

The Lateral Inhibition of Perceived Contrast is Indifferent to On-Center/Off-Center Segregation, but Specific to Orientation

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When a central test patch C , composed of an isotropic spatial texture, is surrounded by a texture field S , the perceived contrast of C depends substantially on the contrast of the surround S . When C is surrounded by a high contrast texture with a similar spatial frequency content, it *appears* to have less contrast than when it is surrounded by a uniform field. Here, we employ two novel textures: T^+ which is designed to selectively stimulate only the on-center system, and T^- , the off-center system. When C and S are of type T^+ and T^- , the reduction of C 's apparent contrast does not vary with the combination of T^+ , T^- . This demonstrates that the reduction of C 's apparent contrast is mediated by a mechanism whose neural locus is central to the interaction between on-center and off-center visual systems. We further demonstrate *orientation specificity*: the reduction of grating C 's apparent contrast by a surround grating S , of the same spatial frequency is greatest when C and S have equal orientation. Using dynamically phase-shifting sinusoidal gratings of 3.3, 10 and 20 c/deg, we measured reduction of apparent contrast using different contrast-combinations of C and S . Results: (1) S gratings, both parallel and perpendicular to C , cause a reduction in C 's apparent contrast relative to a uniform surround. (2) In all of the viewing conditions, the reduction of apparent contrast induced by the parallel surrounds was at least as great as that induced by the perpendicular surrounds. Often it was much greater. (3) Orientation specificity increases with increasing spatial frequency and with decreasing stimulus contrast.

Lateral inhibition Orientation specificity Contrast perception Texture Scale invariance

INTRODUCTION

Previously, we demonstrated that the perceived contrast of a patch of isotropic, random visual texture is diminished when that patch is embedded in a surrounding background of similar texture (Chubb, Sperling & Solomon, 1989). We also demonstrated that, for brief flashes of the center and surround, this contrast inhibition effect is strictly monocular. That is, when the patch and the surrounding texture are presented to different eyes, the apparent contrast of the center will not be diminished. In addition, we showed that this effect is spatial-frequency specific: when the spatial frequency of the patch differs by an octave from the frequency of the surround, then the apparent contrast of the patch is influenced very little by the contrast of the surround. These results suggest the existence, at some level of visual processing, of laterally-interactive neural arrays tuned

to local contrast energy within relatively narrow spatial frequency bands. Neural arrays of this type have also been suggested by other psychophysical and physiological studies (Chubb & Sperling, 1988, 1989; Shapley & Victor, 1978; Enroth-Cugell & Jakiela, 1980; Ohzawa, Sclar & Freeman, 1985; Sagi & Hochstein, 1985; Heeger, 1992).

The present research describes two new phenomena of lateral texture-contrast interactions. The first section (Expt 1) demonstrates that signals from on-center and off-center visual mechanisms are combined prior to processing by the mechanism which mediates the lateral inhibition of perceived contrast. The second section (Expts 2–4) demonstrates that the neural arrays which compose this laterally interactive mechanism are tuned to specific orientations of spatial texture, and measures the orientation specificity as a function of the contrasts of the center and surround.

GENERAL METHODS

Subjects

In each experiment two subjects were run. Each subject was a trained psychophysical observer (JS and

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CC are experimenters). Each had normal or well-corrected vision.

Stimuli

Each stimulus consisted of a circular patch of texture (the *center*) surrounded by another circular patch of texture (the *surround*). The mean luminance of each center and surround was the same, and equal to the background of the display. All displays were presented at 60 frames/sec, and all stimuli were dynamic. That is, new random phases of the textures in the center and in the surround were selected every $\frac{1}{15}$ sec. The images were created using both specially designed programs and the HIPS image-processing software package (Landy, Cohen & Sperling, 1984).

Apparati

The displays for the experiments were presented on three different monochrome graphics monitors using an Adage RDS 3000 image display system. In Expt 1, subject CC used a Leading Technologies 1230V (12 in diagonal) with a mean luminance of 90 cd/m², and subject JS used a US Pixel PX-15 (15 in diagonal) with a mean luminance of 40 cd/m². In Expts 2 and 3, both subjects used a Princeton MAX-15 (14 in diagonal), with a mean luminance of roughly 60 cd/m². In Expt 4, both subjects used the US Pixel.

Calibration

For each monitor, luminance linearization was achieved using a center/surround display comprised of a uniform circular patch surrounded by an annular background containing a squarewave pattern of spatial frequency equal to that of the sinusoidal pattern used in Expts 2–4. A sheet of frosted plastic was placed in front of the monitor. At distances of 1 m or more, this effectively filtered out the high spatial frequencies in the annular surround, and both center and surround appeared uniform. The experimenter set the maximum and minimum luminance values for the light and dark pixels of the surround, and then adjusted the luminance of the center until center and surround were no longer distinguishable. The resulting center luminance is thus halfway between the maximum and minimum luminances of the display. Systematic iterations of this technique yield displays with precisely calibrated contrasts. In order to stabilize the monitor's power draw throughout the linearization process, two separate center/surround displays were shown concurrently. When establishing a relatively high luminance value on one display, the corresponding low luminance value was established on the other.

Procedure

The subject sat in a dark room and viewed the display binocularly. The only source of illumination was the light from the continuously illuminated display. The trial sequence is illustrated in Fig. 1. Upon a key press, a stimulus with a center and a surround was presented. Then, the central texture was presented alone, then the

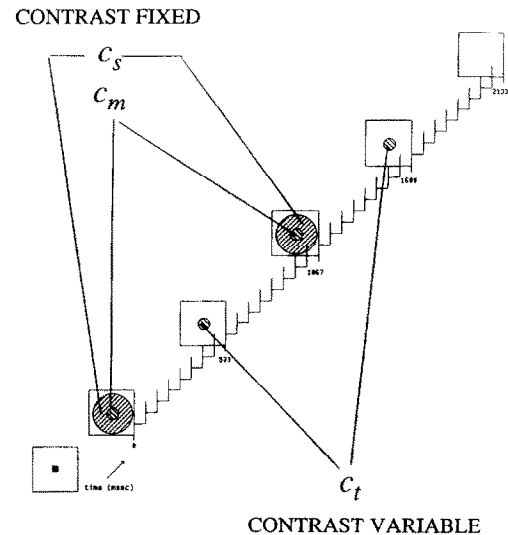


FIGURE 1. Illustration of general procedure. Subject fixates on a cue spot. Following a key press, eight frameblocks (four frames at 60 frames/sec) appear in one of one of the four center/surround texture combinations. They are followed by eight frameblocks of just the center texture (surround contrast equals zero). This 16 frameblock sequence is then repeated. Presentation rate is 15 frameblocks/sec. Immediately following the sequence a blank frame is presented, which is terminated by the subject's response. The subject's task is to indicate whether or not the center texture appeared to have more contrast in the presence of the surround than when viewed in isolation.

center/surround pair again and finally just the center again. Each of the four presentations lasted 533 msec. The subject's task was to make a forced-choice judgment. The subject had to decide whether the central grating had more contrast in the presence of the surround or when it appeared alone. The subject indicated his/her choice by pressing one of two buttons. There was no limit to the time within which the subject had to give his/her answer. In summary: the center appeared four times in a trial, twice with the surround on ("masked center"), and twice with the surround off ("test center"). The subject's task was to decide whether the apparent contrast of the test center was greater or less than the apparent contrast of the masked center.

