether this was a general effect due to the overall presence or absence of orientation contrast, or whether the particular orientations in our stimuli were essential to produce the orientation contrast effect: In other words, do the elements in the contrast texture have to be oriented orthogonally to the center element and do the elements in the uniform texture have to be oriented identically to the center element? To address this issue, we tested 50 cells in Monkey 89c with an additional texture pattern in which each background element was randomly oriented at one of six orientations (Figure 11). This stimulus was similar to the uniform orientation texture in that there was no orientation contrast between the center and surround; the center element was just one of many randomly oriented bars.

Figure 10 (cont.). the 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 ± S.E.M.), 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 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 S.E.M. for the two texture stimuli and compared that to the mean - 1 S.E.M. for the center bar alone. If the mean texture value was smaller than the center bar alone, the cell was classed as General Suppression; otherwise, it was classed as No Effect.

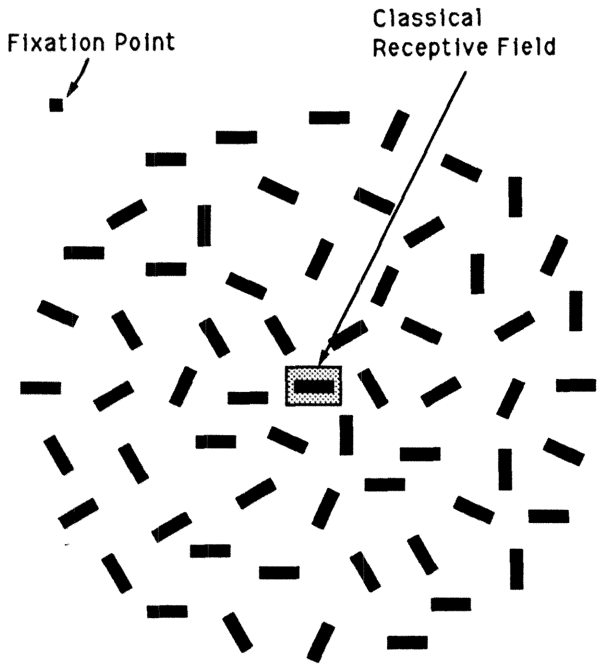


Figure 11. Random orientation texture stimulus.

Random Orientation Differential Suppression Index

In order to quantify the difference in responses elicited by the orientation contrast and random orientation textures, we calculated an index analogous to the Differential Suppression Index by using the values from the random orientation texture in place of the uniform orientation texture in the DSI formula. The distribution of this Random Orientation Differential Suppression Index (RODSI) is shown in Figure 12A. The distribution of DSIs for the same cells is shown in Figure 12B. Although the mean DSI for this subset of cells is smaller than that for the whole sample, the difference is not statistically significant (2-tailed t test, 50 cells in Figure 12 versus 72 remaining cells in sample, $t = 0.68$, n.s.). A comparison of Figure 12A with 12B shows that the distributions of DSI and RODSI are nearly identical. The mean RODSI value was .06, which was significantly larger than 0 (2-tailed t test, $t = 3.00$, $p < .05$). Thus, on average, cells are suppressed more strongly by the random orientation texture than by the orientation contrast texture. The average difference in suppression is 6% of the firing to the center element alone.

Moreover, when one compares the values of DSI for the 10 cells that show a statistically significant orientation contrast effect between the contrast texture and the uniform texture with the values of RODSI for the 9 cells that show a significant orientation contrast effect between the contrast texture and the random orientation texture (these cells

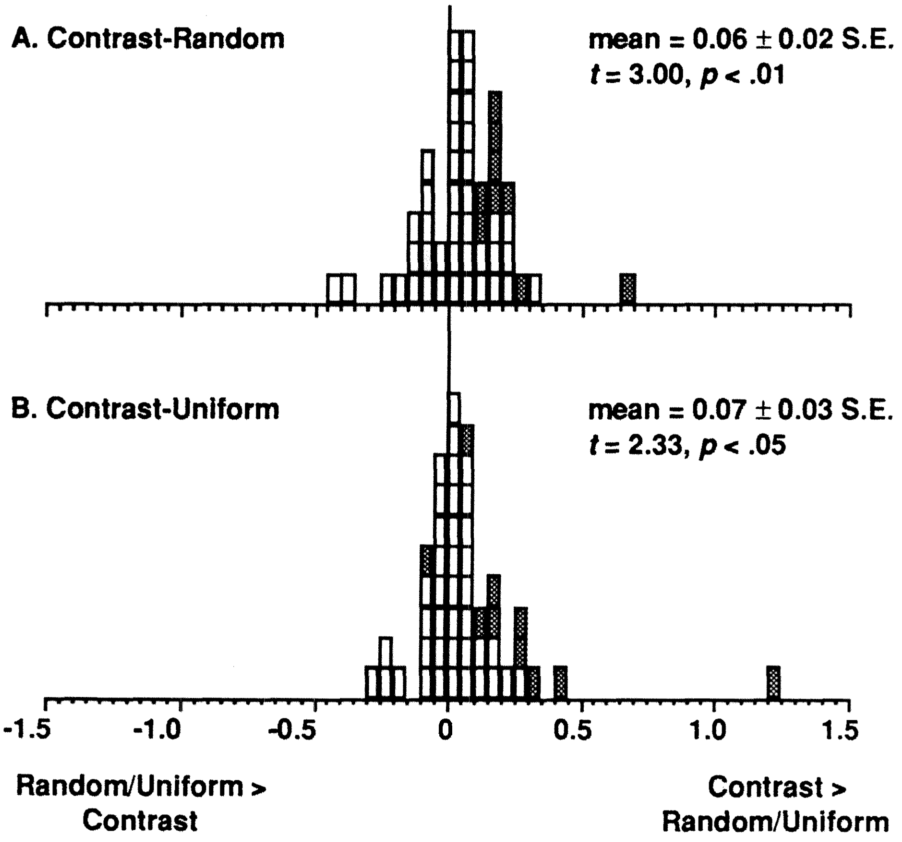
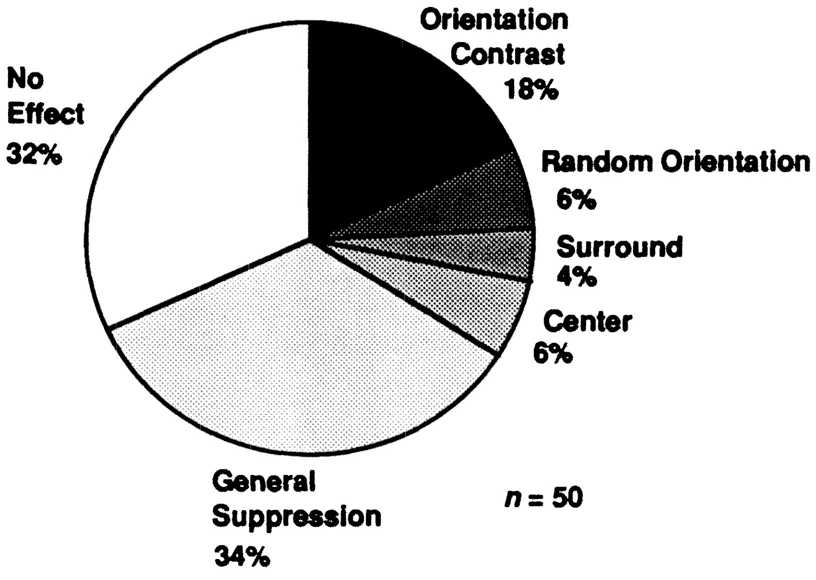


Figure 12. Distributions of Random Orientation Differential Suppression Index (A) and Differential Suppression Index (B) for 50 cells tested with the random orientation texture. Both distributions are statistically greater than 0. The dark shading indicates those cells classified as Orientation Contrast (*A:* C > R; *B:* C > U).

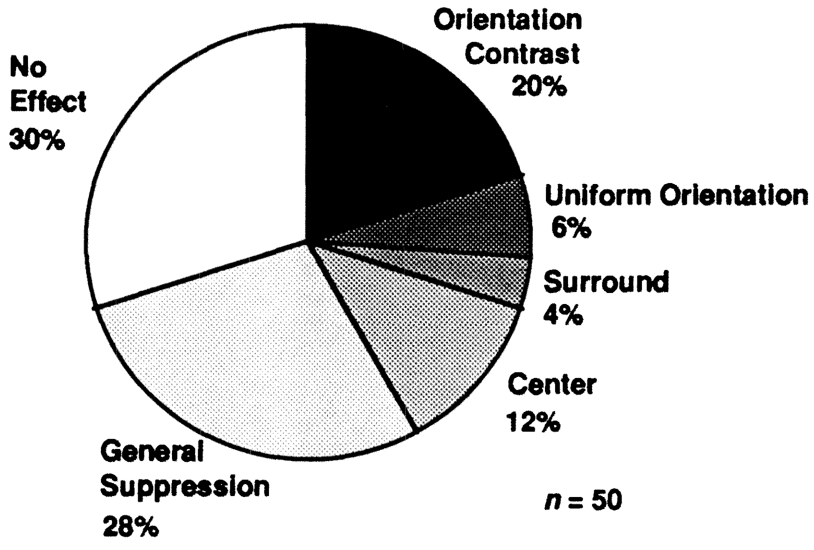
are shaded dark in Figure 12), there is no statistically significant difference in the means (mean DSI = .30 ± .11 S.E.M.; mean RODSI = .24 ± .06 S.E.M.; 2-tailed *t* test, $t = 0.54$, n. s.). Thus, the random orientation texture does not differ from the uniform orientation texture in suppressing the responses of these cells; each noncontrast texture suppresses the response more strongly than the orientation contrast texture.

Cell Classes

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 Figure 13A. Of the 50 cells tested, 9 (18%) responded more strongly to the orientation contrast texture then to the random orientation texture. Only 3 (6%) responded better 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 13B shows the cell groups based on 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 are consistent with the interpretation that it is the presence or absence of orientation contrast in general, rather than the presence of a uniform orientation field, that produces the differential suppression effect. However, we have not ruled out the possibility that the background elements must be orthogonal in orientation to the center element to produce the differential effect. For example, do cells respond more strongly to a texture in which the background elements are oriented at 45° from the center element than to a uniform orientation texture? (See Discussion.)



A. Orientation Contrast vs. Random Orientation



B. Orientation Contrast vs. Uniform Orientation

Figure 13. Breakdown of sample of 50 cells tested with random orientation texture into cell classes based on orientation contrast vs. random orientation response comparison (A) and orientation contrast vs. uniform orientation response comparison (B).

Cell by Cell Comparison of Random vs. Uniform Suppression Effects

One question that arises from these results is whether there is a population of general "orientation contrast detectors" in V1, or whether some cells are sensitive to particular kinds of orientation contrast and insensitive to others. Although, overall, cells in V1 respond more strongly to the orientation contrast pattern than to the two noncontrast patterns, only 3 cells showed a significant orientation contrast effect when comparing the orientation contrast texture with both noncontrast textures. Of the remaining 13 cells that showed a significant orientation contrast effect for either noncontrast texture, 7 showed the effect only with the uniform texture and 6 showed it only with the random orientation texture. An example of each is shown in Figure 14.

Overall, only about half of the cells studied (28/50, 56%) were classified identically when comparing the contrast texture with both noncontrast textures. Table 1 compares the cell classification results for the contrast-uniform comparison with the results from the contrast-random comparison. We see that cells that were classified as General Suppression or No Effect in one comparison tended to keep that classification in the other comparison. The other classes were much more inconsistent, with cells jumping categories from one comparison to the other in no orderly fashion. This is especially true for the Orientation Contrast cells (C > U, C > R). As mentioned before, only 3 cells are classified as Orientation Contrast under both comparisons; the others are scattered fairly evenly among the other categories 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 noncontrast 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).

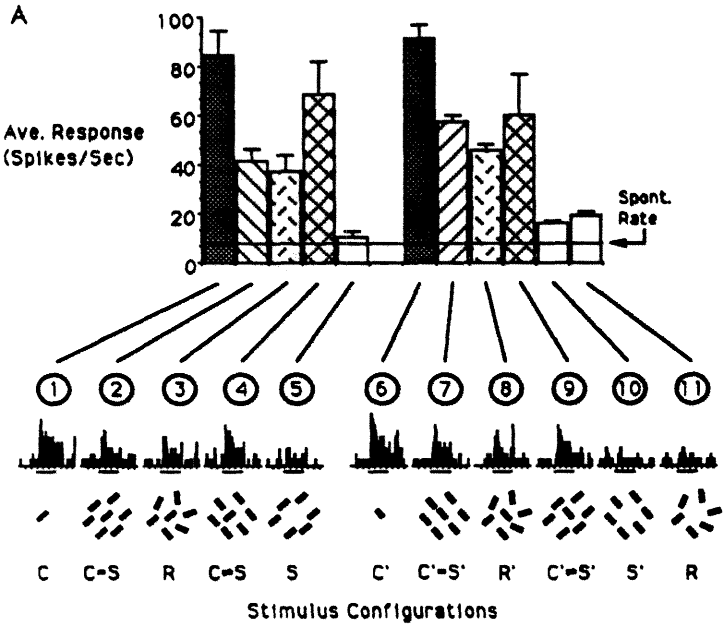


Figure 14. Examples of cells showing differential suppression effects tested with the random orientation surround. (A) Orientation insensitive cell that showed a differential suppression when comparing the orientation contrast pattern (Configuration 4) with both the uniform (Configuration 2) and random (Configuration 3) orientation patterns. For the orthogonal center element (Configurations 6-9) the cell showed a general suppression. Cell 89c46B. (B) Orientation insensitive cell that showed a differential suppression for both center orientations when comparing the orientation contrast pattern (Configurations 4 and 8) with the uniform orientation pattern (Configurations 2 and 7), but a center-dependent suppression when comparing the orientation contrast pattern with the random orientation pattern (Configurations 3 and 8). Cell 89c49A. (C) Orientation selective cell that showed a differential suppression when comparing the orientation contrast pattern (Configuration 4) with the random orientation pattern (Configuration 3) and no effect when comparing the orientation contrast pattern with the uniform orientation pattern (Configuration 2). Cell 89c14B.

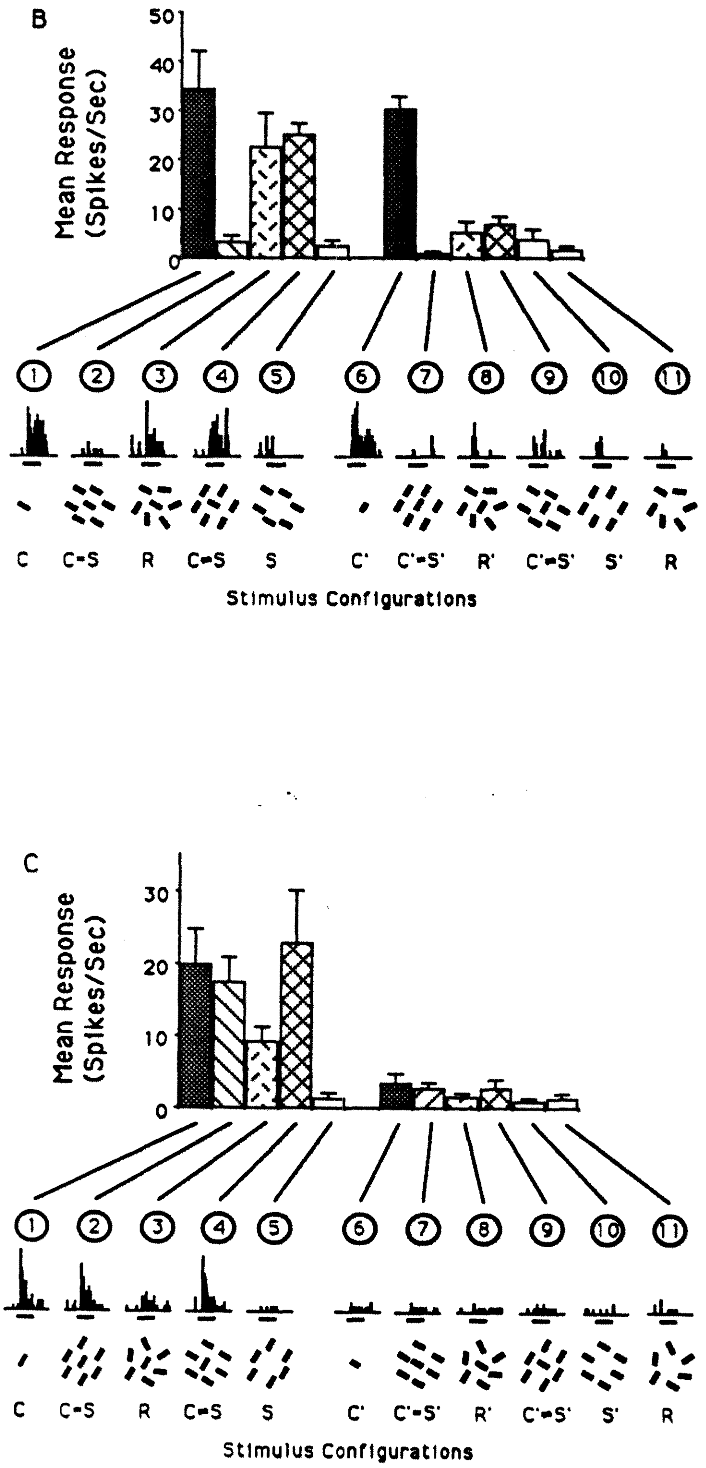


Figure 14 (cont.)

