



Spatial Facilitation Predicted with End-stopped Spatial Filters

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We examined the role of putative end-stopped spatial filters in determining spatial facilitation associated with a line target flanked by square inducers. Results obtained in normal and amblyopic observers were well predicted by end-stopping and other receptive field features of end-stopped spatial filters revealed in a modified Westheimer paradigm. The role of target-inducer collinearity, the effects of inducer polarity, and facilitation associated with non-orientational circular targets, were also studied. Our results suggest that spatial facilitation results from antagonism surrounding spatial filter centers, with end-stopping playing a prominent role. © 1997 Elsevier Science Ltd

Spatial facilitation End-stopping Spatial filter Inducing paradigm Westheimer paradigm

INTRODUCTION

Several recent studies show that the contrast sensitivity to a target object can be increased by nearby spatially separated inducing objects (Dresp, 1993; Kapadia *et al.*, 1995; Morgan & Dresp, 1995; Polat & Sagi, 1993, 1994). Polat and Sagi (1993, 1994) reported that the contrast threshold for a foveal Gabor patch was first elevated (suppression), then reduced (facilitation), by two collinear inducing Gabor patches with increasing target-inducer separation. Thresholds at certain separations were below the baseline level (threshold measured with no inducers) before they finally returned to the baseline level at larger separations. The inducing patches had the strongest facilitation effect when placed end-to-end with the target patch. The authors attributed spatial suppression to spatial integrations within filter receptive fields, in that inducers at small separations excite the same filters and increase the noise level, resulting in masking. Spatial facilitation, which was strongest at a target-inducer separation of 2-3 wavelengths (λ) of the Gabor patch and lasted to more than 6 λ (Polat & Sagi, 1993), was attributed to noise reduction by long-range inhibitory spatial interactions from filters sensitive to different spatial locations. However, it is unclear how long-range inhibition reduces the filter's noise level. Moreover, the strongest facilitation present at a separation of 2-3 λ can be better seen as occurring close to or even within a spatial filter. This is because a separation of 2-3 λ corresponds to a spatial distance varying from 13' ($\lambda = 4.5'$) to 36' ($\lambda = 18'$), and the σ of the gaussian envelope of Gabor patches was 4.5' at the lowest λ (4.5')

and 9' at the largest λ (18'), the target and inducers at this separation were actually somewhat overlapped. Thus, it is uncertain that long-range interactions from spatially non-overlapped filters play an important role in spatial facilitation. Instead, spatial interactions within spatial filters may need to be considered.

Facilitation has also been obtained for a spot (Dresp, 1993) or line target (Kapadia *et al.*, 1995) placed near the end of an inducing line. Facilitation diminished when the target and inducer were not collinear, due to either lateral position offset or orientation difference (Kapadia *et al.*, 1995). Instead of assuming long-range interactions, Morgan and Dresp (1995) suggested that suppression and facilitation actually reflect a pedestal effect. Nachmias and Sansbury (1974) and Foley and Legge (1981) showed that thresholds for a target superimposed on a pedestal of near-threshold contrast are lower than those under no pedestal conditions. However, at higher pedestal contrasts, thresholds increase with the pedestal contrast, following a power law, thus resulting in an overall dipper-shaped function. According to Morgan and Dresp (1995), when the inducer and target are close enough to excite the same simple cell receptive field, the inducer will produce suppression, acting like a supra-threshold contrast pedestal. At larger separations, the inducer will produce weak input to the receptive field, which leads to facilitation, acting like a near-threshold contrast pedestal. Although attractive, the pedestal hypothesis may have difficulty in explaining some existing data. Though the inducer contrast in Morgan and Dresp's study was relatively low (8%), facilitation has also been reported when high contrast inducers were used, and the distances between the target and inducer were very short (e.g., Dresp, 1993; Polat & Sagi, 1993).