We use " $c_t \hat{>} c_m$ " to denote a response indicating that the apparent contrast of the test center was greater than apparent contrast of the masked center and " $c_t \hat{<} c_m$ " to denote the response that the apparent contrast of the test center was less than apparent contrast of the masked center. Consider the psychometric function mapping c_t , the actual contrast of the test center, to $P("c_t \hat{>} c_m")$. We determined two points on this function, the values of c_t for which $P("c_t \hat{>} c_m") = 0.62$ and 0.38 . This allows us to estimate both the point of subjective [the value of c_t for which $P("c_t \hat{>} c_m") = 0.5$] and the slope of the psychometric function, which is a measure of the intrinsic variability of the point of subject of subjective equality. To determine these points, we used a staircase procedure in which the subject's response on trial n is used to determine the contrast of the test center on trial $n + 1$.

For each stimulus, there were two interleaved staircases, designated by their expected points of convergence

on the psychometric function: a 0.62 staircase and a 0.38 staircase. In the 0.62 staircase, the contrast of the test center was decreased by one step size, after every " $c_t > c_m$ " response. The contrast of the test center was increased by one step size, after two consecutive trials yielding " $c_t < c_m$ " responses. In the 0.38 staircase, the contrast of the test center was decreased by one step size, after every " $c_t < c_m$ " response. The contrast of the test center was increased by one step size, after two consecutive trials yielding " $c_t > c_m$ " responses.

Specifically, we measured the reduction of the masked center's apparent contrast induced by the presence of the surround, as a percentage. The calculation of this is shown here

percent reduction in apparent contrast

$$= 100 \left[\frac{c_m - c_t}{c_m} \right] \quad (1)$$

where c_m is the actual contrast of the masked center, and c_t is the actual contrast of the test center.

For each viewing condition in each experiment, subjects ran one block of 50 trials (at least six trials per staircase) using a step size of value $\frac{1}{10}c_t$. Then, with a smaller step size (approximately $\frac{1}{40}c_t$), subjects ran as many blocks of 100 trials as necessary (typically 3–5) until the variance of the reversed points of each staircase, divided by the square root of the number of reversals, was no greater than 2.5%.

EXPERIMENT 1:

ON-CENTER/OFF-CENTER INTERACTION

The fact that Chubb *et al.* (1989) observed the induced reduction of apparent contrast to be strictly monocular in their conditions suggests it is a relatively low level visual process. This raises the possibility that the lateral inhibition underlying the effect might be occurring at the level of on-center and off-center retinal ganglion cells or LGN cells. If so, it seems possible that the inhibition would selectively occur between cells of the same contrast polarity. In other words, perhaps on-center cells selectively inhibit other on-center cells and off-center cells selectively inhibit other off-center cells. Experiment 1 investigates this conjecture.

Stimuli

The on-center and off-center visual pathways work in tandem to efficiently code information about contrast in the visual field. Both on-center and off-center ganglion and LGN cells maintain a steady base rate of firing, which can be increased or decreased by appropriate stimuli. It seems unlikely that contrast information from suprathreshold stimuli can be adequately signaled by *decreases* in the base firing rates. In the extreme, no cell can distinguish between two stimuli, each of which has sufficient contrast to cause a complete cessation in firing. Less extreme stimuli may slow the firing rate down enough so that the rate itself may only become

discernible to subsequent processing stages after some considerable time (Enroth-Cugell & Robson, 1984). However, stimuli of contrast which cause a decrease in the firing rate of on-center cells should simultaneously cause an increase in the firing rate of off-center cells, and vice versa. Thus, contrast information can be adequately coded by an increase in the firing rate of one of the two systems.

Indeed, selective, pharmacological blocking of on-center cells in monkeys has been demonstrated (Schiller, Sandell & Maunsell, 1986) to severely impair detection of bright spots, without affecting dark spot detection. This finding supports the notion that local luminance increments are coded by the on-center system, and local luminance decrements are coded by the off-center system.

Two recent psychophysical studies with human subjects supply further evidence for segregated processing of local luminance increments and decrements. Malik and Perona (1990) demonstrated that when one texture is defined by patches composed of light bars with dark sidebands, and another by dark bars with bright sidebands, a boundary between the two textures is perceived preattentively. Solomon and Sperling (1993) demonstrated that one-third of the population can perceive the motion of gratings defined by the same textures used in the current experiment. A mechanism having a linear function of stimulus luminance as input would not be able to segregate Malik and Perona's textures nor extract motion from Solomon and Sperling's gratings. Neither would one whose input equally weights local luminance increments and decrements. However, performance of these tasks *can* be modeled by a mechanism whose input effectively filters out either local luminance increments or local luminance decrements, and has a soft activation threshold.

Based on the luminance-balanced micro-elements of Carlson, Anderson and Moeller (1980), two novel textures were designed to investigate mechanisms which receive input from either on- or off-center neurons, but not both. These textures consist of bright or dark points on gray backgrounds. In theory, bright points will selectively increase the firing rates of on-center cells in whose receptive field centers they fall, and dark points will increase the firing rates of off-center cells in whose receptive field centers they fall. These textures are somewhat similar to the stimuli used by Zemon, Gordon and Welch (1988), in an attempt to differentially stimulate the on- and off-center systems. Ours differ from the textures used by Zemon *et al.*, in that ours are designed so that the level of adaptation of neurons in each pathway remains constant, independent of the polarity of the texture. This is accomplished by ensuring that the mean luminance of all textures remains constant and that phase (i.e. the positions of the bright and dark points) is randomly determined every $\frac{1}{15}$ sec. Unlike the static textures used by Zemon *et al.* which were not equated for mean luminance, our textures are designed so that any neuron with a receptive field large enough to include several bright or dark points will receive the same stimulation.

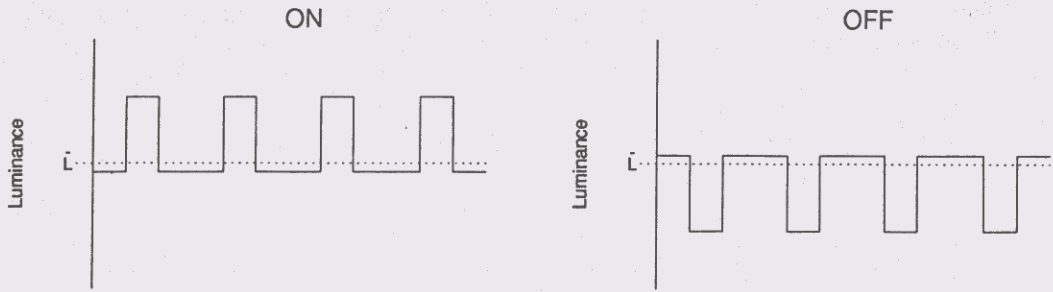


FIGURE 2. Illustration of "ON" and "OFF" textures. A vertical (or horizontal) slice through each texture is diagrammed. Mean luminance \bar{L} , is indicated on the ordinates.