Table 1. Cell classification based on contrast-uniform comparison vs. contrast-random comparison.

Contrast-random classes	Contrast-uniform classes					
	C > U	U > C	S	C	GS	NE
C > R	3		2	1	1	2
R > C				1		2
"S"				1		1
C	1			2		
GS	3	1			13	
NE	3	2		1		10

C > U, C > R: Orientation contrast; U > C, R > C: Uniform orientation; S:Surround-dependent suppression; C: Center-dependent suppression; GS: General suppression; NE: No effect.

NORMALIZED POPULATION RESPONSES

In order to provide an overall picture of how the population responds as a whole to the different texture configurations, we normalized each cell's responses to its response to 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 calculated the mean normalized response rate for each configuration over the sample, and the results are shown in Figure 15. On the right side of the figure, we see the normalized responses for the whole sample of 122 cells. The responses to Configurations 2 and 3 (uniform orientation and orientation contrast) are 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 is 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

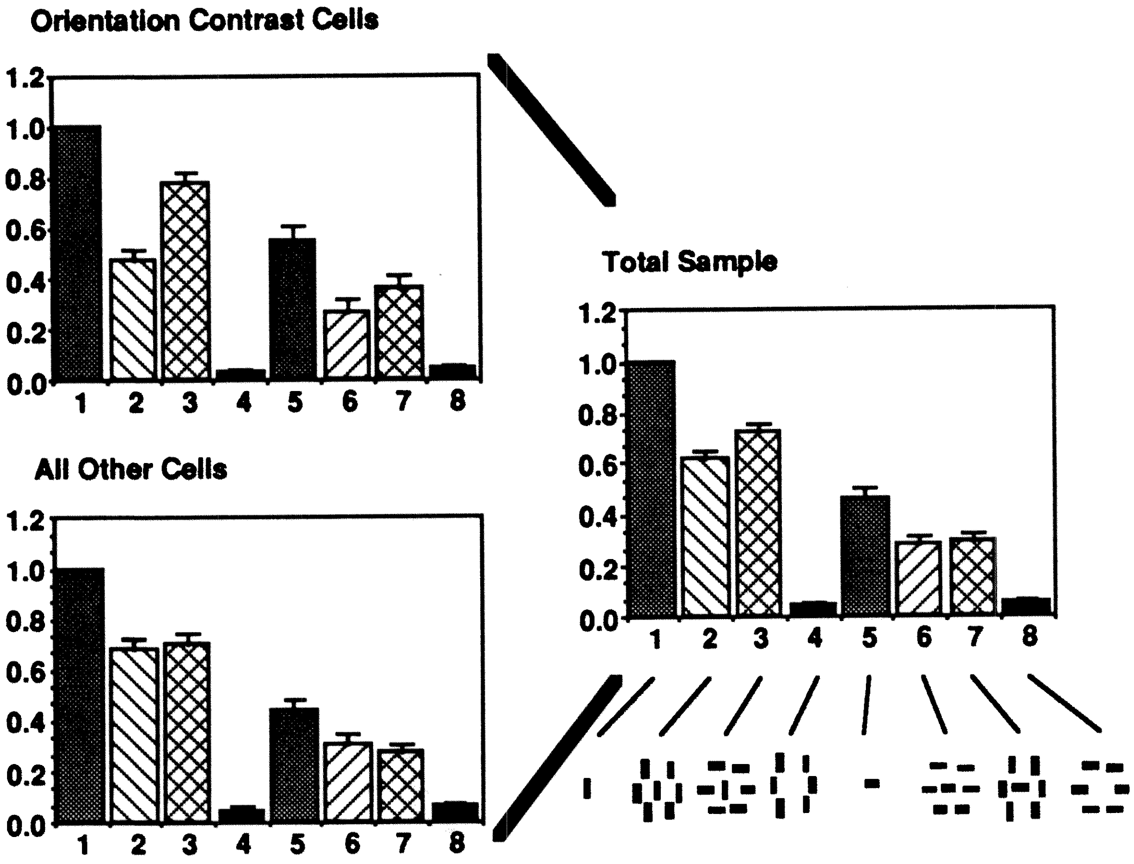


Figure 15. Normalized population responses. Each cell's response pattern was normalized to the cell's response to the optimally oriented center bar alone. The right side of this figure shows the mean normalized responses for the whole sample of 122 cells. A large general suppression and modest but significant orientation contrast effect are evident for the population when comparing Configurations 1-3. The left side of the figure breaks the sample down into the 39 cells classed 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.

a significant orientation contrast effect and the remainder of the sample. The Orientation Contrast cells show a larger difference between the uniform texture and the contrast texture (about 30%) than does the total sample. The other cells show an overall general suppression of about 30% but no significant difference between the two texture patterns. These figures can be taken as average response graphs for V1 as a whole, analogous to the graphs shown previously for individual cells. Overall, V1 is suppressed by the presence of surround textures, and because of the presence of some cells that show a differential suppression, the response of V1 to an orientation contrast texture is significantly larger than its response to a uniform orientation texture.

Figure 16 shows a similar analysis for the 50 cells tested with the random orientation texture. The format of these graphs is similar to Figure 15, except that the random orientation responses (Configurations 3 and 8) have been inserted in 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. We see that the overall general suppression induced by all three texture surrounds is about 25%-30%. The difference in responses between the uniform texture (Configuration 2) and the contrast texture (Configuration 4) is statistically significant (paired t test, $t = 3.00$, $p < .01$) and does not differ statistically from the response difference for the whole sample (Figure 15). In addition, the difference between the random orientation texture (Configuration 3) and the contrast texture (Configuration 4) is somewhat smaller and it barely misses statistical significance at the .05 level (paired t test, $t = 2.00$, $p < .10$). There is no significant difference between the uniform texture and the random orientation texture. The differential effects are more apparent when the sample is broken down on the left side of the figure. The top graph illustrates the 9 cells that showed a significantly greater response to the contrast texture than to the random orientation texture (the Orientation Contrast cells of Figure 13A). The middle graph illustrates the 10 cells that showed a significantly larger response to the orientation contrast texture than to the uniform

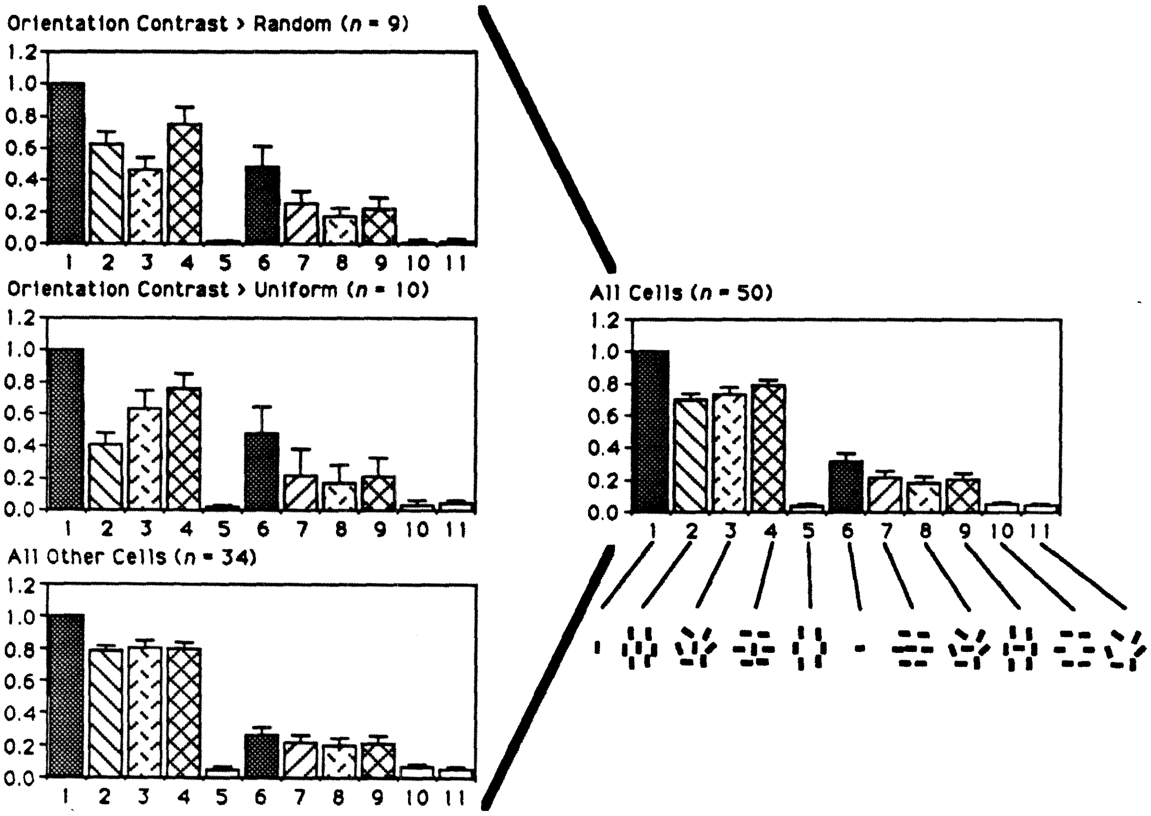


Figure 16. Normalized population responses for the 50 cells tested with the random orientation stimulus. The responses for the whole sample of 50 cells are shown on the right. A small but statistically significant orientation contrast effect is evident between the orientation contrast pattern (Configuration 4) and the uniform orientation pattern (Configuration 2), barely missing significance for the random orientation pattern (Configuration 3). The left side of the figure breaks the sample down into those cells that show a contrast-random orientation contrast effect (top), those cells that show a contrast-uniform orientation contrast effect (middle--includes 3 cells that are also represented in top graph, such as the cell in Figure 14A), and the remainder of the sample (bottom).

orientation texture (the Orientation Contrast cells of Figure 13B). Three cells are shared by both groups. The bottom graph illustrates the 34 remaining cells. These graphs illustrate that V1 as a whole responds more strongly to an orientation contrast pattern that to either noncontrast pattern. This population effect is due to the presence of two moderately overlapping populations of cells that show a much stronger suppression to either the random orientation texture or the uniform orientation texture.

SPATIAL ORGANIZATION OF SURROUND EFFECTS

In order to obtain information about how these suppressive surround effects are generated, we tested cells with stimuli designed to study the spatial organization of the effects. We were specifically interested in 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.

To address these questions, we stimulated the cells with modified versions of the texture patterns used previously. Examples of the stimuli are shown in Figure 17. 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. 17A); 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. 17B).

Figure 18 shows the responses to the surround quadrant stimuli for the same cell illustrated in Figure 4A. Part A shows the responses to the stimuli in which the center element was oriented vertically, and Part B shows the responses to the stimuli in which the center element was oriented horizontally. The first 4 configurations in each part show the responses to the center element alone and to the full-field textures; they are identical to the 8 stimulus configurations shown in Figure 4A. Configurations 5 and 6 show the responses to the texture patterns restricted to the flanking quadrants, and Configurations 7 and 8 show the responses to the texture patterns restricted to the end-zone quadrants. Configurations 5 and 7 are uniform textures, whereas Configurations 6 and 8 are orientation contrast textures.

For each set of surround quadrants, the responses to the orientation contrast textures were larger than the responses to the uniform orientation textures (Configurations 5 vs. 6 and 7 vs. 8). Thus, for this cell, the response patterns for both the flanking quadrants and the end-zone quadrants were similar to the full-field texture: Each showed an orientation contrast effect, although to varying degrees. For the vertical center orientation (Part A), the differential suppression was not as strong for either set of quadrants as it was for the full-field texture, and indeed was not even statistically significant for the end-zones. For

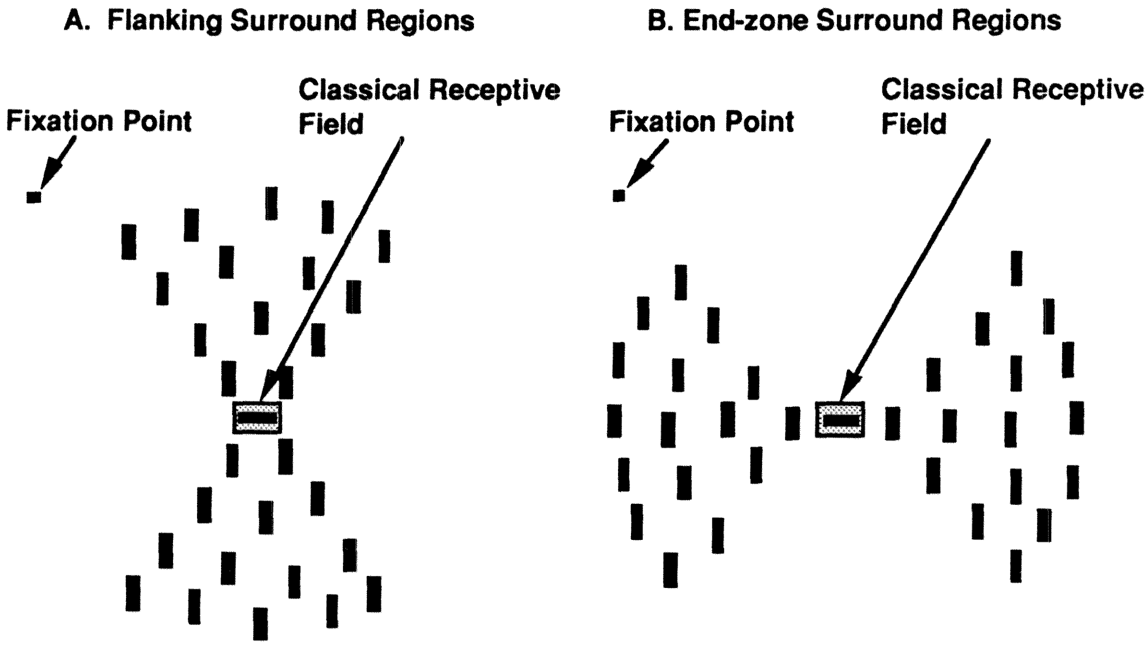


Figure 17. Surround quadrant stimuli. (A) Stimulus in which the surround texture elements are restricted to quadrants along the flanks of the center bar. (B) Stimulus in which the surround texture elements are restricted to quadrants at the ends of the center bar.

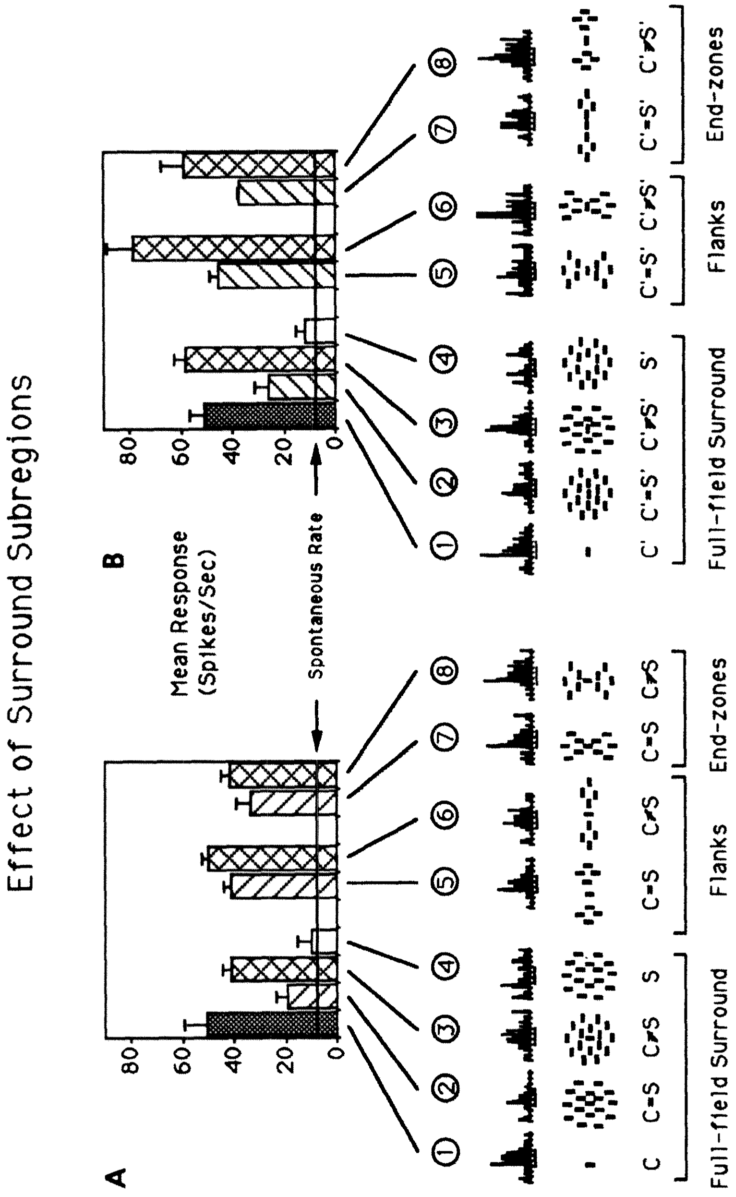


Figure 18. Example of responses to the surround quadrant stimuli. This is the same cell as previously illustrated in Figure 4A. We see that for both center orientations (A and B), both sets of surround quadrants (flanks and end-zones) produce at least a trend toward the orientation contrast effect seen with the full-field texture surrounds. See text for more detail.

the horizontal center orientation (Part B), each set of surround quadrants showed an amount of differential suppression that was similar in magnitude to the full-field surround. For the flanking quadrants, this was due to a rare *enhancement* of the response to the center element alone. For this cell, then, the orientation contrast effect arises from both sets of surround quadrants. However, the amount of differential suppression produced by each set of quadrants alone does not appear to be consistent among all quadrants.