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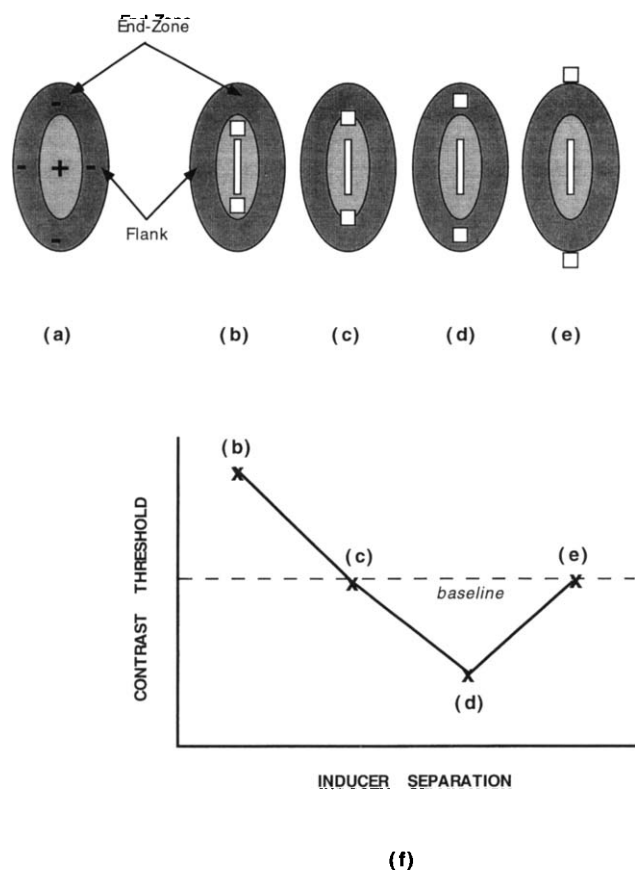


FIGURE 1. (a) The two-dimensional profile of an end-stopped spatial filter. (b)–(e) Inducers placed at these four locations produce distinct inducing effects as shown in (f). (f) A hypothetical inducing function based on predictions of an end-stopped spatial filter.

For example, the inducer contrast in Dresch's study (1993) was near 40%, and the strongest facilitation occurred when the inducer–target gap was 4'. A high contrast inducer so close to the target, if placed in the same simple cell receptive field, might be expected to produce masking rather than facilitation due to the supra-threshold pedestal effect.

In almost all the studies mentioned above, facilitation occurred most often when the target and inducer were located collinearly, or end-to-end. This hints at the possibility that cells with end-stopping might have been involved. Hypercomplex or end-stopped cells (Hubel & Wiesel, 1965, 1968) are characterized by end-zones at the ends of their elongated receptive field centers. Psychophysically, end-stopping has been suggested by Westheimer functions measured with rectilinear stimuli (Yu & Essock, 1996a). Thresholds for a small line centered on a rectangular background are first elevated (desensitization), then reduced (sensitization), until reaching a plateau, with increasing background length. Length desensitization has been taken as suggesting length summation in the center of perceptive fields or spatial filters, and length sensitization as suggesting antagonistic spatial filter end-stopping. Desensitization and sensitization for a line target have also been obtained when the width of the background was changed, and interpreted as

suggesting central width summation and antagonistic flank inhibition. Length and width functions together revealed end-stopped perceptive fields or spatial filters [Fig. 1(a)] resembling the receptive fields of end-stopped simple cells. Later experiments (Yu & Essock, 1996b; Yu & Levi, 1997a) further suggested the cortical origin of end-stopped spatial filters.

Recent literature (Robson, 1988; Albrecht & Geisler, 1991; Bonds, 1991; DeAngelis *et al.*, 1992; Heeger, 1992; Foley, 1994) suggests that the response of striate neurons or spatial filters is in part determined by a nonlinear divisive suppression or normalization process. This orientation non-specific suppressive effect originates from outputs of a pool of neurons in the same cortical region (Heeger, 1992) about the same size as the excitatory receptive field (DeAngelis *et al.*, 1992). In a masking paradigm, adding a mask elevates the contrast threshold because of increased suppressive signals, which reduce the response of the filter to the target (Foley, 1994). This process explains desensitization or threshold elevation in the above Westheimer functions in which the background is within the spatial filter center and serves as a mask. These functions reach a peak when the background is the same size as the spatial filter center because the filter receives maximal suppression. On the other hand, sensitization in length or width Westheimer functions indicates a recovered response or sensitivity of the spatial filter when the background encroaches antagonistic end-zones or flanks. Because orientation non-specific suppression is not overlapped in spatial extent with, and is qualitatively different from, orientation-specific end-stopping and flank inhibition (DeAngelis *et al.*, 1992), the increased sensitivity cannot be attributed to reduced pooled inputs, but rather to antagonistic end-stopping or flank antagonism, which may subtract the suppressive effect of pooled inputs. Therefore, masks have opposing roles on the gain of spatial filters: on the center increasing the divisive suppression, and on end-zones or flanks decreasing it.