Insofar as the on-center and off-center ganglion cells can be modeled as having center-surround antagonism and a (soft) threshold for firing, then the bright spots in our textures will selectively increase the firing rates of

on-center cells in whose receptive field centers they fall, and the dark spots will increase the firing rates of off-center cells. Various plausible assumptions about the responsiveness of on- and off-center systems make a high

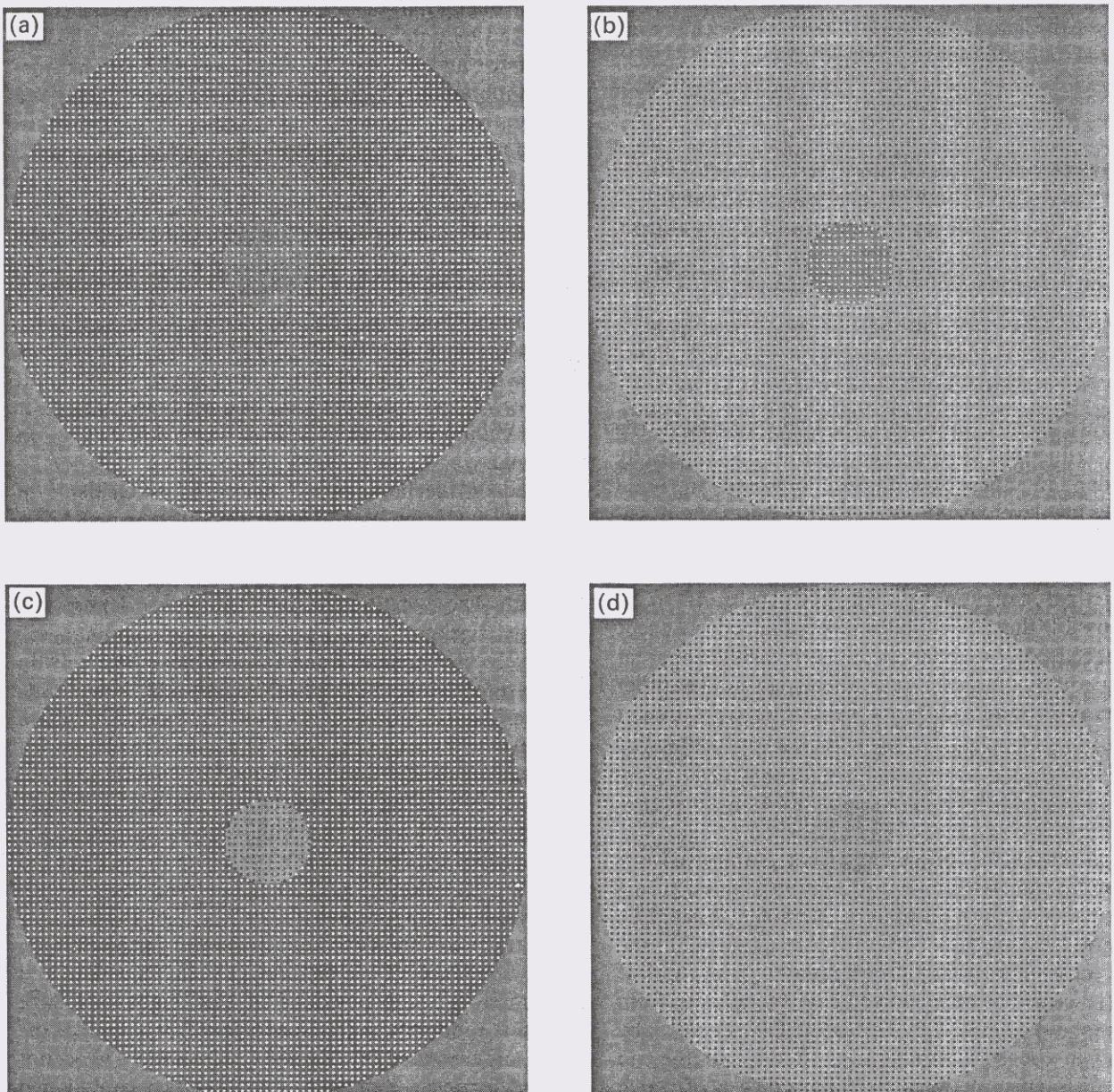


FIGURE 3. Stimuli for Expt 1. (a) On-center stimulating center, on-center stimulating surround (ON/ON). (b) On-center stimulating center, off-center stimulating surround (ON/OFF). (c) Off-center stimulating center, on-center stimulating surround (OFF/ON). (d) Off-center stimulating center, off-center stimulating surround (OFF/OFF).

degree of physiological selectivity likely. For example, if responses are proportional to the second power of contrast of near-threshold stimuli, then stimulation of the on-center system by bright points should dwarf any concomitant stimulation of the off-center system by their background. Nonetheless, the true physiological selectivity of these textures remains to be tested.

The texture designed to selectively stimulate on-center cells is comprised of a regular grid of bright pixels (the pixel at every third row and every third column is bright). This texture is called an "ON" texture. The "OFF" texture is designed to selectively stimulate off-center cells; it is comprised of a regular grid of dark pixels (the pixel at every third row and every third column is dark). The luminances of the other pixels in the textures are chosen so that the mean luminance of the ON texture is equal to the mean luminance of the OFF texture (see Fig. 2).

The stimuli used in this experiment were composed of center/surround combinations of these textures. The positions of the pixel grids in each center and each surround of each block of four frames ($\frac{1}{15}$ sec) were randomly chosen from one of nine possible phases (three horizontal positions times three vertical positions); this produces a dynamically changing display and the appearance of a jittering boundary between center and surround.

There were four stimulus combinations corresponding to two different types of surround texture times two different types of center texture. The four center/surround combinations are shown in Fig. 3. ON masked centers (with a surround) are judged only relative to ON test centers (without a surround), and OFF test centers are judged only relative to OFF masked centers.

The stimuli were viewed from a distance of 0.67 m. At this distance, for JS the surround subtended a visual angle of 9.3 deg, and the center, 1.5 deg. For CC the surround subtended a visual angle of 7.2 deg, and the center, 1.2 deg.

Results and discussion

The results for both subjects are plotted in Fig. 4. Two points, the means of the staircases with the different convergence points, are shown for each center/surround combination. The lower point indicates the percent reduction in apparent contrast, as determined by the 0.38 staircase; the upper point indicates the 0.62 staircase. Symbol size reflects maximum standard error. Most standard errors are much less than symbol size.

For each center/surround combination, both subjects show more than a 50% reduction of the center's apparent contrast induced by the surround. The mean percent reduction (mean of 0.62 and 0.38 staircases) of apparent contrast does not vary with center/surround combination. A surround which is intended to excite only the off-center visual system causes the same degree of reduction in the apparent contrast of a center which is intended to excite only the on-center visual system, as does a surround which is intended to excite only the on-center system, and vice versa.

According to these results, the neural mechanism that mediates the lateral interactions responsible for this reduction of apparent contrast combines information from both the on-center and the off-center pathways. The mechanism for the lateral inhibition of perceived contrast lies central to the point of on-center/off-center integration.