Suppression Indices

In order to look at the separate contributions of the different surround subregions at the population level, we calculated a general suppression index (GSI) and a differential suppression index (DSI) for each set of surround quadrants; these indices are analogous to those computed previously for the full texture surround. The distribution of GSIs for the two sets of surround quadrants and the full-field texture are shown in Figure 19. The mean amount of suppression induced by each set of quadrants is about 25%, which is 10% less than the roughly 35% suppression induced by the full-field surround. Although the mean GSIs for each set of quadrants do not differ, the GSI for each set is significantly lower than the GSI for the full-field texture (paired t tests, t[flank,end] = 1.50, n.s.; t[full,flank] = 5.00, $p < .001$; t[full,end] = 7.00, $p < .001$). Thus, each set of quadrants contributes substantially and equally to the overall general suppression induced by the texture surround, but each individual contribution is less than the effect of the full-field surround.

Just as with the GSI values, the average amount of differential suppression is also equal for the two sets of quadrants, about 8%-9% (Figure 20). The mean DSI for each set is significantly greater than 0 (t[flank] = 4.00, $p < .001$; t[end] = 4.50, $p < .001$), but there is no significant difference between the two. However, unlike the general suppression effect, the full-field differential effect is no stronger than that for either set of quadrants. When one looks at the subset of cells that were classified as Orientation Contrast cells, though, one

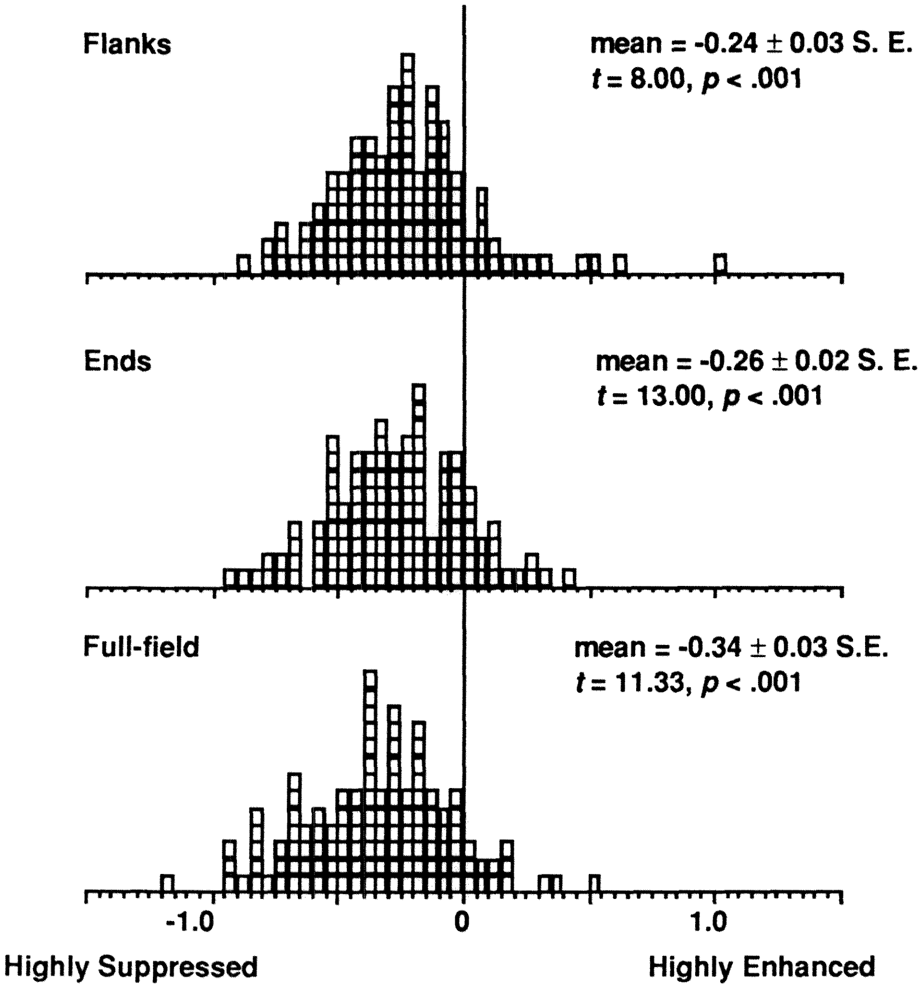


Figure 19. Distribution of General Suppression Index for the flanking quadrants, the end-zone quadrants, and the full-field surround. All three distributions are highly significantly different from 0. Both sets of surround quadrants are significantly different from the full-field, but are not different from each other.

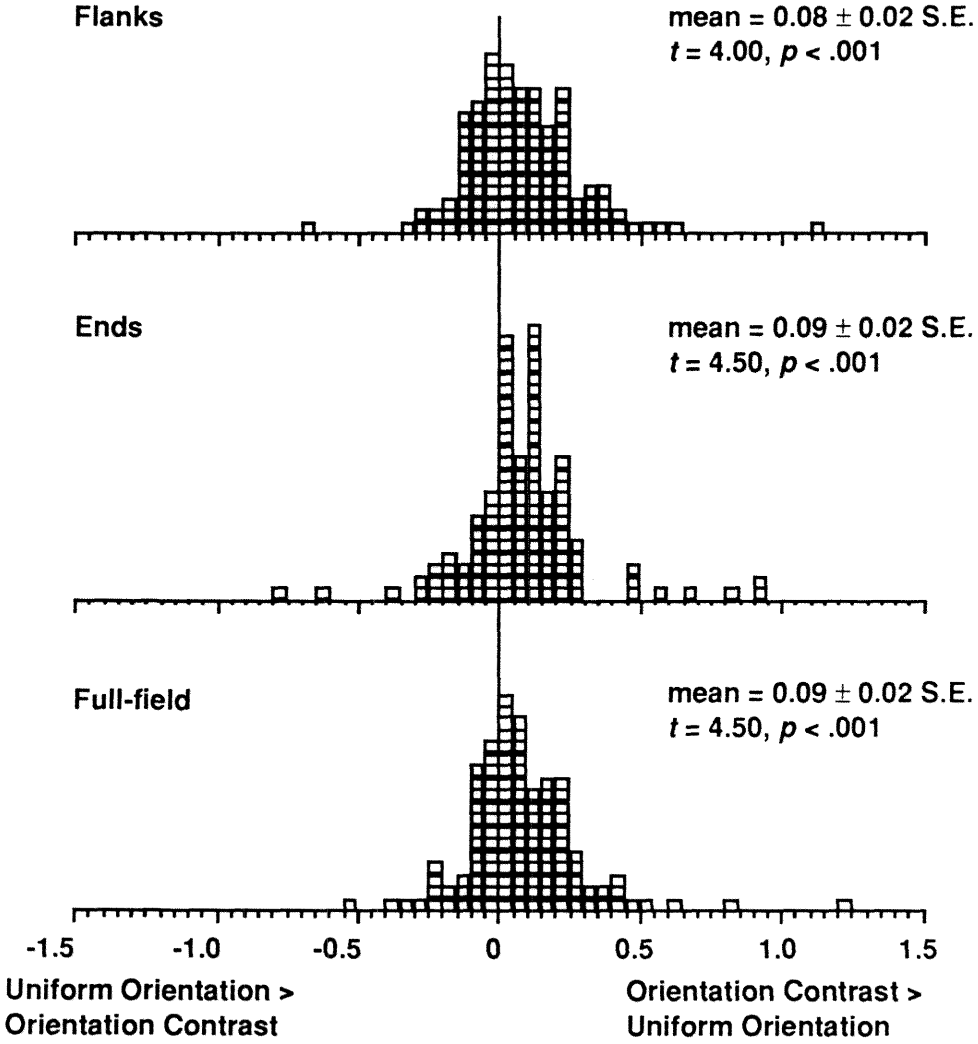


Figure 20. Distribution of Differential Suppression Index for the flanking quadrants, the end-zone quadrants, and the full-field surround. All three distributions are significantly greater than 0, but are not different from each other.

sees a rather different picture (Figure 21). Although, for these cells, both sets of quadrants again show a significant degree of differential suppression, the average amount of differential suppression induced by the end-zone quadrants (17%) is roughly twice that induced by the flanking quadrants (9%) (paired t test, $t = 2.67$, $p < .02$). Moreover, the amount of differential suppression for the full-field texture (28%) is roughly an additive combination of the two sets of quadrants. Thus, it appears that, on average, the orientation contrast effect originates significantly from both sets of quadrants, but more strongly from the end-zones. In addition, the orientation contrast effect is stronger for the full-field texture than for either set of quadrants alone.

Normalized Population Responses

Figure 22 shows the normalized population responses to the full-field texture and the two sets of surround quadrants. The whole population is shown in part A and the subpopulation of Orientation Contrast cells is shown in part B. For simplicity, we have only illustrated the results for the optimally oriented center element.

Figure 22A shows that the population responds identically to the noncontrast flank and end subregions (Configurations 5 and 7) and identically to the contrast flank and end subregions (Configurations 6 and 8). For both the flank and end zones, the responses to the noncontrast texture are smaller than the responses to the contrast texture. The responses to the full-field noncontrast (Configuration 2) and contrast (Configuration 3) textures are smaller than the responses to their counterpart flank and end zone textures. However, the difference between the full-field contrast and noncontrast responses is no larger than the difference between the contrast and noncontrast responses for each set of subregions. Thus, this figure illustrates for the whole population the overall greater general suppression induced by the full-field texture than by either surround subregion alone and the equal amount of differential supression between the full-field, end-zone, and flanking textures.

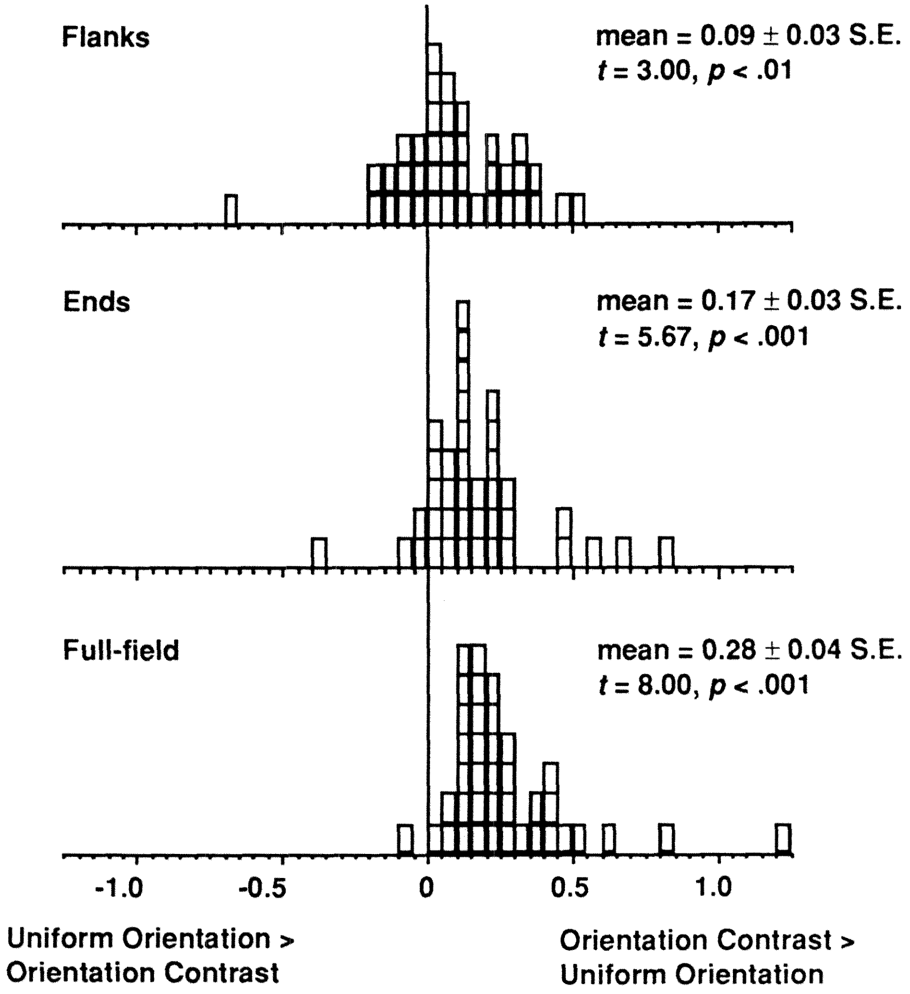


Figure 21. Distribution of Differential Suppression Index for the sets of surround quadrants and the full-field surround for the 39 cells classed as Orientation Contrast. All three distributions are significantly greater than 0 and also significantly differ from each other. The end-zones produce a greater differential effect than the flanks, but neither set of quadrants is as strong as the full-field effect.

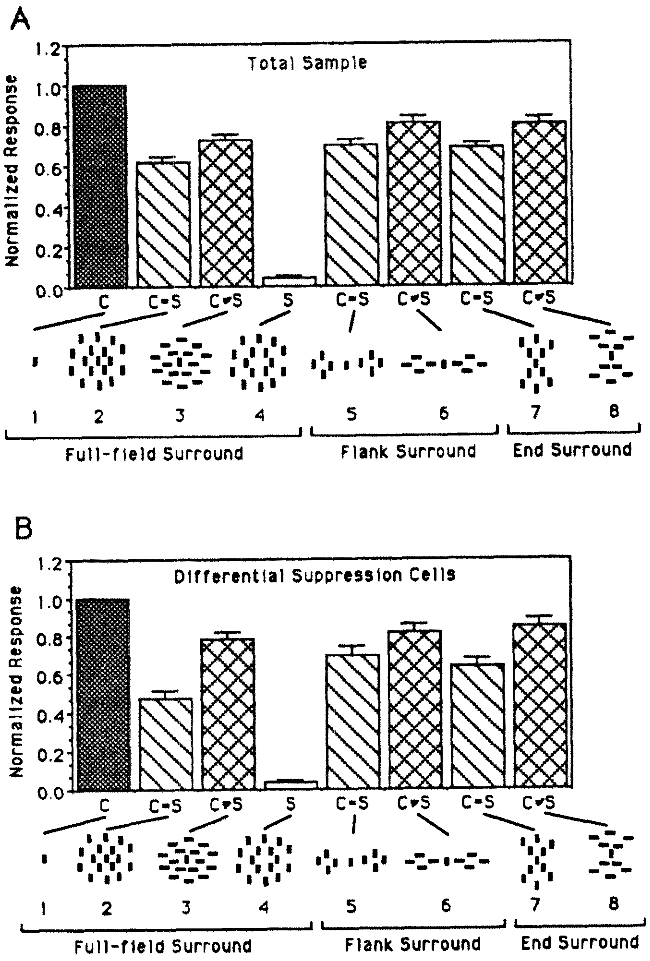


Figure 22. (A) Normalized population responses for the full-field surround and the two sets of surround quadrants. On the population response level, both sets of quadrants contribute equally to both the general suppression effect and the orientation contrast effect. (B) Normalized population responses for the 39 cells classed as Orientation Contrast. For this subset of cells, the differential suppression 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) while the responses to the contrast textures remain about the same (Configurations 3, 6, and 8).

The population response for the Orientation Contrast cells (Fig. 22B) shows that the population responds identically to all contrast patterns (Configurations 3, 6, and 8), at about 80% of the response to the center element alone (Configuration 1). However, the response to the end surround noncontrast pattern (Configuration 7) is smaller than that to the flank surround noncontrast pattern (Configuration 5). The difference between the end surround contrast and noncontrast patterns is statistically larger than that between the flank surround contrast and noncontrast patterns. Moreover, the response to the full-field noncontrast pattern (Configuration 2) is smaller than the responses to either subregion noncontrast pattern (Configurations 5 and 7). Thus, the increased differential suppression of the full-field surround over either set of quadrants is due to an increased suppression of the noncontrast pattern, while the suppression to each contrast texture does not change.

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, these results are much less consistent when one looks at the responses of individual cells. There is a great deal of cell by cell variability in the relative contribution of each set of quadrants to the texture surround effects.

Examples of this variability are shown in Figure 23. One can see from this figure that the responses to the full-field texture for any given cell cannot always be predicted from the responses to the two sets of quadrants (unlike the cell illustrated in Figure 18, in which the responses to each set of quadrants and to the full-field texture are all consistent with each other). In Figure 23a, one sees that only the end-zone regions contribute to the differential suppression, whereas in Figure 23b, only the flanking regions contribute. Figure

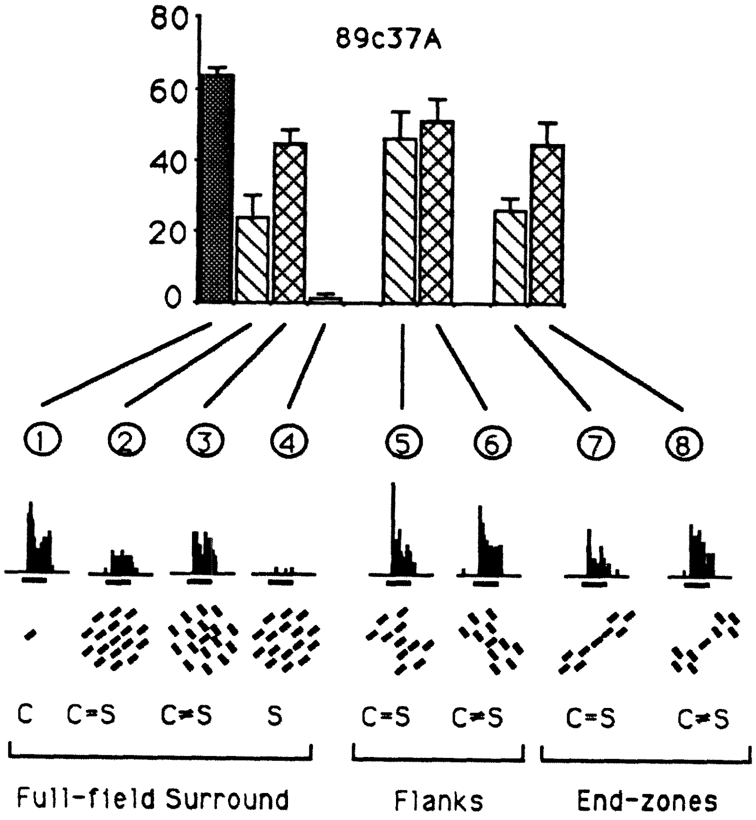


Figure 23. Examples of cells showing inconsistent response patterns among the two sets of surround quadrants and the full-field surround. (A) Cell that showed a differential suppression for the full-field surround and the end-zones but a general suppression for the flanks. Cell 89c37A. (B) Cell that showed a differential suppression for the full-field surround and the flanks but a general suppression for the end-zones. Cell 87a100A. (C) Cell that showed a differential suppression for the full-field surround but a general suppression for both sets of surround quadrants. Cell 89c46B.