According to the above rationale of gain change due to masking on different regions of spatial filters, suppression and facilitation in an inducing paradigm can be readily understood and predicted. Because the increase of suppression due to pooled inputs and the decrease of suppression due to end-stopping occur over different spatial extents and are based on different neural mechanisms (DeAngelis *et al.*, 1992), both processes could function independently. When applied to the inducing paradigm, this independence means that inducers in the filter center would increase the divisive signals over the baseline (no-inducer) level and cause suppression or masking, and in the end-zones would cause suppression below the baseline level and thus produce facilitation. Specifically, when a line target and two square inducers are used, as in the current study, inducers placed within the filter center [Fig. 1(b)] should elevate the contrast threshold above the baseline. Inducers placed on the border of center and end-zones [Fig. 1(c)] should have little or no effect on target

detection, since suppression increase and decrease are canceled out by each other. It is at this point that suppression is changed to facilitation, and the contrast threshold function intercepts the baseline. Inducers placed within the end-zones [(Fig. 1(d))] should reduce the divisive suppression and enhance the filter's sensitivity, driving the contrast threshold below the baseline (facilitation). Finally, when inducers are placed out of the end-zones [Fig. 1(e)], they should no longer affect the spatial filter, and the threshold should return to the baseline. The returning point should indicate the outer limits of end-stopped spatial filters. These predictions are summarized as a hypothetical inducing function in Fig. 1(f).

In this study we examined the above predictions and the roles of end-stopping and other receptive field features in spatial facilitation. We report spatial facilitation results from normal and amblyopic observers, which are well predicted by end-stopped spatial filters measured with width and length Westheimer functions (Yu & Essock, 1996; Yu & Levi, 1997a). Some of these results argue against Morgan and Dresch's (1995) pedestal effect theory, and some may not be easily explained by Polat and Sagi's model of long-range interactions between spatial filters. We also studied the role of collinearity, the effect of inducer polarity, and facilitation associated with non-orientational circular targets. In general, our results suggest that spatial facilitation is the product of antagonism surrounding the spatial filter center, with end-stopping playing a prominent role.

GENERAL METHODS

Observers

Five normal observers (one male, YC; four females, KN, LY, QL and TH, aged 19–32 years) and two amblyopes (one male, RH, one female, AJ, aged 25–27 years) served in this study. All normal observers had normal or corrected-to-normal vision. RH (strabismic) had corrected vision of 20/15 in the preferred eye (O.D.) and 20/48 in the amblyopic eye (O.S.). AJ (strabismic and anisometropic) had corrected vision of 20/15 in the preferred eye (O.S.) and 20/60 in the amblyopic eye (O.D.). QL and TH had no prior psychophysical experience. Others were experienced. Only YC was aware of the purpose of the study.

Apparatus and stimuli

The stimuli were generated by a Vision Works computer graphics system (Vision Research Graphics, Inc.) and presented on a U.S. Pixel Px19 monochrome monitor with a resolution of 1024 × 512 pixels. Pixel size was 0.28 mm horizontal × 0.41 mm vertical (0.17' × 0.25'). The frame rate was 117 Hz. Luminance of the monitor was made linear by means of an 8-bit look-up table. The mean luminance of the monitor screen was 62 cd/m². Experiments were run in a dimly lit room, with a low watt light on the back of the monitor. Viewing was monocular by the dominant eye (right eyes for normal

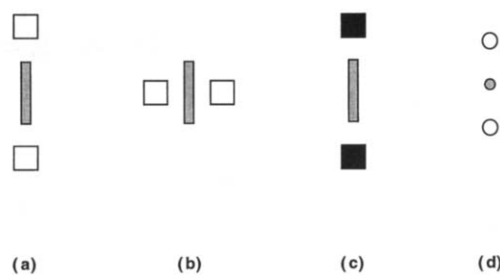


FIGURE 2. Stimulus configuration for each experiment. (a) A 1' × 5' foveal line target with two 3' × 3' square inducers placed end-to-end. (b) Inducers placed side-by-side with the target line. (c) Inducers with the opposite polarity. (d) A 1'-diameter spot target flanked by two 2'-diameter spot inducers.

subjects) or the amblyopic eye, at a viewing distance of 5.64 m.