EXPERIMENTS 2-4: ORIENTATION SPECIFICITY

The procedure we use here was motivated by the initial observation that a surround grating whose overall contrast is temporally modulated will cause an apparent, opposite phase modulation in the contrast of a temporally constant target grating. When two target gratings are used, one with orientation parallel to that of the surround and one with orientation perpendicular to that of the surround, the contrast of the parallel target seems to modulate more than the contrast of the perpendicular target. Further observations suggested that the disparity between contrast inhibition induced by parallel and perpendicular surround gratings was not always pronounced. Some stimulus parameters are better than others at eliciting orientation specific differences in contrast inhibition. The following

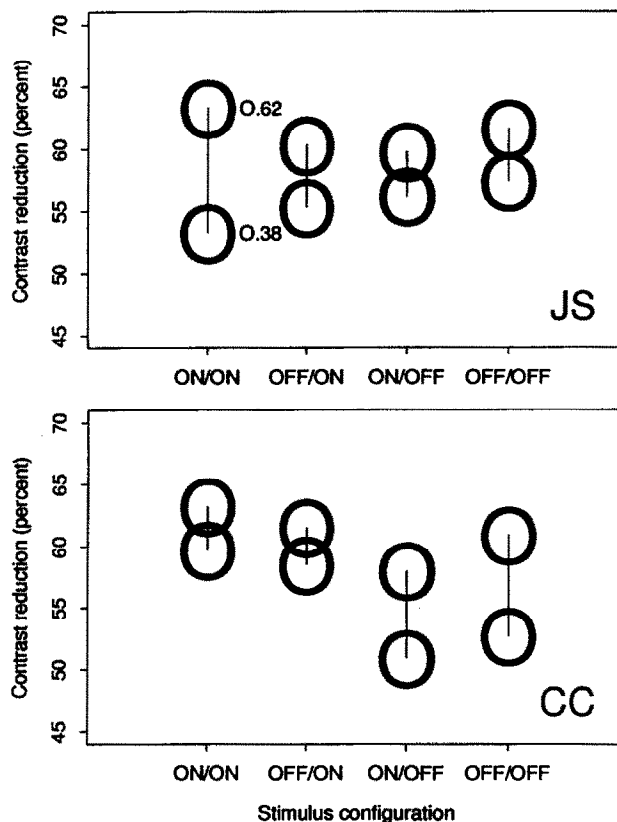


FIGURE 4. Results for subjects JS and CC, Expt 1. For each stimulus configuration, there is a 0.62 probability that the apparent reduction in contrast induced by the presence of the surround is less than that denoted by the upper point. Likewise, there is a 0.38 probability that the apparent reduction in contrast induced by the presence of the surround is less than that denoted by the lower point. Symbol size reflects maximum standard error.

experiments were designed to confirm our initial observations.

Stimuli

All the stimuli were center/surround combinations of sinewave gratings. For each $\frac{1}{15}$ sec frameblock of the stimulus, the phases of both the center and the surround gratings were independent and randomly determined at one of four possible phases. The sinewave gratings were presented in one of two different orientations: either slanted 45 deg in one direction or slanted 45 deg in the other direction. There were four center/surround combinations, corresponding to the two different orientations of surround grating times the two different orientations of center grating. The four stimulus combinations are illustrated in Fig. 5.

Procedures

There were four independent variables: center/surround orientation (parallel, perpendicular), spatial frequency (3.3, 10, 20 c/deg), contrast of the surround c_s , and contrast of the masked center c_m . Spatial frequency was varied by varying viewing distance; this had the virtue of leaving all the physical characteristics of the display intact and varying only the retinal scale. The dependent variable was the *percent reduction in apparent contrast* of the center induced by the presence of the surround, as defined in equation (1). Viewing conditions and results for Expts 2–4 are summarized in Table 1.

The monitor used to display the stimuli in Expt 4 was different from the one used to display the stimuli in Expts 2 and 3. As a consistency check, both subjects performed the 3.3 c/deg, $c_s = 1.0$, $c_m = 0.5$ viewing con-

dition with the new monitor. The resulting data were indistinguishable from the initial data gathered in Expt 2.

Only with the $c_s = 1.0$, $c_m = 0.5$ procedure was the center grating visible at 4 m. (At this, the longest viewing distance, the center grating had a spatial frequency of 20.0 c/deg.) Thus, this viewing distance was omitted from all other procedures. Similarly, with the $c_s = 0.04$, $c_m = 0.03$ procedure, the center grating was invisible from 2 m. Thus, only the shortest viewing distance was used in Expt 4.

Results

There were no systematic differences between the responses to stimuli of reflectively symmetrical orientations; therefore, these data have been pooled. That is, the data from trials in which the center and surround shared the same orientation have been pooled (*parallel configuration*), and the data from trials in which the center and surround were perpendicularly oriented have been pooled (*perpendicular configuration*).

The results for Expts 2–4 are plotted in Figs 5 and 6. As in Expt 1, two points are plotted for each configuration to indicate the points of convergence of the 0.62 staircases and the 0.38 staircases.

Each individual graph compares the reduction in apparent contrast for the parallel stimulus configuration with that for the perpendicular stimulus configuration.

Trends in the data. (1) For every stimulus configuration, in every viewing condition, there is a statistically significant ($P < 0.005$) percent reduction of the center's apparent contrast induced by the surround.

(2) The difference between the heights of the parallel-configuration points and the perpendicular-

TABLE 1. Viewing conditions and results for Expts 2–4

Experiment	Subject	Contrast		dva		Spatial frequency (c/deg)	Mean luminance (cd/m ²)	Contrast reduction (%)			
		c_s	c_m	Surround	Center			Parallel		Perpendicular	
								0.707	0.293	0.707	0.293
2	AS	1.0	0.5	9.9	1.64	3.3	60	47.2	41.9	44.6	40.6
2	AS	1.0	0.5	3.3	0.55	10.0	60	51.5	45.4	42.9	34.0
2	AS	1.0	0.5	1.6	0.28	20.0	60	52.9	37.1	21.7	6.0
2	AS	0.2	0.1	9.9	1.64	3.3	60	38.1	28.5	30.0	22.2
2	AS	0.2	0.1	3.3	0.55	10.0	60	52.6	36.7	17.4	4.4
2	JS	1.0	0.5	9.9	1.64	3.3	60	29.3	19.7	27.5	19.0
2	JS	1.0	0.5	3.3	0.55	10.0	60	37.7	27.4	28.5	18.1
2	JS	1.0	0.5	1.6	0.28	20.0	60	54.2	28.7	22.9	4.6
2	JS	0.2	0.1	9.9	1.64	3.3	60	26.3	19.3	23.0	8.1
2	JS	0.2	0.1	3.3	0.55	10.0	60	41.4	29.3	19.6	7.7
3	AS	1.0	0.1	9.9	1.64	3.3	60	49.6	41.4	40.0	31.5
3	AS	1.0	0.1	3.3	0.55	10.0	60	58.1	47.8	37.0	24.4
3	AS	0.2	0.1	9.9	1.64	3.3	60	35.6	27.4	29.6	24.4
3	AS	0.2	0.1	3.3	0.55	10.0	60	52.6	43.7	26.3	17.0
3	JS	1.0	0.1	9.9	1.64	3.3	60	44.4	34.8	42.6	29.3
3	JS	1.0	0.1	3.3	0.55	10.0	60	41.1	30.4	28.5	4.4
3	JS	0.2	0.1	9.9	1.64	3.3	60	26.6	19.3	23.0	8.1
3	JS	0.2	0.1	3.3	0.55	10.0	60	41.1	29.3	19.6	7.7
4	AS	1.0	0.04	9.9	1.64	3.3	40	64.6	60.9	62.0	56.9
4	AS	0.04	0.03	9.9	1.64	3.3	40	37.8	31.3	27.8	12.8
4	JS	1.0	0.04	9.9	1.64	3.3	40	48.5	43.0	42.5	28.5
4	JS	0.04	0.03	9.9	1.64	3.3	40	40.5	24.4	23.6	6.6