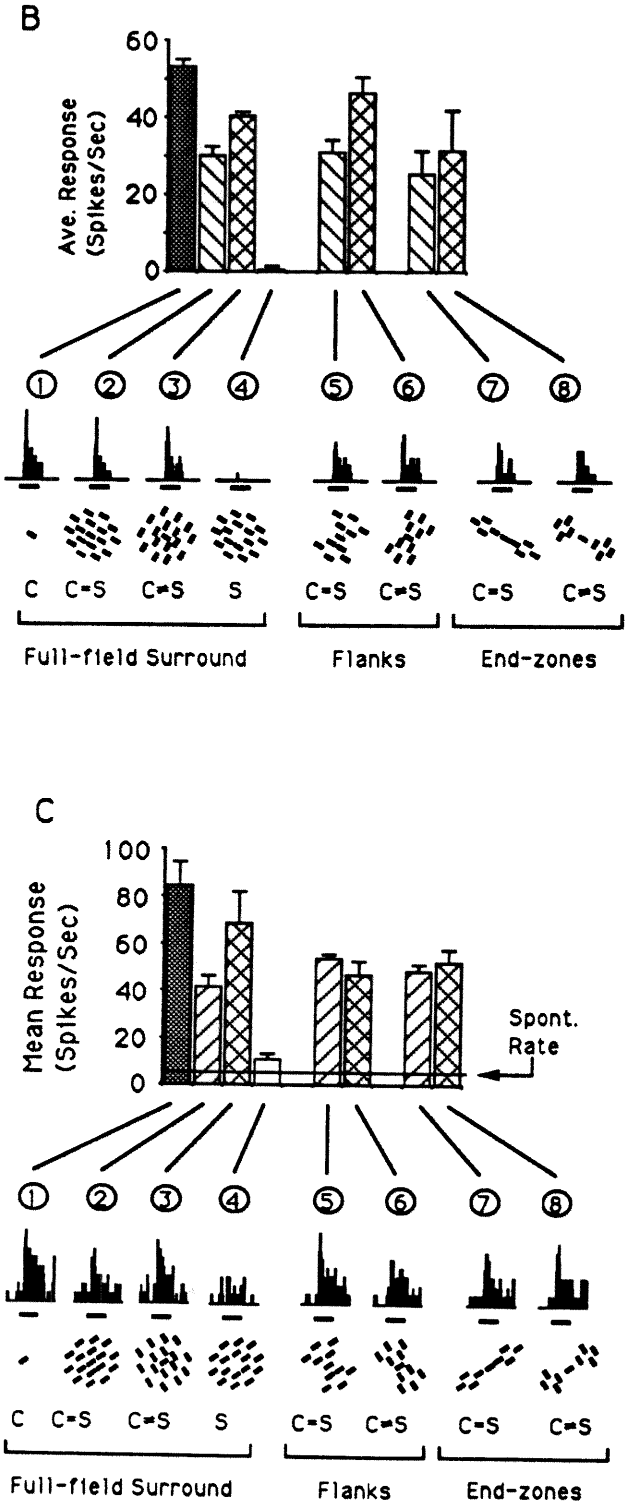


Figure 23 (cont.)

23c shows a cell in which neither set of quadrants shows a differential suppression, whereas the full-field texture induces a strong differential effect.

This cell by cell variability in the relationship between the surround subregions and the full surround is summarized in Table 2. In this table, individual cells are grouped according to their classification based on the pattern of responses to the full-field textures and according to the degree of consistency between responses to the full-field textures, the end-zone quadrants, and the flanking quadrants. For the latter grouping, a cell was put in the *Both consistent* group if both sets of quadrants showed the same qualitative effect as the full-field texture (e.g., all three textures showed a significant general suppression or all three textures showed no effect). Similarly, cells were put into one of the other three groups if neither set of quadrants showed the same pattern as the full-field, if only the flanking quadrants showed the same pattern, and if only the end-zone quadrants showed the same pattern.

Table 2. Consistency of response patterns between the surround subregions and the full-field surround.

Response Class	Both consistent	Neither consistent	Flank consistent	End consistent
C > U	10	12	7	10
U > C	0	6	1	0
C or S	6	2	2	4
GS	14	1	11	7
NE	23	1	3	2
Total	53	22	24	23

C > U: Orientation Contrast; U > C: Uniform Orientation; C or S: Center- or Surrround-dependent suppression; GS: General suppression; NE: No effect

Looking at the results of the whole sample, only 53/122 cells (43%) had consistent response patterns for all three surround textures. The rest of the cells were divided equally among the "inconsistent" categories. Thus, for any given cell, the pattern of responses to either or both of the surround subregions is a poor predictor of the response to the full-field texture. When broken down into the full-field response classes, this observation holds true for all except the *No effect* class. For these cells only, the lack of any surround effect was consistent for both the full-field surround and for the two sets of quadrants.

One question that arises is whether this inconsistency in individual cellular responses reflects real differences in the spatial organization of the surround effects in different cells, or whether it is due merely to the inherent variability in the neuronal responses. To address this question, 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. Thus, one factor in the ANOVA was the spatial organization of the texture elements (full, flank, and end) and the other was the presence or lack of orientation contrast. There was a significant ($p < .05$) main effect of the spatial organization 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 5 cells (4%) showed a significant interaction between the two factors, a number that would be 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, the inherent unreliability of individual cell responses to these texture stimuli. Although at the population level the responses to the different texture patterns are consistent with perceptual salience, the responses of individual cells are quite variable. Thus, one needs to look at the responses of the whole population of neurons to determine reliably how the cortex responds to these texture patterns.

TEXTURE DENSITY

Psychophysical experiments (Nothdurft 1985; Sagi and Julesz 1987) have shown that the magnitudes of texture segregation and pop-out effects are reduced as the density of texture elements decreases. In order 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 texture elements was made increasingly larger. Five different spacings were tested. 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 caused the surround elements to encroach upon the CRF. The three largest spacings were all well outside the CRF. Because the size of the individual elements and the number of surround rings remained constant, the patterns with larger spacing were overall larger than those with smaller spacing.

As might be expected by now, the pattern of responses of individual cells to the different texture densities was quite variable. Examples of this variability are shown in Figure 24. Part A shows a cell that showed a significant orientation contrast effect at all densities tested; Part B shows a cell that showed an orientation contrast effect only at the tightest spacing, with a general suppression at higher spacing (note that for this cell, the surround elements even at the smallest spacing did not encroach upon the CRF); Part C shows a cell that showed no effect of the texture surround at small spacings, but a general suppression at larger spacings; and Part D shows a cell that showed a general suppression at smaller spacings that became weaker as the spacing increased.

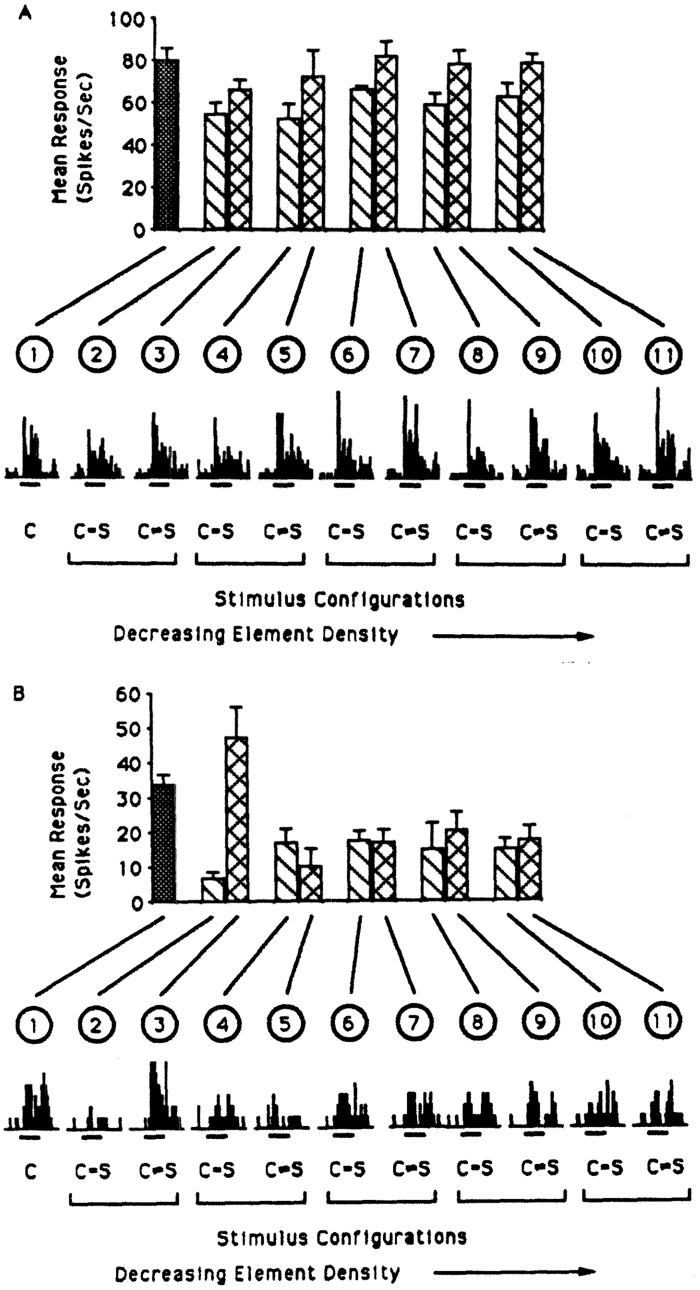
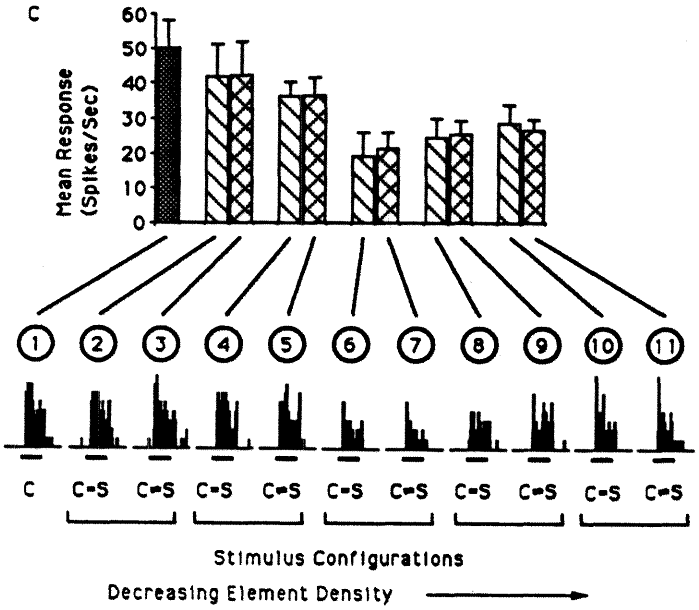


Figure 24. Examples of individual cellular responses to the texture stimuli at different texture element densities. (A) Cell that showed an orientation contrast effect at all densities tested. Cell 89c6E. (B) Cell that showed a large orientation contrast effect at the tightest density tested and a general suppression at all other densities. Cell 89c1B. (C) Cell that showed an increasing general suppression as the texture density decreased. Cell 89c40A. (D) Cell that showed a decreasing general suppression as the texture density decreased. Cell 89c44B.



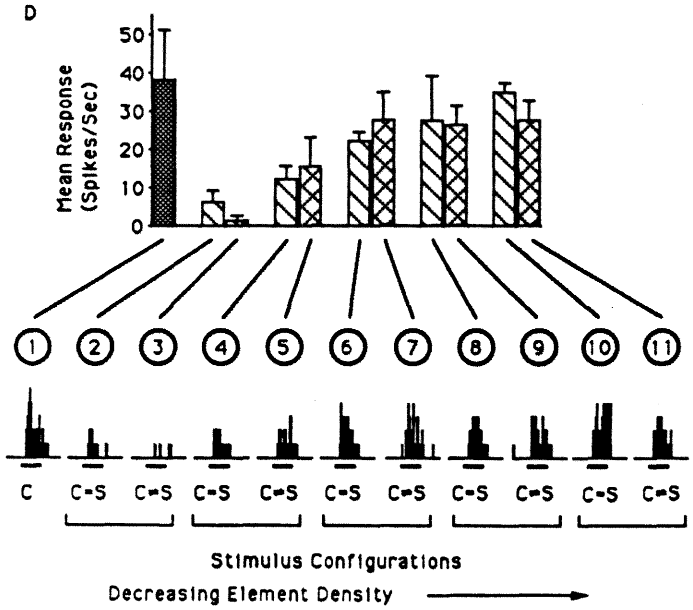


Figure 24 (cont.)

Normalized population responses for the density test are shown in Figure 25. The general suppression effect is largest at the smallest spacings, and it gets increasingly weaker as the spacing increases. For these 23 cells, on average there is no significant differential suppression at any of the 5 spacings tested. Although 4 of the cells were classified as Orientation Contrast cells, only 1 of them showed a very strong effect. Because of the absence of strong orientation contrast effects in this sample, we cannot make any claims about the effect of texture density on the population level orientation contrast effect. However, Figure 24A shows that at least some cells show an orientation contrast effect over a wide range of texture densities; whereas Figure 24B shows that some cells lose the contrast effect as the spacing becomes too sparse. This latter effect is consistent with the psychophysical pop-out experiments.

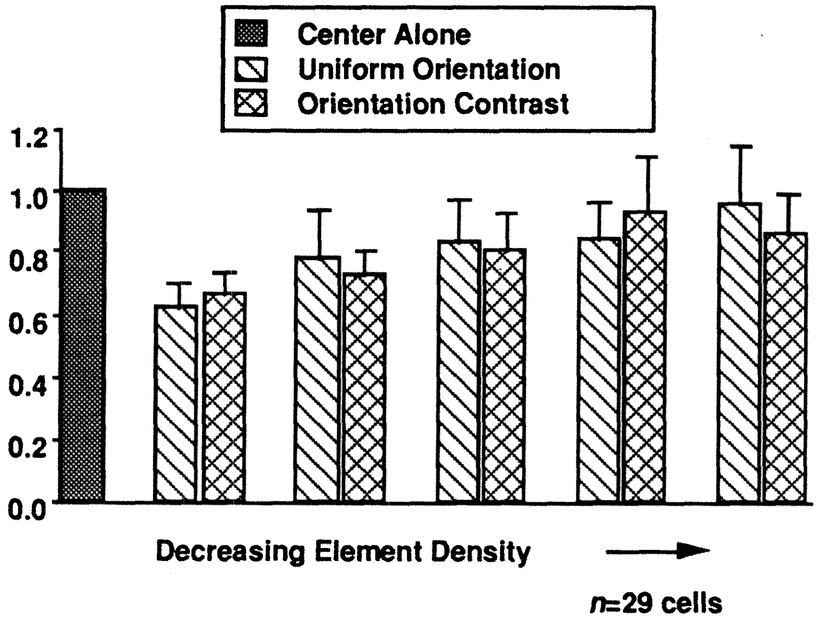


Figure 25. Normalized population responses for the texture density test. Overall, as the texture element density decreases, the general suppression effect for the population response also decreases. There is no evidence of a differential suppression at any texture density for these cells.

To quantify the suppressive effects at the different densities, we calculated GSIs and DSIs for each cell at each density, analogous to the indices calculated for the earlier tests. Figure 26 shows the average GSI for the 5 different densities. For these cells, the amount of general suppression ranged from .35 at the smallest spacing to .1 at the largest. The decrease in GSI as the spacing increased was significant (one-factor repeated-measures ANOVA, $F(4,88) = 2.75$, $p < .05$). Figure 27 shows the average DSI for the different densities. There was no significant differential effect at any density for these cells.

Thus, overall, a decrease in texture density tends 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 differential suppression effect overall, we cannot make any statements about the effect of texture density on differential suppression effects.