The stimuli in the first two experiments consisted of a 1' × 5' foveal line target and two 3' × 3' square inducers at a contrast of 33.3%, placed either end-to-end [Fig. 2(a)] or side-by-side [Fig. 2(b)] with the target. In Experiment 3 dark inducers (0 cd/m²) were used to examine the effect of the opposite polarity [Fig. 2(c)]. In Experiment 4 a 1'-diameter foveal spot target was flanked by two 2'-diameter spot inducers at a contrast of 33.3% [Fig. 2(d)]. A target-only condition was also included in each experiment for setting the baseline, in which a 0.5' thick dark ring (diameter = 48') was used to help observers locate the target and thus reduce spatial uncertainty (Pelli, 1985). The Michelson contrast of the target, defined as $(L_{\text{target}} - L_{\text{mean}})/(L_{\text{target}} + L_{\text{mean}})$, was varied by a staircase procedure as the dependent measure.

Procedure

A successive two-alternative forced-choice (2AFC) staircase procedure with a convergence rate of 75% was used. The inducers were present in each of the two stimulus intervals (400 msec each) separated by a 400 msec inter-stimulus interval. In one of the two intervals the target was also presented for the same duration. Each trial was preceded by a 6.3' × 6.3' fixation cross in the center of the screen which disappeared 100 msec before the beginning of the trial. Audio feedback was given on incorrect responses.

Each staircase consisted of four practice reversals and six experimental reversals. The initial contrast was set at 15% for normal observers and 33% for amblyopes. The step size in practice reversals was set at 1.25% and in experimental reversals at 0.25% for normal observers, and respectively 2.5% and 0.5% for amblyopes. The contrast went down one step after a correct response but went up three steps after an error response. The mean of the six experimental reversals was calculated as the contrast threshold. An experimental session usually consisted of 9–10 randomly presented conditions of various target–inducer separations, and lasted for about 35 min. Each datum represents the mean of 4–6 replications for each condition, and the error bars represent ±1 SEM.