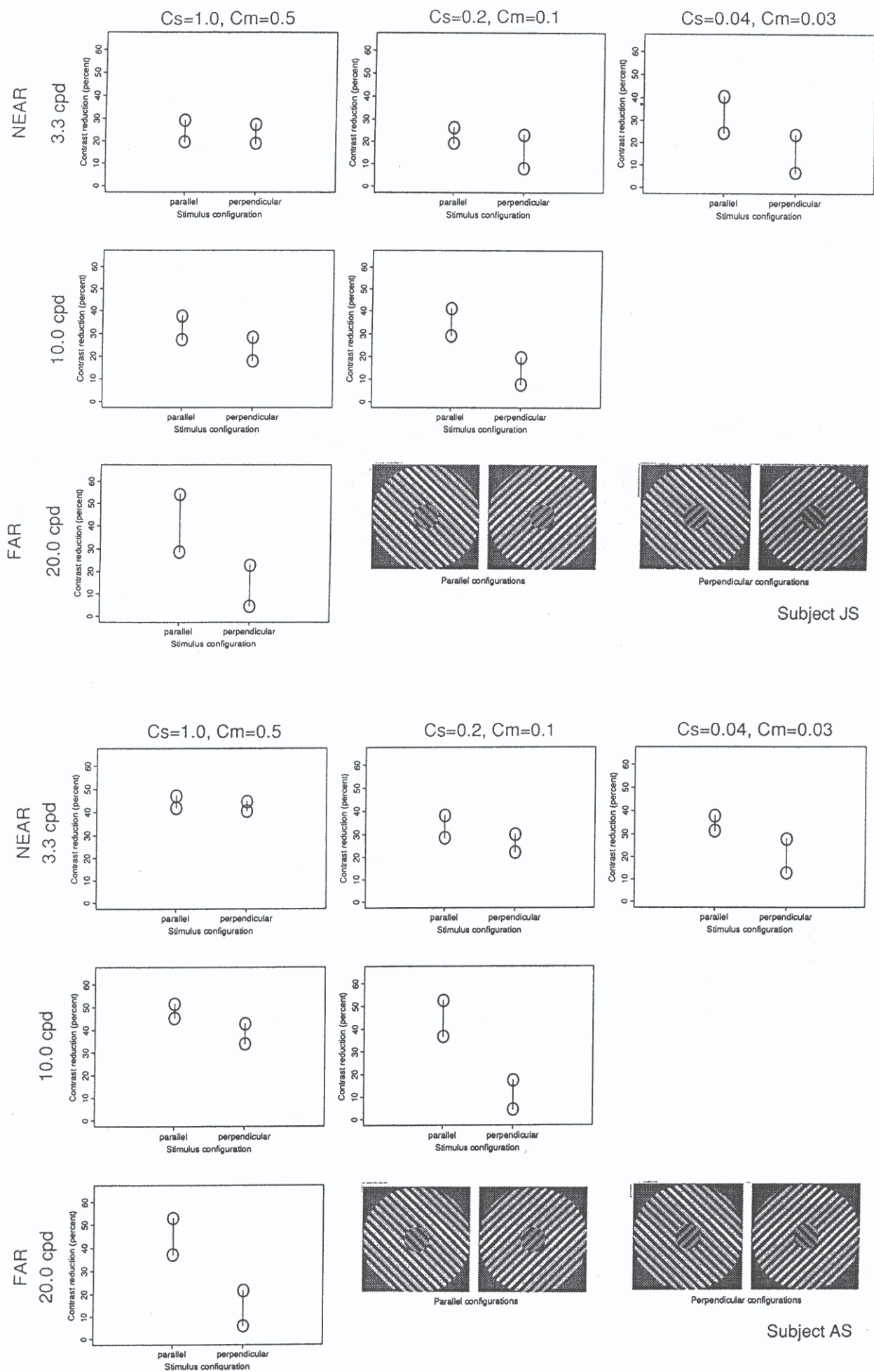


FIGURE 5. Results for subjects JS and AS, Expts 2 and 4. Six experimental conditions, four types of stimulus (see insets). Data from reflectively identical center/surround combinations are collapsed.