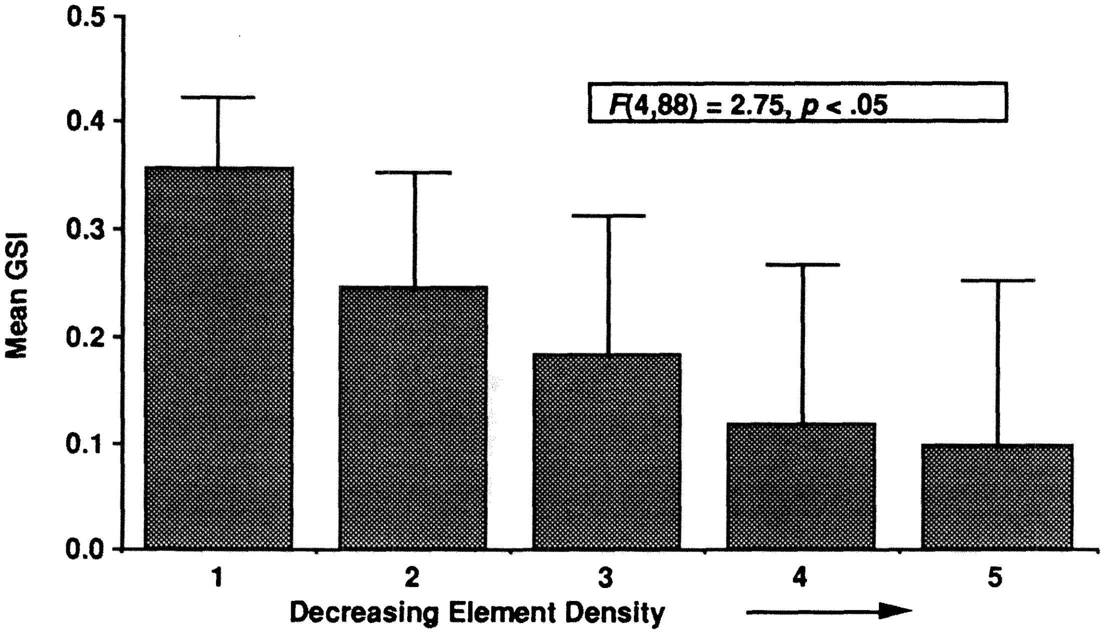


Figure 26. Mean GSIs for each texture density, showing a significant main effect of texture density on general suppression.

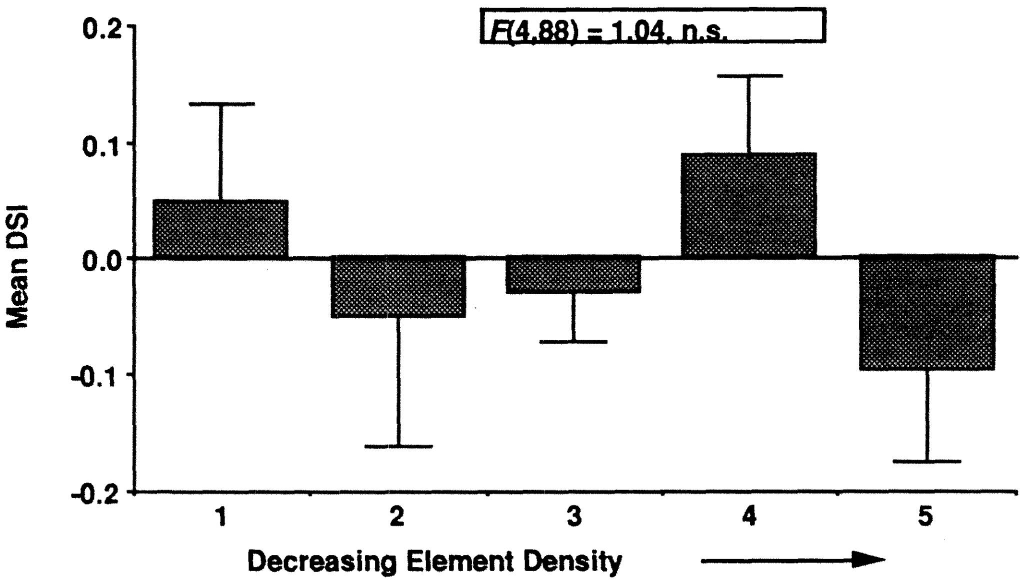


Figure 27. Mean DSIs for each texture density, showing no significant differential effects at any texture density for this sample of cells.

TEMPORAL ANALYSIS

The results reported so far are consistent with the notion that these response properties of V1 cells may underlie the perceptual pop-out phenomenon, at least in the domain of orientation pop-out. To test this idea further, we examined certain temporal aspects of the responses of cells to the texture stimuli. Since human observers are able to detect the presence of a pop-out target in very brief, masked stimulus presentations (see Introduction), we reasoned that the surround effects reported here should be evident very early in a cell's response to a stimulus, if these responses are indeed related to the perception of pop-out.

Differential Suppression in First 100 msec of Response vs. Full 500 msec

To address this question, we grouped the sample of cells into the classification scheme described earlier based on the first 100 msec of response for each cell. The results of this classification are shown in Figure 28. The largest group comprised those cells showing an orientation contrast effect (29%). Only 11% of cells showed a uniform orientation effect, 20% of cells were suppressed in general by both texture backgrounds, and 26% showed no effect of any background. If one compares this figure with Figure 10, the two pie charts are very similar (chi-square = 3.98, n.s.). (Note that in using the chi-square test, we make the false assumption that the two samples are independent; the question of individual cellular variability in responses is addressed in the next section.) Perhaps the only important difference is the smaller ratio of Orientation Contrast to Uniform Orientation cells in Figure 28 than in Figure 10. Even so, there is still a 2.5-fold larger number of Orientation Contrast cells than Uniform Orientation cells based on the 100 msec classification, indicating that V1 cells do respond differentially to the orientation contrast and uniform orientation patterns within 100 msec.

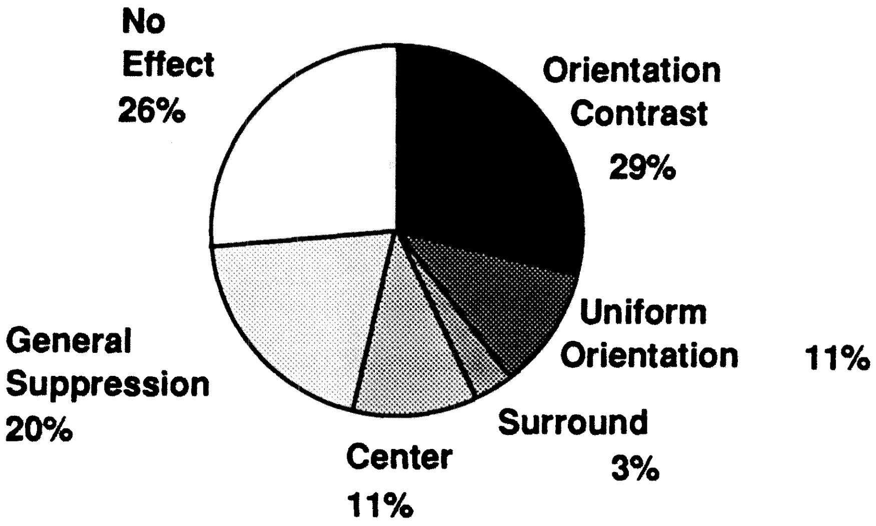


Figure 28. Breakdown of sample into 6 cell classes based on the first 100 msec of each cell's response. This distribution resembles closely that of Figure 10, where the cells were classified on the basis of their full 500 msec responses.

Cell by Cell Variability

Although the overall frequency of cell types is consistent regardless of whether one looks at the full 500 msec response or at the first 100 msec, once again the picture is less clean-cut when examined at the individual cell level. Just under half of the cells (17/36, 47%) classified as Orientation Contrast cells based on the first 100 msec maintained the differential effect when their responses were looked at over the full 500 msec. Conversely, less than half of the cells (17/39, 44%) that were classified as Orientation Contrast cells based on the full 500 msec were also classified as such based on the first 100 msec; the other 22 cells (56%) did not show the differential effect early on, but over time acquired it. This could be due to either a real latency before the onset of the differential suppression or the result of an increased signal-to-noise ratio when the response is integrated over a larger time period. The full comparison of cell classes based on the first 100 msec versus the full 500 msec is shown in Table 3. Examination of this table reveals again a great deal of 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., Figure 28 vs. Figure 10).

Time Course of Suppressive Effects

Having shown that these surround effects can occur within the first 100 msec of a cell's response, we were interested in determining whether it took a certain amount of time for these effects to develop in a cell's response, or whether they were apparent from the beginning of the response. To address this question, we calculated peristimulus time histograms for each cell and each stimulus configuration, and added these histograms together for the whole sample of cells. The cumulative histograms for the center bar alone,

Table 3. Cell classification based on responses during full 500 msec vs. responses during first 100 msec.

	Full 500 msec					
First 100 msec	C > U	U > C	S	C	GS	NE
C > U	17	1	1	3	6	8
U > C	3	2	1	2	4	1
S	1		2		1	
C	5	2		2	1	2
GS	6	1		2	15	
NE	7	1		1	5	18

C > U: Orientation Contrast; U > C: Uniform Orientation; S: Surround-dependent suppression; C: Center-dependent suppression; GS: General suppression; NE: No effect.

the uniform orientation texture, and the orientation contrast texture are shown superimposed on each other in Figure 29A. It is clear that by the time the population has reached its peak response (~57 msec after stimulus presentation), both texture patterns evoke a smaller response than does the center bar alone. Moreover, the response to the orientation contrast texture is already larger than that to the uniform orientation texture. Thus, at peak response, both the general suppression effect and the orientation contrast effect are evident in the population response.

When one expands these cumulative histograms in order to analyze more closely the time period leading up to the peak response (Figure 29B), it appears that it does take a finite time for these effects to be generated. The response starts about 40 msec after stimulus onset. All three histograms are roughly superimposed up until around 47 msec after stimulus presentation, whereupon the two texture conditions evoke smaller responses than does the center bar alone. At about 58-60 msec post-stimulus, the uniform orientation texture response becomes smaller than the orientation contrast texture. To analyze the statistical

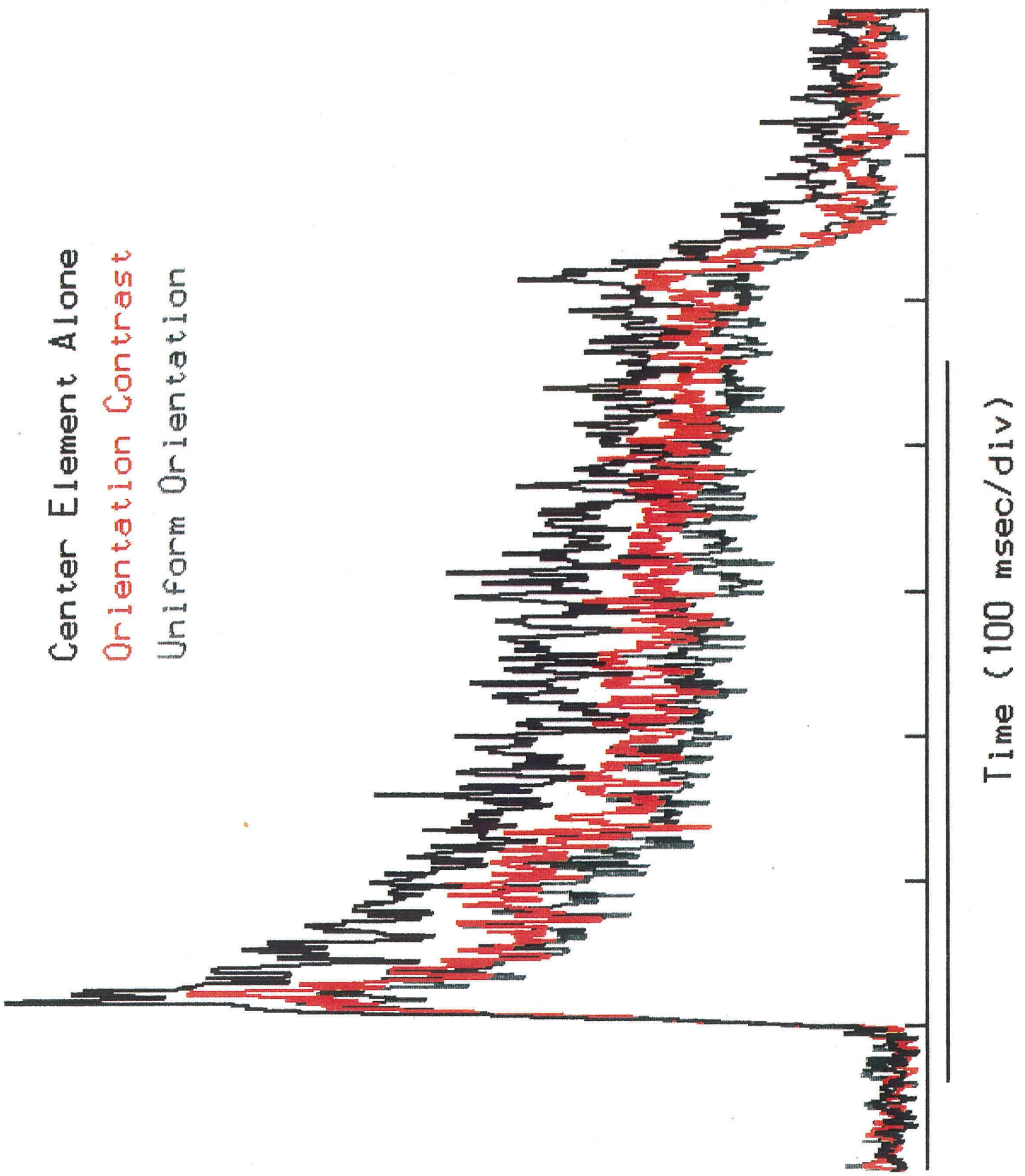


Figure 29A. See caption two pages ahead.

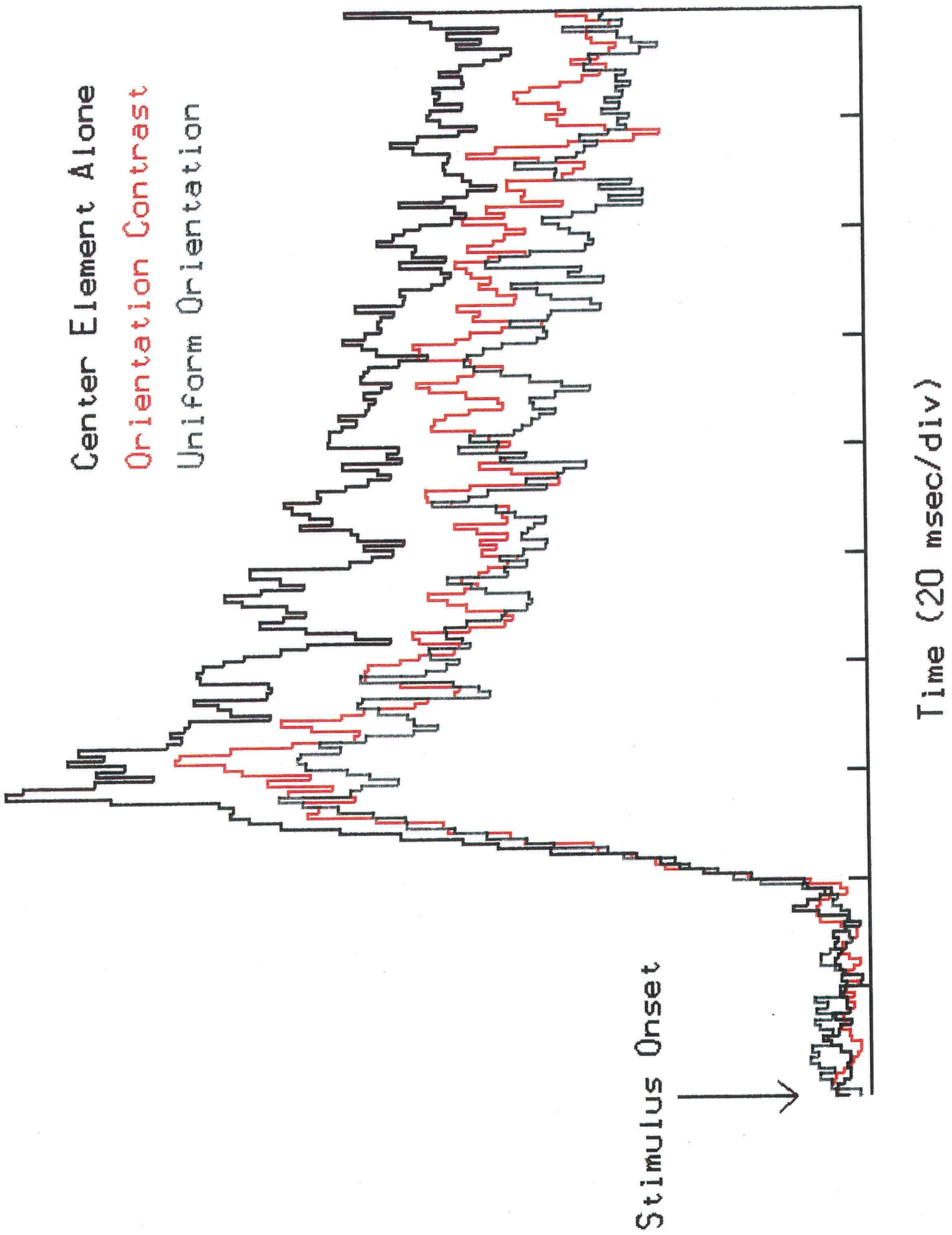


Figure 29B. See caption on next page.

significance of these differences, we calculated the mean response rate for each neuron during three short time intervals after stimulus onset: 41-48 msec, 49-56 msec, and 57-64 msec. If a cell did not respond to any stimulus during a particular time interval, then it was not included in the analysis for that interval. Table 4 shows the results of the statistical comparisons between the responses to the different stimuli at each time interval. It shows that there were no differences between the responses to all three stimuli during the first 8 msec interval; that both texture stimuli elicited weaker responses than the center element alone stimulus but were no different from each other during the second 8 msec interval; and that all three stimuli elicited different responses during the third 8 msec interval. Thus, the surround effects are not present from the onset of the population response to the texture patterns, but they do become evident very quickly. The general suppression effect appears earlier than the orientation contrast effect, and both of them are present by the time the population has reached its peak response.