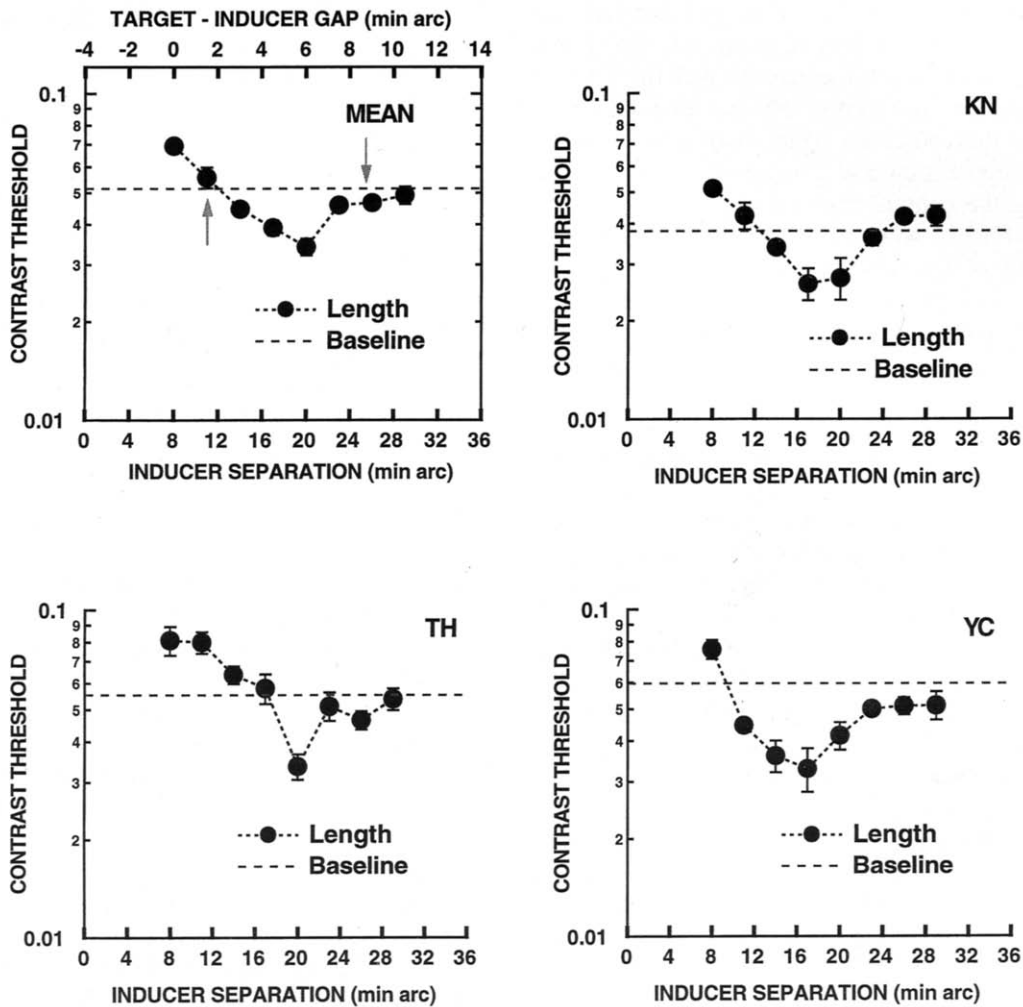


FIGURE 3. Contrast threshold for a $1' \times 5'$ line as a function of the center-to-center separation between two inducers placed end-to-end with the line target. The corresponding gap distance between target and inducer is also presented in the mean figure (top, x-axis). The arrows in the mean figure indicate predicted start and end of spatial facilitation.

EXPERIMENT 1: THE ROLE OF END-STOPPING IN SPATIAL FACILITATION

For a $1' \times 5'$ line, thresholds in the length Westheimer function reached a peak at a background length of $11'$, which then decreased until reaching a plateau at a background length of about $23'$ (Yu & Essock, 1996a). These data have been taken to suggest an $11'$ long summation center and two $6'$ long end-zones of the end-stopped spatial filter most sensitive to a $1' \times 5'$ line. Thus, in an induction experiment, for the same $1' \times 5'$ target line, if two small $3' \times 3'$ square inducers are placed end-to-end to it [Fig. 1(a)], suppression should be observed when the inter-inducer separation (center to center) is smaller than about $11'$, and the crossing point should be at a separation of about $11'$. Beyond that separation, facilitatory effects should be seen until the separation reaches about $26'$ (i.e., $23' + 3'$, or $23' + 2 \times 1/2$ of the size of the square inducers), where the inducers are just out of the outer limits of the end-zones and facilitatory effects should end.

We conducted such an experiment on three normal observers to examine the above prediction. Contrast thresholds were measured for a $1' \times 5'$ line with two $3' \times 3'$ square inducers separated from $8'$ to $29'$ (center-to-center distance between two inducers, or $0'$ to $12'$ gap distance between the line end and the inner edge of the inducer). Results are shown in Fig. 3. Although individual differences are present, the mean curve shows suppression until the inducer separation reaches $12'$, where the contrast threshold function intercepts the baseline. Beyond $12'$ the curve shows facilitation until the contrast threshold returns to the baseline again at a separation of $29'$, with the bulk of the facilitation occurring before $23'$ and the strongest facilitation at $20'$. In general, the extent of the inducing effect is predicted quite well by the end-stopping hypothesis. The total length of the spatial interaction area is within a range of about $29'$, well within the size range of end-stopped cells in primate visual cortex reported by Peterhans and von der Heydt (1993). They found that the optimal stimulus length for end-stopped cells in the central 1° to 6° visual field of area V2

in the macaque ranged from 6' to 181'. In terms of the gap distance between the target end and inducer end, spatial facilitation starts to occur at a gap distance of 2.5', and ends at a gap distance of 10.5'. The latter matches Dresp's (1993) report that facilitation disappeared at a gap distance of 10'–13'. Note too that it is well within the range of Polat and Sagi's facilitation effects observed with Gabor patches. Thus, it appears that end-stopping may be sufficient to account for spatial facilitation.