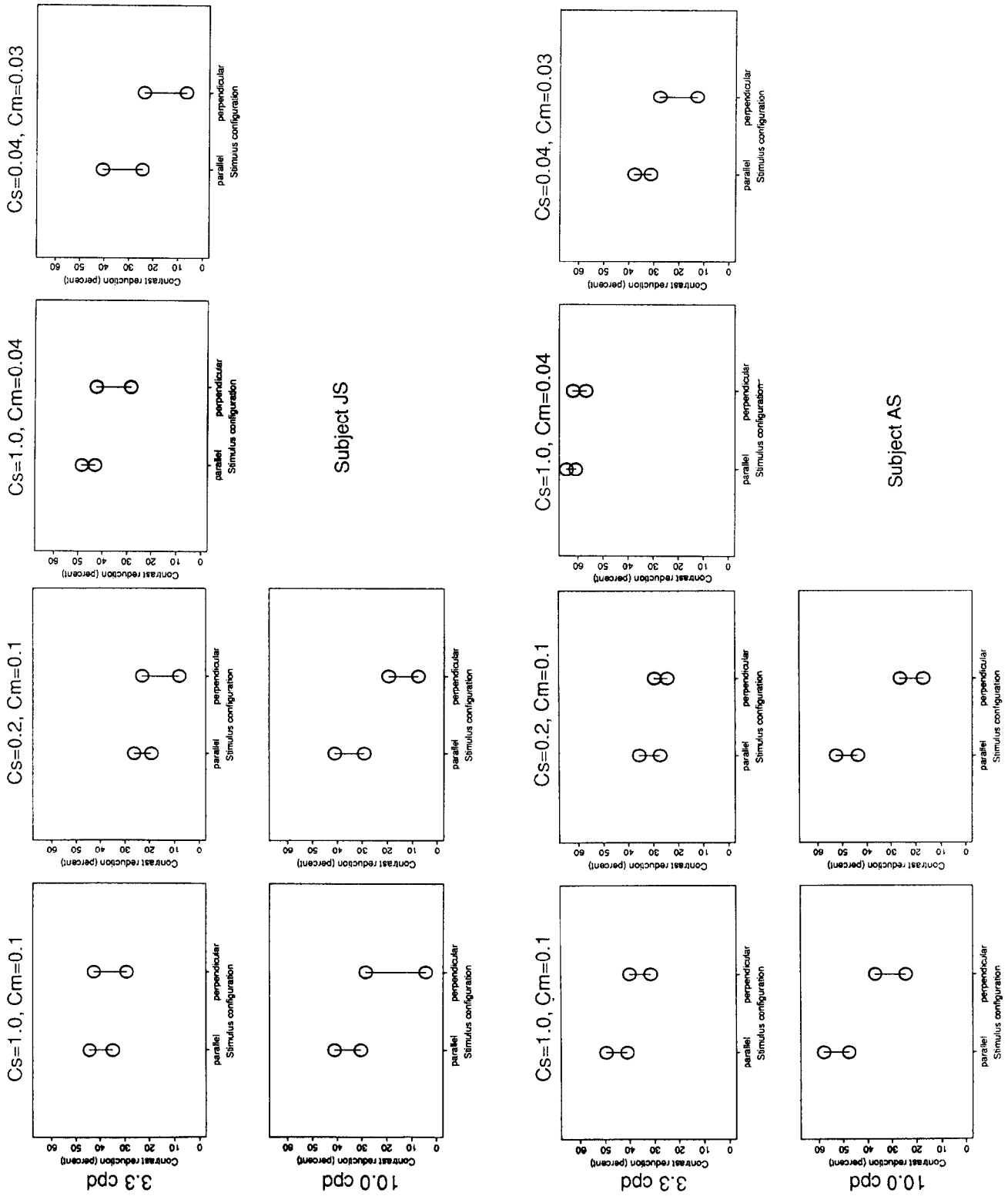


FIGURE 6. Results for subjects JS and AS, Expt. 3.

configuration points on each graph is a measure of the orientation specificity in that viewing condition. In all of the viewing conditions, the percent reduction of apparent contrast induced by the parallel surrounds is at least as great as that induced by the perpendicular surrounds. Often it is much greater.

(3) The left column of Fig. 5 represents all of the data from the trials in which $c_s = 1.0$, $c_m = 0.5$. Note that *an increase in the viewing distance (and hence an increase in the retinal spatial frequency of the gratings) results in greater orientation specificity*. This general trend obtains for the other combinations of c_s and c_m (middle column of Fig. 5, two leftmost columns of Fig. 6).

(4) The first and fourth rows of Fig. 5 represent data from trials in which the retinal spatial frequency of the gratings was 3.3 c/deg, and the ratio of $c_s:c_m$ was 2:1. Note that *a decrease in stimulus contrast results in an increase in orientation specificity*. This general trend also holds for the 10.0 c/deg stimuli (second and fifth rows of Fig. 5).

GENERAL DISCUSSION

Chubb *et al.* (1989) conducted similar experiments to those reported here. However, they used patches of isotropically filtered visual noise rather than sinusoidal gratings. Their principal findings were: (i) for high contrast surrounds, when c_m was roughly equal to half the surround contrast, percent reduction of apparent contrast was around 40%, *provided* that center and surround were filtered into the same frequency band; (ii) if the center and surround were presented to opposite eyes, no induction occurred; (iii) if center and surround were filtered into octave-wide frequency bands, with center frequencies one octave apart, the percent reduction of apparent contrast dropped down to 15%. This third result indicates that the reduction of apparent contrast induced by the presence of the surround is spatial frequency specific.

The current experiments investigate the degree to which this reduction of apparent contrast induced by the surround is *orientation* specific.

Channels, tuned filters, neurons

Since the pioneering work of Campbell and Robson (1968), it has been recognized that the visual system filters the visual signal into a number of relatively narrow spatial frequency bands, which they termed *channels*. Each of these channels can be modeled approximately as an array of linear filters with all filters in the array sharing the same receptive field profile, but centered at different retinal locations so as to cover the visual field. Each of these filters produces a positive or negative output in response to any given stimulus. Apparent contrast is proportional to the absolute value of filter output.

One way of understanding the results of Chubb *et al.* (1989) is to suppose that the output values produced by the filters in these arrays are subject to lateral inhibition from other filters in the same array. In particular, the

higher the *absolute value* of the output of a filter in such an array, the greater its inhibitory effect on other filters near it in the array. Thus, high contrast regions of a narrow band texture produce regions of high absolute value in the filter array tuned to that texture; in turn, these regions of high absolute value output act laterally to damp the magnitude of the output values produced by filters in nearby regions of the array, thereby lowering the apparent contrast of the inhibited region.

In the visual system, filters are realized by neurons. We assumed that, in each of our experimental conditions, the observed percent reduction of apparent contrast depends on the amount of lateral inhibition delivered to neurons tuned to the center texture by neurons tuned to the surround texture. For any viewing condition, the observed reduction of apparent contrast induced by a parallel surround is always at least as great as that induced by a perpendicular surround; we thus infer that the neurons tuned to the parallel surround deliver at least as much inhibition to the similarly tuned neurons being stimulated by the center texture than do the neurons tuned to the perpendicular surround. That is, neurons tuned to the same orientation deliver more inhibition to each other than do neurons tuned to different orientations.

Relations to physiology

Physiological studies of macaque and cat have yielded no evidence for any precortical orientation specificity (Hubel & Weisel, 1977). This restricts the neural locus of the interaction between texture-sensitive neurons. Equally restrictive is the result that surround-induced apparent contrast reduction is a strictly monocular effect.

When we first reported that the lateral inhibition of perceived contrast does not spread interocularly (Chubb *et al.*, 1989), we used tests involving only band-passed isotropic texture to support our claim. To insure that this result held true for high frequency gratings as well, we re-ran our "interocular induction" experiment with two subjects. In this procedure the center and surround, both 20 c/deg, were presented to different eyes in a continuous display. Here, and in the interleaved same-eye control trials, center and surround were separated by a thin gray annulus to prevent rivalry. The surround flashed either on or off every 500 msec. Subjects adjusted the contrast of the surround-on center, until it appeared equal to that of the surround-off center. As before, this manipulation was effective in removing any noticeable interaction between the contrast of the surround and the appearance of the center. Thus, we maintain that the neural locus for the lateral interaction between texture-sensitive neurons lies at an early cortical or precortical level of processing.

Physiological studies of the functional architecture of macaque and cat visual cortex have revealed that, outside of layer IV in area 17, binocularly driven cells greatly outnumber monocularly driven cells. Thus we propose that it is the neurons of this layer which combine texture information, in a spatially antagonistic