Figure 29 (preceding pages). (A) Cumulative response histograms for the optimally oriented center element alone (black), the orientation contrast texture (red), and the uniform orientation texture (green). The bars underneath the histograms represent the stimulus on time. Individual cell histograms were initially constructed by adding all spikes in each 1 msec 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 to produce a population cumulative response histogram. This histogram was then smoothed using a boxcar algorithm (with a boxcar width of 3 msec). The output of the smoothing algorithm is shown here. (B) Expanded version of the histograms in A. The hint of oscillatory responses in the center element alone histogram is a reflection of the neuronal sensitity to the 60 Hz refresh rate of the graphics monitor.

Table 4. Analysis of temporal onset of general suppression and orientation contrast effects: Results of paired *t* test comparisons.

Time interval	*n*	Configuration Comparison	Mean Difference (Spikes/Sec)	S.E.M	*t*	*p*
1-8 msec	58					
		3 - 2	-0.59	7.53	-.08	n.s.
		1 - 3	13.60	8.49	1.60	n.s.
		1 - 2	13.01	7.12	1.83	n.s.
9-16 msec	96					
		3 - 2	2.38	7.06	0.34	n.s.
		1 - 3	22.99	8.67	2.65	< .01
		1 - 2	25.38	8.51	2.98	< .01
17-24 msec	107					
		3 - 2	21.66	6.74	3.21	< .01
		1 - 3	21.63	7.22	3.00	< .01
		1 - 2	43.29	7.30	5.95	< .01

Configuration 1: Center bar alone; Configuration 2: Uniform orientation texture; Configuration 3: Orientation contrast texture.

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. Such a relationship might be helpful in determining whether the surround effects we saw occurred in the earliest-responding cells in V1 or only in late-responding cells, whose responses would presumably reflect the result of a number of levels of processing in V1. Such differences may be tied to the laminar location of the cells. We calculated the response latency for each cell based on its responses to the optimally oriented center element alone, using the method of Seal et al. (1983). The distribution of response latencies for the sample of cells is shown in Figure 30A. Figure 30B shows the mean response latencies for each class of cells described earlier. There were no significant differences in latency among all six classes.

To investigate this further, we broke the sample into 3 groups based on latency: early (< 50 msec), middle (50-65 msec), and late (> 65 msec). We then classified the cells in

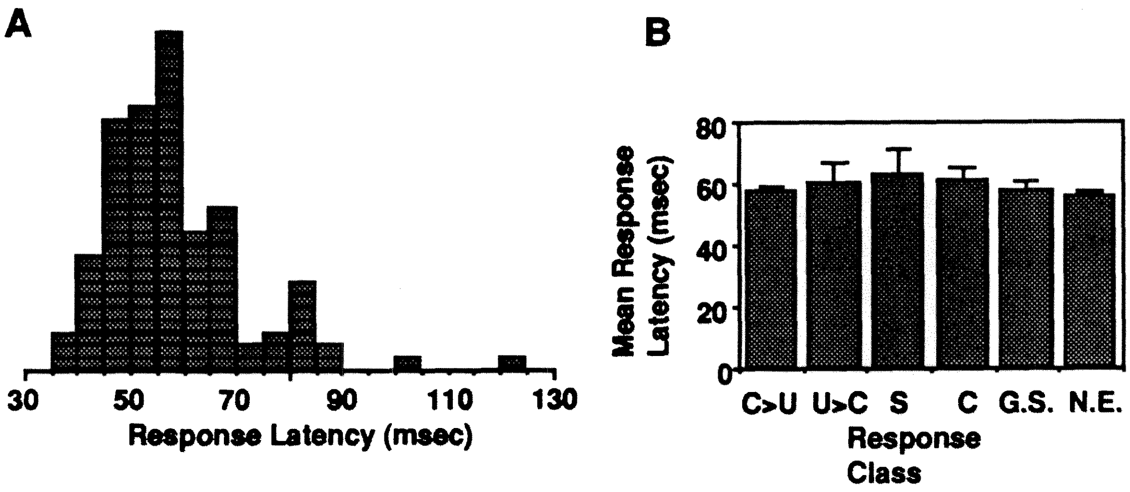


Figure 30. (A) Distribution of response latencies for sample of cells. (B) Mean response latency for each response class.

the early and late groups according to their responses to the texture patterns. The results are shown in Figure 31. The distribution of response types are very similar in both latency groups. There are nearly equal numbers of all response types (chi-square = 1.5, n.s.). Taken with the results of Figure 30, there appears to be no relationship between response latency and the effects of the texture surrounds. All surround effects are seen in similar proportions in early and late responding cells.

RELATIONSHIPS TO OTHER CRF CHARACTERISTICS

Orientation Selectivity

Although the different surround effects were apparent in both highly orientation selective cells and nonselective cells (see examples in Figs. 2, 4, and 14), we were interested

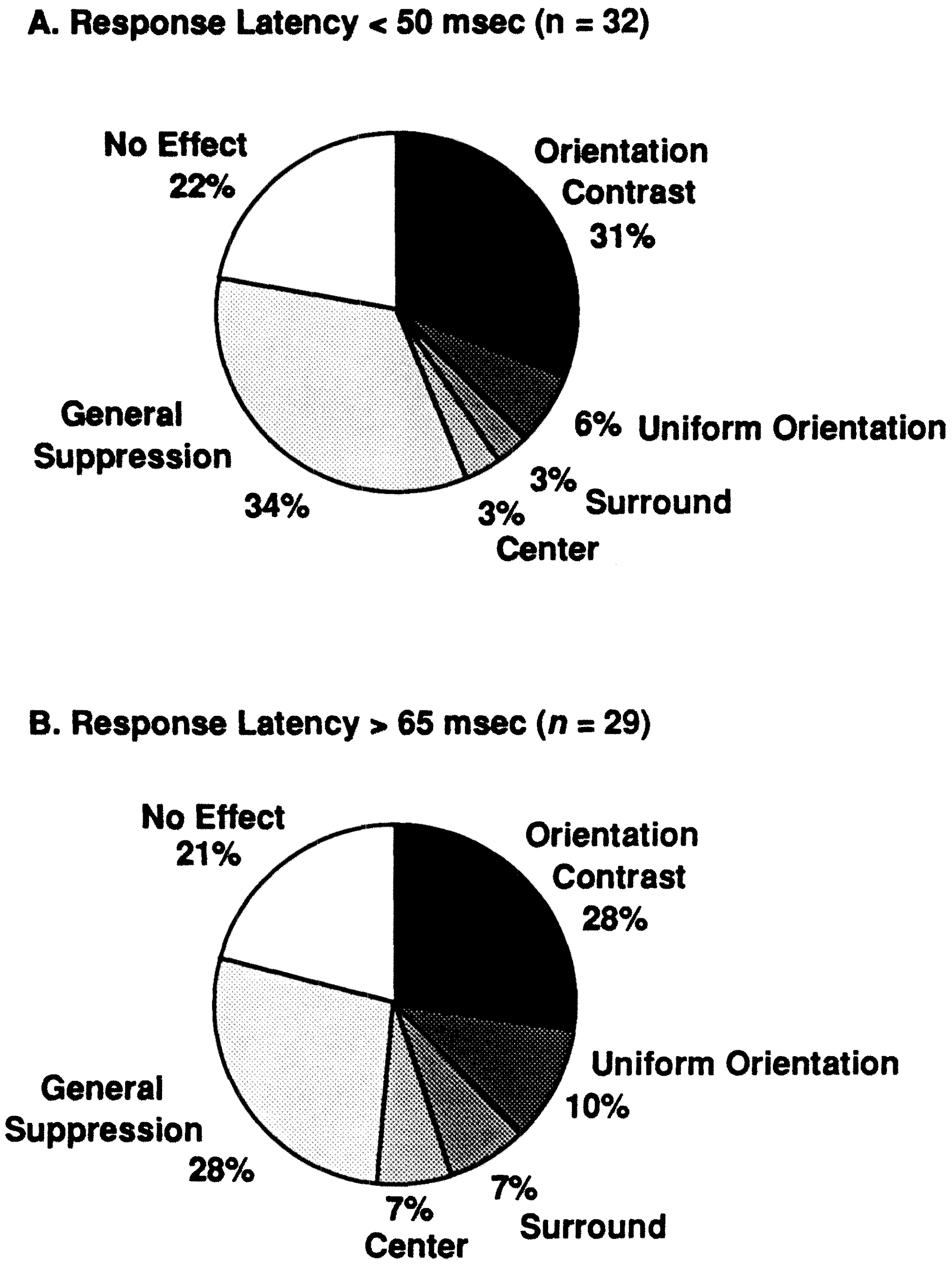


Figure 31. (A) Breakdown of cells with response latency < 50 msec into 6 cell classes. (B) Breakdown of cells with response latencies > 65 msec into 6 classes. The breakdowns of A and B are not significantly different.

nonetheless in whether there was an overall relationship between a cell's selectivity to orientation of the center element alone and its responses to the texture patterns. We calculated an orientation selectivity index (OSI) for each cell (1-Orthogonal/Preferred) and compared these values with the General Suppression Index and Differential Suppression Index calculated earlier. The scatterplots in Figures 32A and 32B show that there is no correlation between a cell's OSI and either its GSI or DSI.

CRF Size

In order to ascertain whether the surround effects depended on the size or location of a cell's CRF, which may give an indication of the laminar location of cells showing strong effects, we correlated each cell's GSI and DSI with the ratio of its CRF size (the square root of its area) divided by its eccentricity in the visual field. The scatterplots in Figure 33A (GSI) and Figure 33B (DSI) show that there is no correlation between the surround effects and the size of the CRF.

Response Transiency

We were interested in whether there was any correlation between the texture surround efects and the transiency of a cell's response. Since cells of the magnocellular pathway tend to have transient responses and cells of the parvicellular pathway tend to have sustained responses (see Maunsell, 1986), such a relationship between the general or differential suppression effects and response transiency might indicate that these effects were predominant in one of the two pathways. For each cell we calculated a Sustained Response Index (SRI), defined as the firing rate during the third 100 msec interval of the cell's response divided by the firing rate during the first 100 msec interval (Response[200-300 msec] / Response[0-100 msec]). A high SRI indicated that the cell's response was

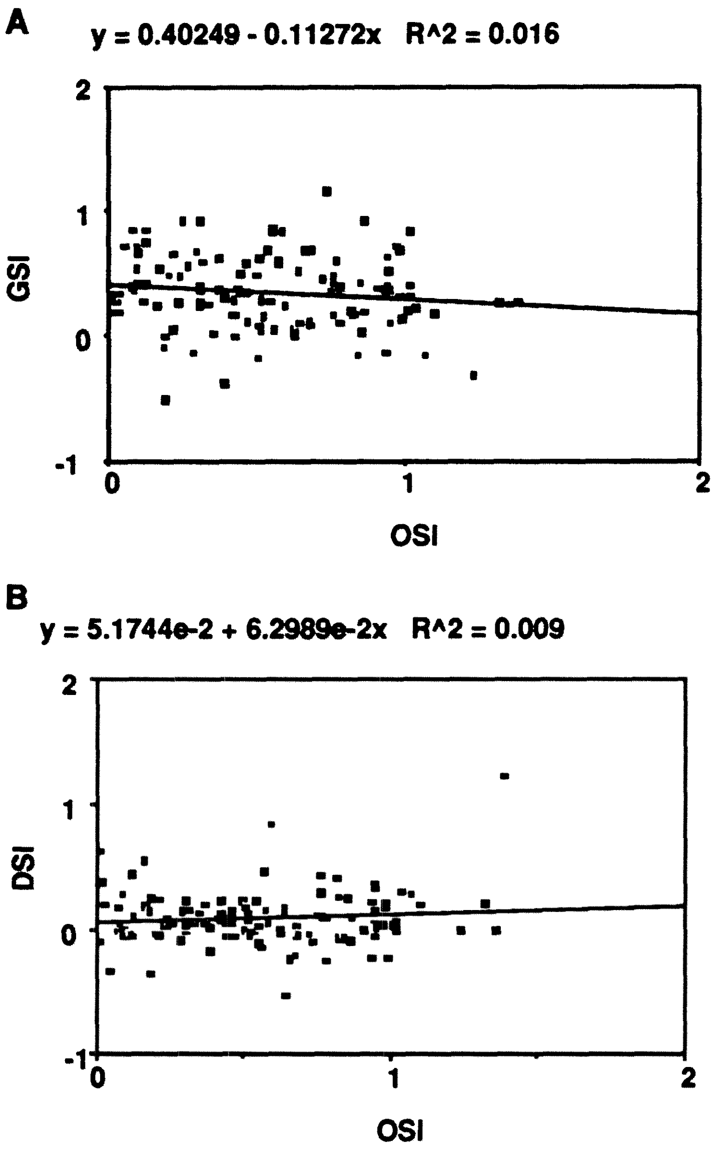


Figure 32. Scatterplots showing no correlation between a cell's orientation selectivity index (OSI) and its (A) general suppression index (GSI) or (B) differential suppression index (DSI).

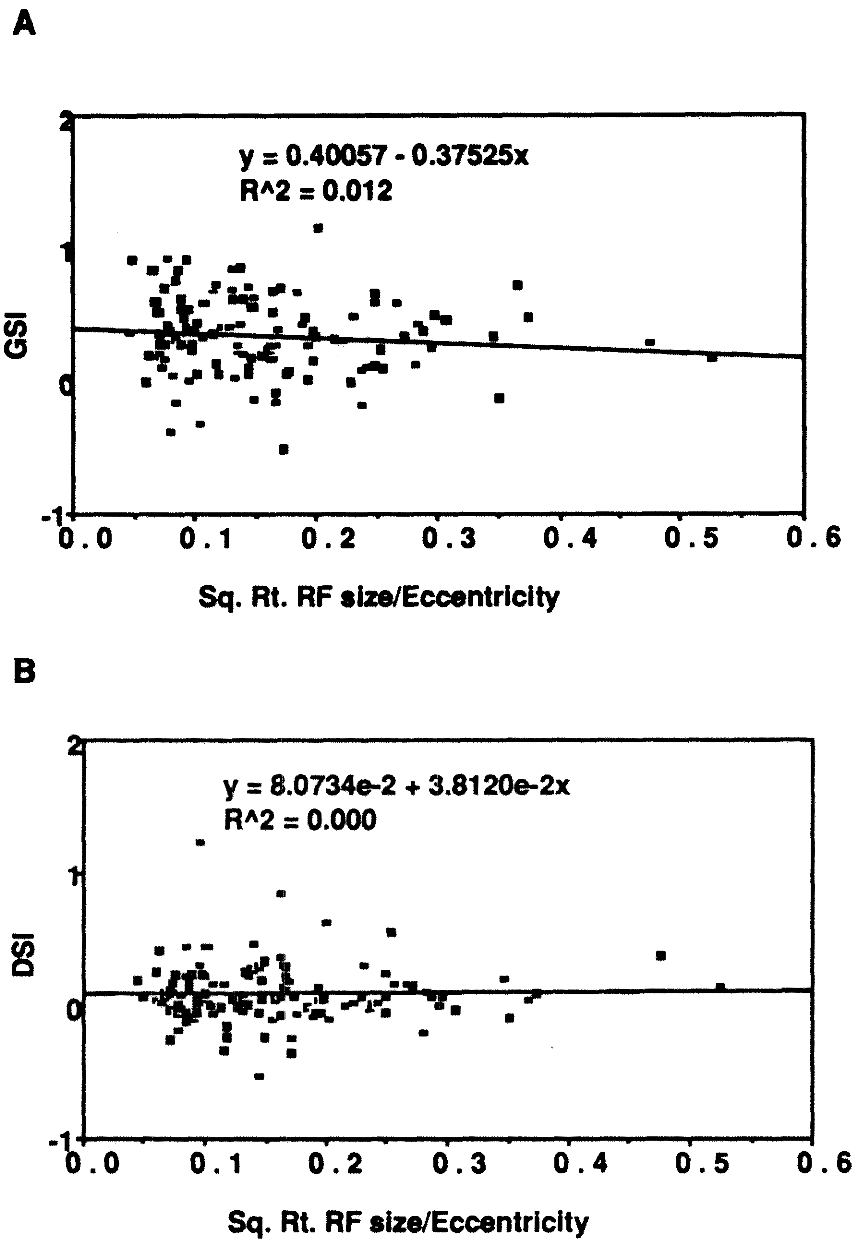


Figure 33. Scatterplots showing no correlation between a cell's CRF size (square root of area / eccentricity in visual field) and its (A) GSI and (B) DSI.

sustained; a low SRI indicated a transient response. Figure 34 shows scatterplots comparing the SRI with GSI (A) and DSI (B). It is obvious from these graphs that there is no relationship between a cell's response transiency and its degree of general or differential suppression.