To ensure that the nice match between the experimental results and the prediction was not a coincidence, we measured the same function on two amblyopes. Previously, when the length Westheimer function was measured on the same two amblyopes (Yu & Levi, 1997a), their results only showed threshold elevation which peaked at a background length a few minutes larger than the normal value, after which there was no threshold decrease, even at very large background lengths. In other words, end-stopping appeared to have been absent in these two observers with amblyopia. In the current inducing paradigm, the end-stopping theory predicts that their inducing functions should reach the baseline at a separation a few minutes larger than the normal value, but should show no facilitation. This is exactly what their results show (Fig. 4)! The contrast thresholds in the two amblyopic functions stop decreasing at a separation of around 17', and the familiar dipper shape of the conventional spatial inducing function is absent. Similar results were also obtained from one observer (RH) when the inducer contrast was reduced to be 20% and 10%, except that suppression was weaker at lower inducer contrasts. There are two possible interpretations for this result: either amblyopia abolishes long-range interactions from other spatial filters (Polat and Sagi, 1993), or it eliminates end-stopping. However, given the close similarity between these results and those obtained using the Westheimer paradigm, we favor the latter explanation. We believe that spatial interactions measured with the Westheimer paradigm and the inducing paradigm may be based on similar neural mechanisms, and spatial facilitation may be comparable to spatial sensitization in a Westheimer function, both resulting from antagonism surrounding the receptive field center. Thus, the inducing paradigm and the Westheimer paradigm are both useful tools for examining the organization of spatial filter receptive fields.

These amblyopic results also argue against Morgan and Dresp's (1995) pedestal effect model. Studies on contrast discrimination of amblyopes (Bradley & Ohzawa, 1986; Levi *et al.*, 1994) demonstrate the same dipper-shaped function of pedestal effects in amblyopes (including current observer RH (Levi *et al.*, 1994)). The normal and amblyopic functions are actually superimposed when the amblyopic functions are scaled by the contrast threshold, so that the processes underlying contrast discrimination in normal and amblyopic vision are similar. Morgan and Dresp (1995) suggested that spatial facilitation occurs when the input from the inducers is sufficiently weak to produce a pedestal effect.

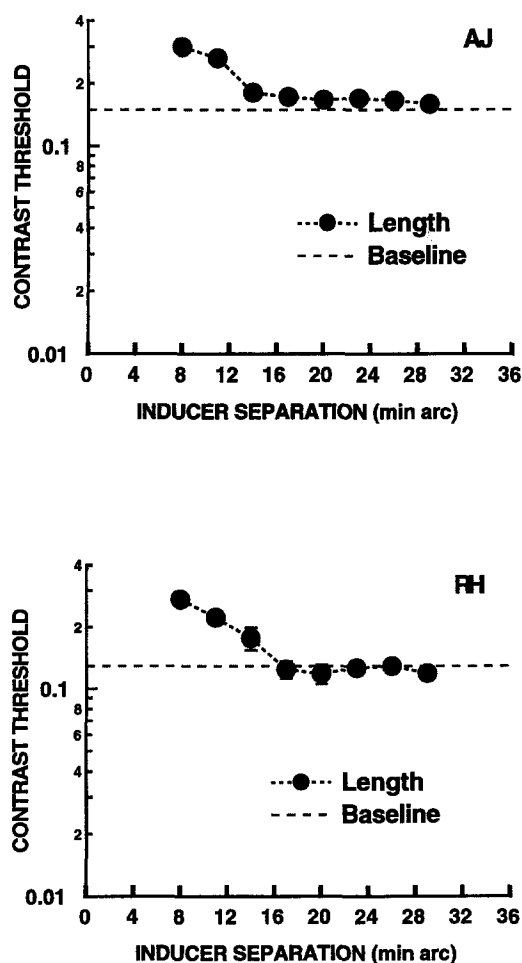


FIGURE 4. The same functions as in Fig. 3 measured in two amblyopes. Notice the scale change of the y-axis due to elevated overall threshold level.

If this model were correct, inputs from two inducers in our experiments, which were strong enough to cause suppression when placed close to the target (Fig. 4), should have produced facilitation at some larger separations, where the inducers' inputs should have become sufficiently weak to facilitate. Thus, the simple pedestal model would predict facilitation, rather than functions with no facilitation at all.