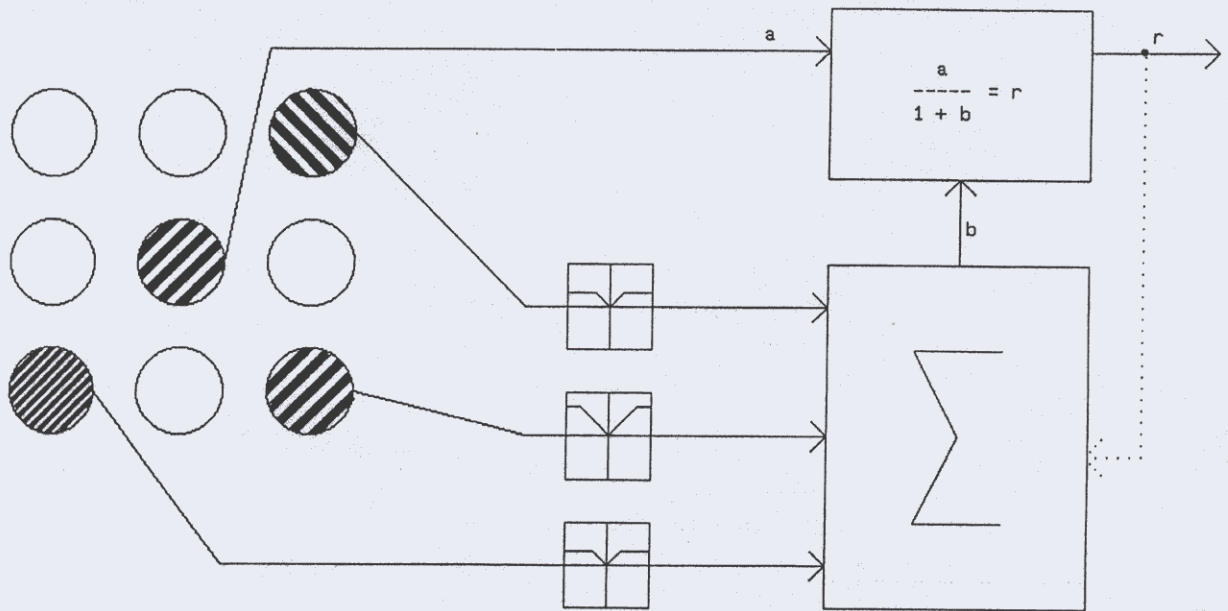


FIGURE 7. Model for the lateral inhibition of perceived contrast. Central unit tuned to specific spatial frequency and orientation. Excitatory component a , is the dot product (correlation) of the stimulus with the receptive field of the central unit. Surrounding units are tuned to a variety of frequencies and orientations. Their outputs are rectified and summed, giving preferential weighting (indicated by the filters in the small boxes) to those units with spatial location, frequency and orientation tuning similar to that of the central unit. The response r , of the central unit is scaled with respect to this combination b . The dotted arrow indicates a more complex model, in which the responses of surrounding units are scaled with respect to the response of the central unit.

way, resulting in surround-induced apparent contrast reduction.

A model

Simple theory: one-way interactions. Figure 7 diagrams proposed interactions between various texture-sensitive units. We use the term *units* (rather than *neurons*) because neurons transmit only positive firing rates (positive signals); it requires a push-pull pair of neurons (a neural *unit*) to transmit both positive and negative signals. Also, we do not differentiate here between a single neuron and many similar neurons that may be acting in concert.

The central unit is tuned to a specific spatial frequency and orientation. The excitatory component a is the dot product (correlation) of its receptive field with the stimulus. The surrounding units are tuned to a variety of spatial frequencies and orientations. Their outputs are first rectified (absolute value) and then added together giving preferential weighting (indicated by the filters diagrammed in the small boxes) to those units with spatial location, frequency and orientation tuning similar to that of the central unit. The output response r , of the central unit is scaled with respect to the rectified sum of surrounding outputs b . We consider this simple model first, and then a more complex model in which the interactions are reciprocal, the output of the surround units being scaled by the rectified output of the center unit.

Since virtually every viewing condition results in some reduction in apparent contrast, it is possible to construct a model that attributes a proportion p of this effect

to a balanced mixture of parallel and perpendicularly oriented units that have precisely equivalent properties and occur in precisely the same numbers. Consequently, any orientation specific effect must be attributed to parallel and perpendicular units that have different properties and may occur in different numbers. Alternatively, one could attribute a proportion $q \leq p$ of the total observed reduction in apparent contrast to a population of unoriented receptive fields. For conceptual simplicity, for the proportion p of orientation-balanced units, we do not discriminate the balanced mixture of parallel and perpendicular receptive fields from a functionally equivalent mixture of unoriented receptive fields.

The model portrays inhibition as a divisive (shunting) form of gain control (Sperling & Sondhi, 1968; Sperling, 1970), for which *percent reduction in apparent contrast* is the natural dependent variable. The model is similar in spirit to the models proposed by Sperling (1989) and Heeger (1992). It differs in three respects: it deals in detail with the contrast saturation functions that limit lateral interactions, it allows for orientation specific normalization, and reciprocal inhibitory interactions between center and surround are treated explicitly.

To apply the simple model to the current experiments, we consider the equilibrium state when a masked center (contrast c_m) with its surround (contrast c_s) is equated in apparent contrast to the isolated test center (contrast c_t). Because the surround inhibits the masked center, the match is represented as

$$c_t = \frac{c_m}{1 + b'}, \quad b' = \sum_i w_{i,\theta} g_{\theta}(c_s). \quad (2)$$

The functions g_θ are monotonically increasing functions that represent the influence of the surround on the center; $g_\theta = g_\parallel$ or g_\perp depending on whether the orientation of the center is parallel (\parallel) or perpendicular (\perp) to the surround. The values of the weights $w_{i,\theta} \geq 0$ depend on the relative orientations θ of the units, as well as their retinal locations i . Solving equation (2) for c_i and substituting for c_i in equation (1) yields

percent reduction in apparent contrast

$$\begin{aligned}
 &= 100 \left[\frac{c_m - c_i}{c_m} \right] = 100 \left[\frac{c_m - \frac{c_m}{1 + b'}}{c_m} \right] \\
 &= 100 \left[1 - \frac{1}{1 + b'} \right]. \tag{3}
 \end{aligned}$$

One obvious implication of equation (3) is that the percent reduction in apparent contrast should be independent of the contrast level c_m of the matching stimulus. This can be checked against the available data: $c_s = 1, c_m = 0.5$ (Fig. 5) and $c_s = 1, c_m = 0.1$ (Fig. 6). There is a tendency, quite large in some instances (e.g. subject, JS, 3.3 c/deg) for a smaller reduction in apparent contrast to be associated with higher levels of c_m . The observed variation of percent reduction in apparent contrast with c_m requires an elaboration of the simple theory.

An approximation to a theory of fully reciprocal interactions. A quite natural elaboration of the theory of equation (2) is to consider that not only does the surround inhibit the center but the center reciprocally inhibits the surround. Because of its smaller size and contrast, the center may exert less effect on the surround than vice versa. A first-order approximation to this reciprocal theory is simply to elaborate the term b' [equation (2)] to a b (no prime) that incorporates reciprocal inhibition from the center:

percent reduction in apparent contrast

$$\begin{aligned}
 &= 100 \left[1 - \frac{1}{1 + b} \right] \\
 &= 100 \left[1 - \frac{1}{1 + \frac{\sum_i w_{i,\theta} g_\theta(c_s)}{1 + h(c_m)}} \right] \tag{4}
 \end{aligned}$$

and to use this b instead of only its numerator [b' in equation (3)]. The function $h(c_i)$ is a monotonic increasing function that represents the inhibitory effectiveness of the center as a function of its output magnitude.

Equation (4) is an approximation because it uses only the first two terms of an infinite series of indirect effects in which the reciprocal feedback of the center affects the surround which affects the center, etc. Indeed, the situation is far more complex. The center is represented by a large aggregate of diverse neurons, as is the surround. Every neuron is involved with all of its neighbors in

reciprocal feedback interactions. This fully interactive model is far beyond the scope of the present paper, both in complexity and in the number of assumptions that would be needed to fully specify the model. So, we stop with the first two terms. In this two-term approximation, the effects of varying the contrast of the center (which are represented in the denominator) are separable from the effects of varying the contrast of the surround (which are represented in the numerator). The function h absorbs the effect of level of matching contrast c_m on percent reduction in apparent contrast.