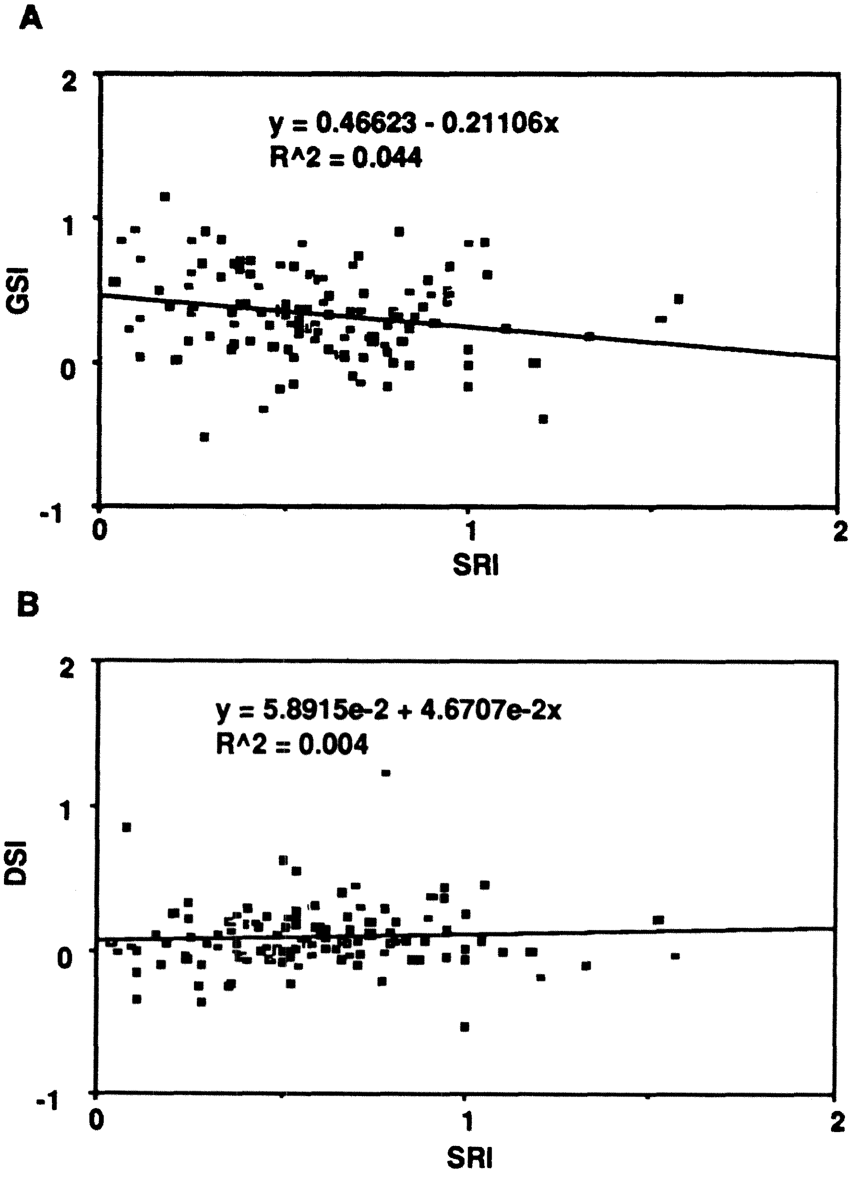


Figure 34. Scatterplots showing no correlation between a cell's SRI and its GSI (A) or DSI (B).

Depth of Penetration

It is difficult to reconstruct electrode penetrations and obtain accurate laminar information about the location of recorded cells in the alert monkey preparation without going to extraordinary lengths. However, we were able to make some very rough estimates of the depth of recording based on our microdrive readings and experimental log records indicating the passage of the electrode through various landmarks, e.g., layer 4, white matter, etc. Using these estimates, we wanted to see if there was any relationship between the estimated depth of recording and the texture surround effects. Figure 35 shows that there was no correlation between estimated depth and GSI (A) or DSI (B). Based on experimental log notes, layer 4 was located around 750-1000 μm recording depth, although this number varied widely depending on exact experimental conditions. Thus, it appears that both the general suppression effect and the orientation contrast effect can occur in both superficial and deep layers; however, our resolution of recording depth is inadequate to discern whether the incidence of the effects is different between the two regions.

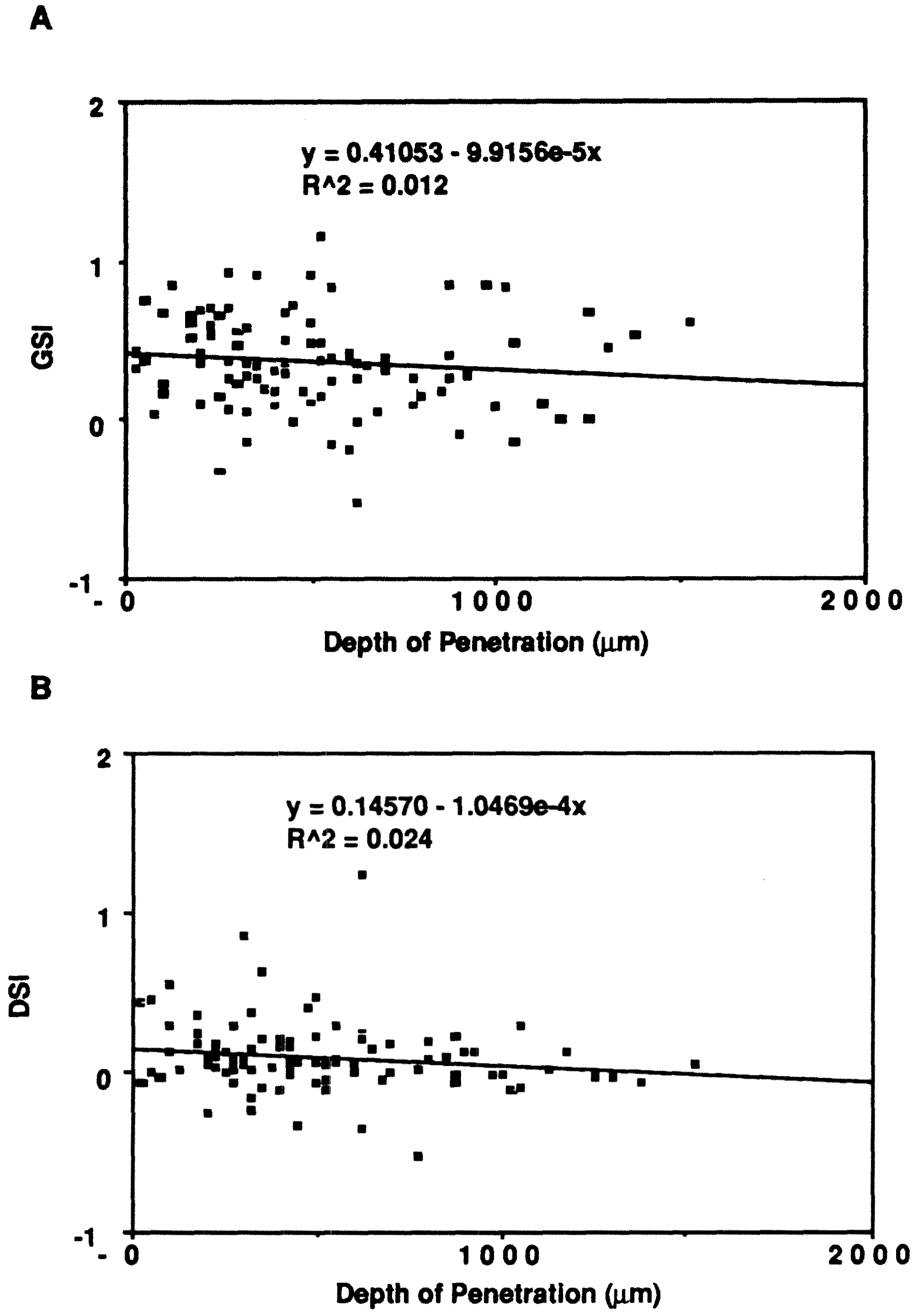


Figure 35. Scatterplots showing no correlation between a cell's estimated depth in the cortex and its GSI (A) or DSI (B).

4 Discussion

CHAPTER SUMMARY

The present results demonstrate a modulatory effect of neuronal responses from stimuli placed outside the classical receptive field. A number of such effects have been discovered over the years, forcing a reevaluation of the meaning of a receptive field for a cell. In addition, the present results also suggest a neurophysiological mechanism for the perceptual pop-out effect, at least in the orientation domain. Perceptual pop-out may occur because, on average, cells in V1 respond more strongly to an orientation contrast pattern than to a noncontrast pattern. It is possible that the local cortical "hot spot" of activity corresponding to the location of the orientation contrast target may be what attracts focal attention to that location in the visual field. It is also tempting to speculate that the response properties of these cells may be involved in the detection and segregation of texture borders based on orientation differences. Experiments are underway to test this notion.

A number of possible anatomical substrates for the suppressive surround effects are considered. These effects may be generated subcortically, before the input even reaches V1. Convergent input from LGN fibers may play some role in the general suppression effect induced by the innermost ring of elements, but it is unlikely that they play a major role in the orientation-specific differential suppression. Interlaminar projections within striate cortex may also play a role, analogous to the proposed role of projections from layer 6 to higher layers to produce the end-stopping effect. Once again, this substrate would seem to be restricted to influences from the innermost ring of elements. Long-range horizontal connections in V1 might allow more outer rings of elements to exert an influence on the response to the center element, but the role of these connections in the generation of suppressive effects is questionable, given the findings in cats that these connections tend to be *excitatory* and to connect areas with similar orientation preferences. Finally, feedback connections from V2 would provide a pathway for both the innermost and the outermost rings of elements to exert an influence on the response to the center element. The spatial extent of these surround effects is not known, however.

A number of unresolved issues remain. In addition to the question of the spatial extent of the suppression, it would be interesting to know the effect of systematically varying the amount of orientation contrast between the center and surround; whether cells in V1 have similar suppressive surround effects in other modalities, such as color, and whether the same cells signal contrast regardless of modality; whether cells showing the different types of surround effects are concentrated in specific cortical laminae; whether a detailed mapping of both excitatory and inhibitory regions of V1 receptive fields would explain much of the present results; whether decreasing the density of texture elements would reduce the differential suppression effect, as predicted by psychophysical experiments; and whether there are any effects of focal attention on these response properties.

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 such modulatory effects induced by diverse stimuli such as random noise surrounding the CRF (Hammond and MacKay, 1975, 1977); oriented gratings (Maffei and Fiorentini, 1976; Fries et al., 1977; Nelson and Frost, 1978); color (Desimone et al., 1985); and moving random dot patterns (Allman et al., 1985b, 1990). Our results show that textured surround stimuli composed of identically 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 selective, such that the strength of the response is often stronger when there is a contrast in orientation between the center element and the texture surround compared to when there is no such contrast. Such responses correlate with the perceptual salience of the center element. The prevalence of these outside-the-CRF modulatory effects suggests that center-surround interactions are a very important, 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, 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 readily 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 (< 50 msec) followed 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. If the target and distractors differ only in more complicated ways (e.g., they are mirror images of each other) but not in these elementary ways, then subjects must perform a serial item by item search of the pattern to locate the target. Somehow, the presence of a contrast in one of these features in the display causes the subject's attention to be directed immediately to the location of the contrast.

The response properties of cells in V1 reported here are well-suited to rapidly signal the presence of orientation contrast, potentially driving a process that produces the involuntary, "reflexive" shift of attention to the area of contrast. For example, for the whole population of cells studied, the response to the orientation contrast textures 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 perception must remain tenuous until more data are obtained. One thing that must be shown is that 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 mechanism for attentional control is still unknown, and indeed may not occupy a single anatomical locus. Thus, at best all we can do now is demonstrate a correlation between the response properties of these neurons and psychophysical results and see if the neuronal responses reasonably match predictions expected from the psychophysics.

If these response properties do indeed underlie the perception of pop-out, though, they raise a number of possible models for the automatic directing of attention to areas of contrast. The simplest model is one in which the 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 portion which is the most active. 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 spiking activity would be 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 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 a color or motion contrast. Presumably, if one were to look for results analogous to those reported here for the color, motion, spatial frequency, etc. domains, one would 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.

RELATIONSHIP TO TEXTURE SEGREGATION

The pop-out effect has been studied by psychophysicists not only as a perceptual phenomenon in its own right but also as a limiting case of the more general effect of texture segregation. The natural question arises, then, of whether the response properties of V1 neurons reported here are involved in the perceptual segregation of texture borders. One would predict that if these cells were stimulated with a texture pattern in which a border was defined by orientation differences, the cells would tend to 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). This prediction is currently being tested experimentally by Nothdurft, Van Essen, and Gallant.

POSSIBLE MECHANISMS

Although the experiments reported here were not designed to test explicitly the mechanisms responsible for the generation of the surround effects, we can glean some insight into possible mechanisms based on the analysis of the results. We will consider in turn the following possible anatomical substrates for the surround effects: 1) subcortical origin of effects; 2) convergence of input from LGN fibers; 3) interlaminar connections within striate cortex; 4) long-range horizontal connections; and 5) feedback connections from V2.

Subcortical Origin

Modulatory effects from stimuli well outside the classical receptive field have been demonstrated as early in the visual pathway as the retina (e.g., the shift effect of McIlwain, 1964). It is therefore possible that some of the surround effects reported here have a subcortical origin. However, the delay before the suppressive effects become evident in the population response histograms suggests that at least some of the processing generating these effects is done cortically, after initial nonmodulated responses reach V1. Whether in addition to this there is a role played by subcortical processing cannot be discerned from the present results.

Convergence of Input from LGN

LGN fibers terminate mostly in layers 4C, 4A, and 2/3, with smaller terminations in layers 1 and 6. Individual fibers usually terminate in 1-2 bundles that can be separated by as much as 1 mm in cortex, sometimes encompassing more than one ocular dominance band (Blasdel and Lund, 1983). In addition, some LGN fibers projecting to layer 1 seem to spread out over an even larger horizontal distance, > 2mm. These distances are larger than the average dendritic spread of their recipient neurons, and are apparently larger than the size of the CRFs in V1 would predict. Thus, it is possible that some component of the suppressive effects may derive from this "excess" spread. However, it would seem that only the innermost ring of elements could have an effect using this mechanism; the outer rings are too far away. In addition, it is unlikely that this mechanism could account for the orientation-specific differential suppression, for LGN fibers and most layer 4 cells (except some in layer 4c-alpha) are not sensitive to orientation.

Interlaminar Connections: End-stopping and Side-band Suppression

End-stopping and side-band suppression are two well known "classical" properties of visual neurons that may account for the present findings. Since the property of end-stopping has been linked to interlaminar projections from layer 6 (Bolz and Gilbert, 1986), I will discuss the possibility that end-stopping, side-band suppression, and the present results share a common mechanism. End-stopping was original discovered by Hubel and Wiesel (1965) in their studies of cat areas 18 and 19, in which they found that for some cells, the response to a bar of light became weaker as they increased the length of the bar beyond the limits of the cell's receptive field; in some cases, a sufficiently long bar would suppress the cell's response completely. In their early classification scheme, Hubel and Wiesel originally termed these cells hypercomplex, but it became apparent later that simple cells could also share this end-stopping property. Bishop et al. (1973) performed a more thorough analysis of the inhibitory regions surrounding the receptive field. They found that many simple cells had inhibitory regions along the flanks of the excitatory receptive field center; these flanks were revealed by the suppression of the response to a conditioning stimulus in the excitatory RF when a test stimulus moved through the inhibitory flank. Subsequent analysis revealed that the inhibitory region completely surrounded the "excitatory receptive field" (ERF) and was many times larger in areal extent than the ERF. In addition, Jones (1970) demonstrated a modulatory effect from outside the CRF in cats by comparing the response of a bright-dark edge within the CRF to a bright bar on a dark background. In the latter case, the second edge of the bar was located well outside the CRF, and when presented alone (as an edge) it did not drive the cell. However, when the two edges were combined to form the bar, the response to the edge in the CRF could be either facilitated or suppressed.

Thus, modulatory effects from outside the ERF center are not a new phenomenon, and it is worthwhile to see whether the present results and these "classical" results may possibly share a common mechanism. One problem in attempting this, though, is that most studies on end-stopping and side-band suppression have been done on cats, whereas the present results are from monkeys. However, it is reasonable to assume that the two species may share common mechanisms, given the similarity in responses between cat and monkey neurons at different cortical levels (e.g., both have simple cells in striate cortex). In addition, Hubel and Wiesel (1968) and Schiller et al. (1976) have shown that striate neurons in monkey also exhibit end-stopping.

The inhibitory regions surrounding the RFs of simple cells in the Bishop et al. (1973) study were not orientation dependent. However, Hubel and Wiesel (1965) showed that some hypercomplex cells in cat area 18 showed an end-stopping effect that was orientation selective. The cell was suppressed maximally when a long continuous edge extended over both the excitatory and inhibitory regions of the RF. When the edge was bent at the border between the two regions, making the edge stimulating the inhibitory region a different orientation than the edge stimulating the excitatory region, the suppression was reduced. Orban et al. (1979) subsequently found that the end-zone inhibitory regions of cat striate cortex cells were also orientation selective. Such an orientation dependent end-stopping mechanism might be sufficient to explain the results from our texture patterns.

Many authors have suggested that end-stopped cells may be involved in a number of perceptual tasks, including the detection of corners or borders (Hubel and Wiesel, 1965); the representation of curvature (Hubel and Wiesel, 1965; Dobbins et al., 1987); and the perception of illusory (subjective) contours (von der Heydt and Peterhans, 1989; Peterhans and von der Heydt, 1989). The perception of orientation contrast and borders defined by orientation differences is another possible role for end-stopped cells. The mechanisms underlying end-stoppping are not yet known, although Bolz and Gilbert (1986) have shown that the inactivation of layer 6 in cats reduces or eliminates end-stopping in cells located in layers 2+3 and layer 4. This result provides evidence that the elongated receptive fields of layer 6 cells provide the inhibitory input to the end-stopped cells of layers 2-4. One might do a similar experiment with the texture patterns used in the present study to see if the suppression effects are similarly attenuated when layer 6 is inactivated.

Long-range Horizontal Connections

Anatomical studies in both the monkey (Rockland and Lund, 1983; Fitzpatrick et al., 1985; Blasdel et al., 1985) 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 up to 4 mm or more (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 mm to 1.5 mm. The majority of evidence in the cat suggests that these long-range connections are excitatory (Kisvarday et al., 1986; Gabbott et al., 1987) 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. For example, Krüger and Aiple (1988) show evidence for inhibitory interactions between neurons of similar orientation selectivity 300-400 µm apart. On the other hand, T'so and Gilbert (1988), using a cross-correlation analysis, show evidence only for excitatory interactions betwen cells of like orientation preferences in monkey striate cortex, similar to results they see in cat.

These long-range horizontal connections may be anatomical substrates for the surround effects reported here. To address the feasibility of this suggestion, it is necessary to translate the extent of the connections from millimeters to degrees in the visual field. At the eccentricity of the majority of cells recorded in the present study (3-5 degrees), the cortical magnification factor is roughly .3-.5 deg/mm (Van Essen et al., 1984; Tootell et al., 1988). In addition, estimates of the cortical point size image range from 0.4-0.5 mm in linear dimensions (Van Essen et al., 1984) to 1-2 mm (Hubel and Wiesel, 1974; Dow at el., 1981) at this eccentricity. On average, the distance between the texture elements in our displays was 1 degree in visual angle, with a wide range of variability. However, from these numbers, it appears that the horizontal connections are indeed capable of linking the area of cortex stimulated by the center element with those areas stimulated by at least the innermost ring of elements, possibly the second ring as well. However, it would appear unlikely that the outermost rings would have a direct effect on the cell under study by way of the horizontal connections. On the other hand, they could operate through a cascade effect, whereby those cells stimulated by the outermost ring affect the cells stimulated by the third ring, which affect the cells stimulated by the second ring, and so on. We do not have any direct information on the relative contributions of the innermost and outermost rings to the surround effects. If the outermost rings contribute substantially, then it is unlikely that horizontal connections play a major role in that contribution, although they may still play a role in the contribution from inner rings. What is needed is a direct test of the influence of each ring. This issue is discussed below. However, one relevant piece of information comes from the density tests reported above. On average, as the spacing between elements increased, the general suppression became weaker. This might indicate that the innermost elements are responsible for the suppression, and as they are placed further away from the CRF, they lose their suppressive influence. Alternatively, the loss of suppression may be due to the overall decreased density of elements in the surround. Our results cannot distinguish between these two possibilities. In addition, we cannot conclude anything about the differential suppression effect, for the particular subset of cells tested with the density test were not very sensitive to orientation contrast. 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. Although it is not obvious how to fit such a model into the orientation dependent suppressive effects reported here, these types of connections may help 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 Figures 2 and 9). Under this scheme, the typical single bar stimulus used to plot a CRF does 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 is 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 locations relative to the CRF. They interpreted these results as a possible mechanism for certain perceptual completion phenomena. In any case, it is unclear how these results may fit into the known anatomical picture.

Feedback from Higher Cortical Areas

A final possible anatomical substrate for these suppressive surround effects are the connections to V1 from other cortical and subcortical 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). It is not known, however, whether the cells in V2 inherit these properties from V1, or whether the effect is generated in V2 and passed back to V1 by the feedback pathway. Alternatively, the real mechanism may incorporate both of these possibilities: Cells in V1 may be influenced by feedback from oriented cells in V2 representing the regions outside the V1 cell's CRF, thus generating the surround effects; in turn, the V2 cells may then acquire the surround sensitivity from the V1 cells. This "cortical loop" model of information processing is attractive, for it gives a possible functional role to the ubiquitous feedback pathways in visual cortex, that of providing a broader context for the firing of cells in lower areas. This is, of course, only speculation at this point. One would need to selectively eliminate the feedback projections to test whether or not V1 cells still display the surround effects without the input from V2. I know of no clean way to do this in the macaque, where most of V2 is buried deep within the lunate sulcus and the inferior occipital sulcus. However, some insight into this question may be gained by comparing a temporal analysis of the surround effects in both V1 and V2, such as in Figure 29. For V1, the delay before the population displays the general suppression effect and differential suppression effect is consistent with this proposed role of feedback connections. Interareal conduction times are on the order of 5-10 msec (Maunsell, 1986; Raiguel et al., 1989), which fits roughly with the 7-10 msec delay before the general suppression effect becomes evident and the ~20 msec delay before the onset of the differential suppression effect. A similar analysis of the V2 population response might provide some clues to the role of V2 feedback. If V2 cells show the differential effect immediately, then this argues that the processing is done either in V1 before projecting to V2 or is done at the level of divergent feedforward projections from V1 to V2, immediately endowing the V2 cells with the suppression effects. If the suppression effects take time to develop in V2, but quicker than in V1, this may indicate that the effects are generated in V2 and then fed back to V1. This type of analysis is unlikely to provide a conclusive answer, however, because of the fundamental limitation that we do not know whether the cells showing the suppression effects are the cells that project to V2 (or back to V1). A laminar analysis of the different effects may help untangle this question, but that information is not available from the present results. We do have the information potentially available from our previous experiments on anesthetized monkeys, though, so it may be possible to address this issue. A relevant report in this regard is from Edelstyn and Hammond (1988), who showed in the cat that the complex cells strongly sensitive to texture are concentrated in layers 3 and 5, the major output layers to higher areas and subcortical areas, respectively.

The anatomy of reciprocal projections between V1 and V2 seems capable of supporting this role of integrating information over a wide visual range. Single axons from V1 terminate in clusters in V2 that can be separated by 1 - 1.2 mm (Rockland and Virga, 1990). Intrinsic connections in V2 can run horizontally by more than 3 mm (Rockland, 1985). Finally, axons feeding back from V2 to V1 can run horizontally along layer 1 in V1 for distances greater than 4 mm (Rockland and Virga, 1989). By this anatomical route, a cell in V1 may be influenced by visual stimuli well outside the cell's CRF. Although the feedback projections have commmonly been believed to be excitatory, they can still exert a suppressive influence on the cell by synapsing on an inhibitory interneuron. In addition, McDonald and Burkhalter (1990) have recently shown that in rat visual cortex, a significant minority of inter-areal axons are inhibitory. Thus, feedback pathways may well contribute to the suppressive surround efects.

RELATIONSHIP TO OTHER RESULTS

The results from this study in the alert monkey are quite consistent with the results of similar experiments in both anesthetized monkeys and cats. Although the effects of the surround texture are somewhat more robust and more prevalent in the alert monkey that in the anesthetized monkey (DeYoe et al., 1986), they are qualitatively the same. These results also agree with the studies of orientation-dependent surround effects in cat visual cortex, described in the Introduction. 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, cells responded more strongly to a stimulus if there was a contrast in orientation between the center and surround regions. Maffei and Fiorentini (1976) reported prevalent 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. A number of factors might account for this discrepancy. Maffei and Fiorentini compared the response to their center + surround gratings against a center-alone stimulus presented on a diffusely illuminated background. In the present study, the center-alone condition was a bar presented on a blank background. If the diffusely illuminated background of Maffei and Fiorentini caused an inhibition of the response to a central grating alone, then their enhacement effect in relation to this stimulus might be a suppression effect if compared to a central stimulus on a blank background. In addition, their center-alone gratings 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 also account for their enhancement effects. It is informative that in the Fries et al. (1977) study, their three classes of responses correspond identically to the three major classes of results reported here (Orientation Contrast, General Suppression, and No Effect).

It is also impressive how well the present 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). If one compares the normalized population responses of the present study (Figure 15) with the optical recordings of the Grinvald et al. study (their Figure 4), the pattern of results looks remarkably similar, the only difference being a slightly weaker general suppression effect.

Gilbert and Wiesel (1990) recorded from cells in cat striate cortex using contextual stimuli very similar to the flanking surround quadrant stimuli of the present study. They measured the tuning curve for the orientation of the center element while systematically changing the orientation of the surround elements, and found that for 9/27 cells studied, the peak of the tuning curve shifted when the surround elements were close (within 30°) to the center orientation. The average shift was 11°. Gilbert and Wiesel suggest that this orientation tuning shift may be related to the perceptual tilt illusion. More relevant to the present study, though, was their finding 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 oriented orthogonally or nearly orthogonally to the center element, contrary to the results of the present study and the results of the similar studies in the cat (reviewed in the Introduction). The reason for these differences in results is unclear, perhaps related to the particular visual stimuli employed.

UNRESOLVED ISSUES

As is often the case in a study such as this one, more questions and unresolved issues remain than answers. In this section I will address the most crtical unresolved issues and suggest possible experiments to address them.

Spatial Extent of Surround Effect

As discussed above, one critical unknown is the spatial extent of the suppressive surround effects. Do the outer rings in our stimuli contribute to these effects, and if so, how much? An answer to this question would help in trying to determine the anatomical basis of the surround effects. If the outermost rings contribute substantially to the effect, then it is likely that the widespread horizontal and feedback connections are involved. On the other hand, if only the innermost ring is involved, then more local connections cannot be ruled out.

There are a few obvious experiments that will address this question. One is to record responses of cells to stimuli with only 1, 2, 3, or 4 rings and see if the surround effects grow stronger wth larger numbers of rings. Variations on this theme would include starting out with only the outermost ring and adding rings from the outside in, seeing which outer ring starts to produce the suppression. Finally, one can test the effect of a single ring of elements at different surround distances. All of the experiments taken together should reveal the spatial extent of the surround, and might even reveal some interesting surround interactions. The results of Allman et al. (1990) are relevant to this question. These authors found that for some cells in V1 of the owl monkey, direction-dependent surround effects came from areas as far as 15° away from the CRF.

As mentioned above, the density tests performed in this study suggest that most of the suppressive effect comes from the innermost rings. However, this test is confounded because the increased spacing between the center element and the surround also leads to a decrease in the density of the surround elements, and it is possible that this surround density is a critical parameter. The experiments proposed above would overcome this confound by maintaining a constant local surround density.

Effect of Varying Surround Orientation

The present results look at the effects of surround elements that are oriented either identically to the center, orthogonally, or randomly. It would be interesting to test the effect of the surround when the elements are at other orientations. Does the orientation contrast effect gradually decrease as the center and surround orientations become more similar? Or is there a threshold level above which all surround orientations produce a similar orientation contrast effect? At what surround orientations does the orientation contrast effect disappear? Psychophysical results would lead one to predict that it would start to diminish when the surround elements are oriented at around 30° or less from the center (Nothdurft, 1985; Bergen and Julesz, 1983b). Experiments in cats would predict that the surround effect would grade as a function of the center-surround orientation difference, but it is possible that the effects might differ in the two species.

Pop-out in Other Modalities

Many psychophysical experiments have demonstrated pop-out effects in domains other than orientation: color (Treisman and Gelade, 1980), motion (Nakayama and Silverman, 1986), size (Nothdurft, 1990a), and depth (Nakayama and Silverman, 1986), for example. There are even examples of pop-out based on high-level surface cues, such as shape-from-shading (Ramachandran, 1988). It would be of interest to determine whether there are analogous surround effects in V1 or other areas to these types of pop-out. If so, does one population of cells encode orientation pop-out, for example, while a separate population encodes color pop-out? Or does the same population of cells encode many forms of pop-out, while other cells are insensitive to all forms.

Laminar Organization of Surround Effects

It would be interesting to know whether the cells showing the surround effects were located in all cortical layers or were confined to a subset of them. Since the different cortical layers have different projection patterns, this information may help in interpreting the functional significance of these effects. In many of the orientation contrast studies in the cat (see Introduction) simple cells were affected by the surround patterns whereas complex cells were not. It would be of interest to know whether the same distinction holds for simple and complex cells in the monkey using our stimuli. It would also be valuable knowing what anatomical types of cells exhibit the surround effects, e.g., inhibitory (GABAergic) interneurons, pyramidal cells, etc., and where these cells project. This would entail recording from cells and then intracellularly injecting the same cell with a dye to reconstruct its projection pattern. Although this is a technically difficult experiment, it is possible. Such an experiment would reveal whether the orientation contrast information is sent from V1 to higher cortical areas and/or to subcortical areas. An intriguing possibility is that the information is sent to subcortical areas implicated in selective attention (e.g., pulvinar). The possible role of these effects in the guidance of selective attention is discussed further below.

Detailed Mapping of CRFs in Relation to Pop-out Stimuli

An unresolved issue is whether these surround effects are true nonclassical receptive field effects or whether they can be explained by classical mechanisms, e.g., end-stopping or inhibitory side bands. This issue can be addressed by making detailed maps of the CRF, using appropriate stimulation to unmask inhibitory regions as well as excitatory regions, such as was done in the Nelson and Frost (1978) study. If one still sees effects from outside the detailed CRF, as did Nelson and Frost, then it would be difficult to explain these in terms of CRF mechanisms. It may be, though, that the surround effects displayed by at least some of the cells are due to surround elements falling within the classical inhibitory regions. This type of experiment would be more suitable to an anesthetized preparation, for the small eye movements of fixation in an alert animal might tend to make a fine-grained RF plot inaccurate.

Effect of Texture Density on Differential Suppression

Finally, the density test performed here gives us some clues regarding the generation of the general suppression effect, but since the sample of cells tested with these stimuli did not show a strong orientation contrast effect, we do not know the effect of increasing interelement distance on the orientation contrast effect. This test should be extended to a larger sample of cells that show stronger contrast effects to see if this effect diminishes as the density of elements in the surround decreases.

POSSIBLE ATTENTIONAL EFFECTS

One of the central points of many theories of texture segregation is the distinction between the preattentive and attentive modes of vision. Preattentive vision works in parallel across the whole visual scene. Its function is to detect areas of contrast (luminance, motion, orientation, etc.) in the scene and to direct attentive processing to that location, whereupon a more detailed analysis of the visual information can be performed. Since the monkeys in the present study were trained to fixate a spot of light and to virtually ignore the texture stimuli, it is likely that the texture stimuli were being processed preattentively. The results obtained fit in well with this idea, for overall the responses were stronger to orientation contrast stimuli than to noncontrast stimuli. A natural question, then, is what would happen to the cellular responses if the monkey's attention was directed to the visual stimulus. Would the cells retain the same suppressive effects, or would they show different effects as a result of the attentive processing? Are some cells used only for preattentive processing, while others perform attentive processing, or does the same cell have two modes of operation, a preattentive and an attentive? We are currently starting experiments to address these types of questions.

RELATIONSHIP TO COMPUTATIONAL MODELS OF TEXTURE SEGREGATION

The results of psychophysical research (Enns, 1986; Gurnsey and Browse, 1989) and computational models (Malik and Perona, 1990; Gurnsey and Browse, 1989; Caelli, 1985) have revealed that both sides were partially correct in the early debate over texture segregation being a local or a global process. Texture segregation appears to rely on the distribution of local features of the image extracted from neural filters, but the context in which the local features are present plays an important role in the discriminability of the textures. It appears that this context dependence can explain the foreground/background element asymmetries mentioned earlier (Gurnsey and Browse, 1989). In addition, Malik and Perona (1990) concluded that such a context dependence, in the form of local inhibition between neural filters, was necessary to make their model's performance equivalent to human performance.

The present results show that the texture context in which an oriented bar is presented can inhibit the response of the cell to the bar in a differential way, depending on whether there is a contrast in orientation between the target and the surround. This orientation-dependent surround inhibition bears some resemblance to the local inhibition of Malik and Perona, in that their oriented filters inhibited only identically oriented filters. The motivation behind their local inhibition stage was to eliminate weak "spurious" responses to image features from filters that were not tuned for that feature, by raising the output threshold of the filters and suppressing responses below the threshold. The suppressive effects shown in the present study might be involved in such a function.

INDIVIDUAL CELLULAR UNRELIABILITY/VARIABILITY IN RESPONSES 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 show both the general suppression and orientation contrast effects (see Figure 22A); however, as shown in Table 2, at the individual cell level, there is no such consistency of responses. At the population level, cells respond more strongly to the contrast pattern than to either noncontrast (uniform and random) pattern; at the single cell level, most cells that show an orientation contrast effect for one noncontrast pattern do not show it for the other. At the population level, at all time periods shortly after response onset both effects are present; at the single cell level, some cells show the effect when looked at over the whole stimulation period, whereas others show it only during the first 100 msec. This variability in single-cell responses is probably due to the small size of the surround effects (35% general suppression overall, 10% differential) compared to the inherent variability in neuronal responses to any stimulus. One might expect that all the variability might cancel out any effect when the responses are added up over the whole population, but instead 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, due to this inherent single-cell variability in responses, the amount of information transmitted by most single neurons about the presence of orientation contrast in a single trial would appear to be quite small. It is only from a population of many neurons that a consistent, reliable decision about orientation contrast can be made. 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), using signal-detection theory techniques, showed that some of these neurons can reliably signal small orientation differences that are near the limit of human and primate perceptual performance. How reliably the responses of single V1 neurons can signal the presence of orientation contrast awaits such an analysis using appropriate stimuli. Some of the cells showing a strong differential effect may be able to signal the presence of contrast quite reliably, but it is doubtful that the vast majority of cells can do so.

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