Orientation specificity. The surround, of course, has the biggest role in determining the percent reduction of apparent contrast of the center. We now consider the complex effects of surround contrast c_s , spatial frequency f of the center and surround, and relative orientation (\parallel, \perp) of center and surround. These are mediated by the functions $g_\parallel(c_s)$ and $g_\perp(c_s)$. The data allow us to distinguish between three complementary explanations of the relationship between inhibitory connections between pairs of texture-sensitive units with parallel receptive fields and pairs of texture-sensitive units with perpendicular receptive fields (see Fig. 8).

(i) *Early saturation:* $g_\parallel(c_s) = g_\perp(c_s)$ and $w_\perp = k_1 w_\parallel, 0 < k_1 < 1$ [Fig. 8(a)]. The function $g_\parallel(c_s)$ mapping input contrast to lateral inhibition for parallel surrounds and the function $g_\perp(c_s)$ for connections between units tuned to perpendicular surrounds are identically the same, only their weights differ. The functions saturate at contrasts $< \pm 1$.

(ii) *Low efficiency (same intercept):* $g_\parallel(c_s) = g_\perp(k_2 c_s)$ and $w_\perp = w_\parallel, 0 < k_2 < 1$ [Fig. 8(b)]. The function mapping contrast to lateral inhibition reaches the same maximum level for connections between units tuned to different orientations as it does for connections between units tuned to equal orientations, but it has a smaller slope (lower efficiency) for connections between units tuned to different orientations than it does for connections between units tuned to equal orientations.

(iii) *Low efficiency (non-saturating)* [Fig. 8(c)]. The linear functions shown in Fig. 8(c) satisfy the conditions on g and w defined in both (i) and (ii). That is, the function mapping contrast to lateral inhibition is *strictly* increasing. It reaches a different maximum level for connections between units tuned to different orientations than it does for connections between units tuned to equal orientations, and it has a smaller slope (lower efficiency) for connections between units tuned to different orientations than it does for connections between units tuned to equal orientations.

While each of these assumptions about the nature of g_\parallel and g_\perp can account for much of the data, none of them accounts for all. We consider now empirical criteria which, when are satisfied, would refute each of these interpretations. One way to refute early saturation is to demonstrate that, at high levels of surround contrast (e.g. $c_s = 1.0$) there is no indication of orientation specificity. To refute low efficiency (same intercept), it is sufficient to demonstrate that, at high levels of surround contrast there is distinct orientation specificity.

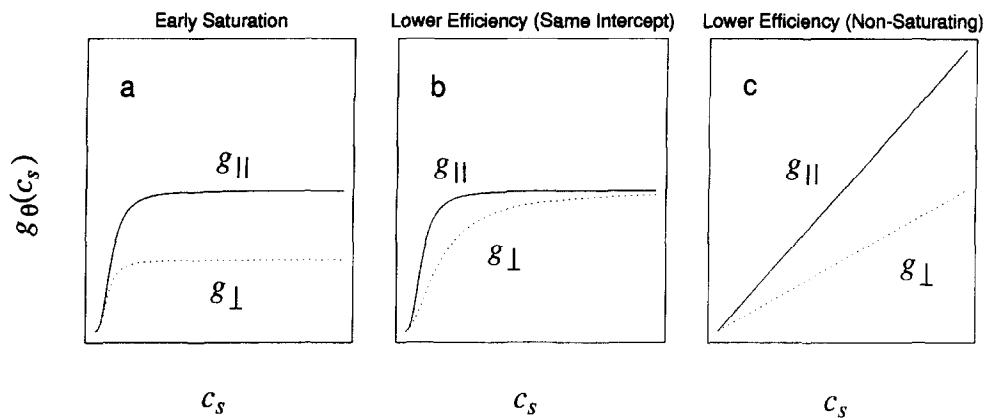


FIGURE 8. Three complementary relationships between the inhibition delivered by lateral connections to neurons of equal and different orientations: (a) Early saturation, the function mapping contrast to lateral inhibition has a lower intercept (earlier saturation) for connections between neurons tuned to different orientations (dashed line) than for connections between neurons tuned to equal orientations (solid line). (b) Low efficiency (same intercept), the function mapping contrast to lateral inhibition reaches the same maximum level for connections between neurons tuned to different orientations as it does for connections between neurons tuned to equal orientations (solid line), but it has a smaller slope (lower efficiency) for connections between neurons tuned to different orientations (dashed line) than it does for connections between neurons tuned to equal orientations (solid line). (c) Low efficiency (non-saturating), the function mapping contrast to lateral inhibition is *strictly* increasing, reaches a different maximum level for connections between neurons tuned to different orientations as it does for connections between neurons tuned to equal orientations (solid line), and has a smaller slope (lower efficiency) for connections between neurons tuned to different orientations (dashed line) than it does for connections between neurons tuned to equal orientations (solid line).

Low efficiency (non-saturating), can be refuted by demonstrating that, for a given c_m , an increase in surround contrast does not result in any increase in percent reduction in apparent contrast.

For 20.0 c/deg stimuli, only one value of c_s was tested, so we cannot refute low efficiency (non-saturating). However, we can refute low efficiency (same intercept) because, for both subjects, distinct orientation specificity is apparent in the data (Fig. 5).

For 10.0 c/deg stimuli again we are able to refute low efficiency (same intercept). There is distinct orientation specificity when $c_s = 1.0$ for both subjects, especially when $c_m = 0.1$ (Fig. 6). For 10.0 c/deg stimuli we are also able to refute low efficiency (non-saturating). There is no appreciable difference between the data from the $c_s = 1.0$, $c_m = 0.1$ viewing condition and the $c_s = 0.2$, $c_m = 0.1$ viewing condition, for either subject.

For 3.3 c/deg stimuli, however, things are much less clear cut. Both subjects' data display distinct increases in percent reduction in apparent contrast with an increase in c_s . This prohibits us from discrediting low efficiency (non-saturating). For JS, only with $c_m = 0.03$ does there appear to be some orientation specificity, when surround

contrast is maximal. Whether or not this orientation specificity is distinct enough to refute low efficiency (same intercept) is a matter for debate. The most parsimonious judgment is to accept all three explanations as possibilities. For AS, only with $c_m = 0.1$ does there appear to be any significant amount of orientation specificity, when $c_s = 1.0$. Here again the best policy is not to discredit any of the three explanations. A summary of the possible explanations for each subject's data, at each spatial frequency, is given in Table 2.

CONCLUSION

Chubb *et al.* (1989) demonstrated that the lateral inhibition of perceived textural contrast is mediated by arrays of neurons that are narrowly tuned for spatial frequency. The results of these experiments indicate that they are tuned for orientation as well. This research also clearly indicates that the mechanism responsible for the lateral inhibition of perceived textural contrast receives equal inputs from both the on-center and the off-center visual pathways.

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TABLE 2. Possible explanations of orientation specific lateral inhibition

Subject	Spatial frequency (c/deg)		
	3.3	10.0	20.0
AS	ES; LE(SI); LE(NS)	ES	ES; LE(NS)
JS	ES; LE(SI); LE(NS)	ES	ES; LE(NS)

Explanations not discredited by the data are given in each cell.

ES, early saturation; LE(SI), low efficiency (same intercept); LE(NS), low efficiency (non-saturating).

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