EXPERIMENT 2: COLLINEARITY IN SPATIAL FACILITATION

Inducing experiments often reveal the importance of collinearity in spatial facilitation. Whenever the requirement of collinearity is not met owing to position or orientation offset, spatial facilitation is markedly diminished (Kapadia *et al.*, 1995). According to our theory, such a degradation could occur because the offset moves part or all of the inducers out of the end-zones so that inducers would have little or no effect on the sensitivity of the spatial filter. The question which needs to be answered here is this: is collinearity a necessary condition for facilitation? In an end-stopped spatial filter, antagonism surrounding the filter center includes not only

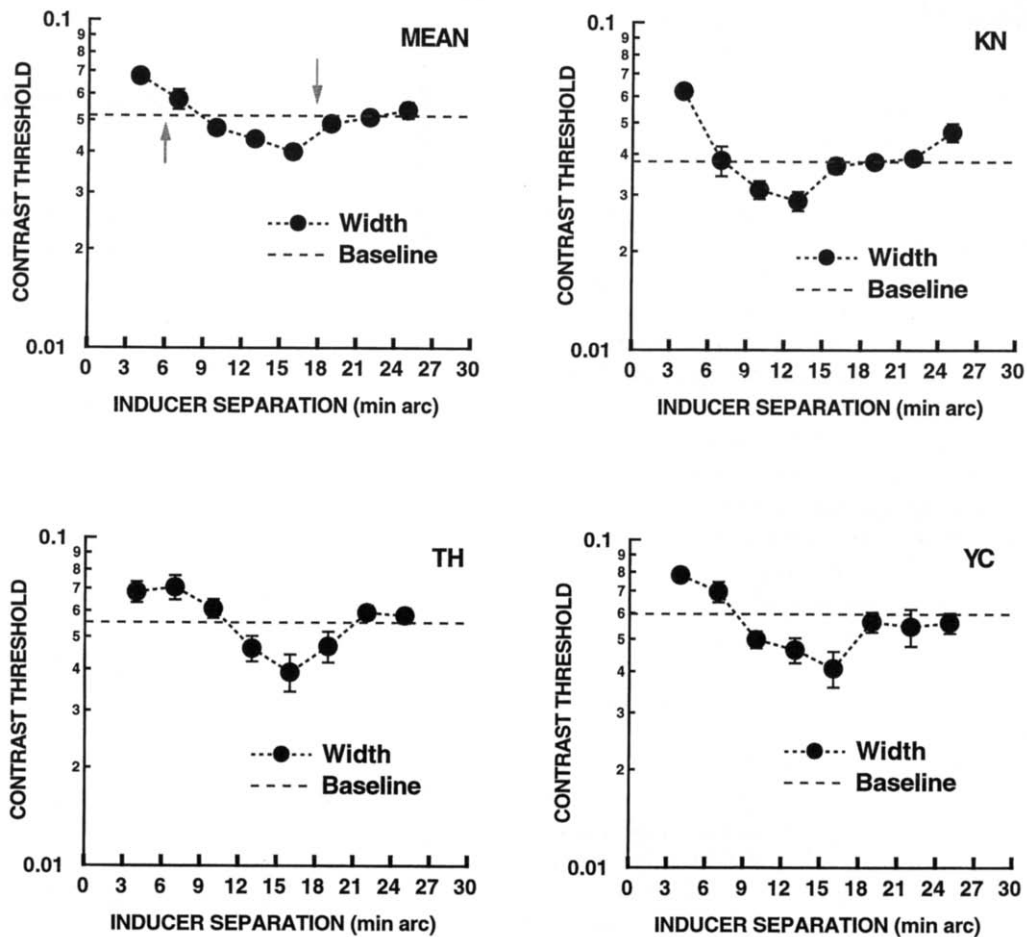


FIGURE 5. Contrast threshold for a $1' \times 5'$ line as a function of the separation between two inducers placed side-by-side with the line target. The arrows in the mean figure indicate predicted start and end of spatial facilitation.

end-stopping, but also flank inhibition side-by-side with the filter center. Like end-stopping, flank inhibition would also be able to produce facilitation, since inducers placed within the inhibitory flanks might affect the spatial filter in similar ways to those placed in the end-zones (see Introduction).

We conducted an experiment on the same three normal observers to test this prediction. The contrast thresholds for the same $1' \times 5'$ line were measured as a function of the separation of the same two $3' \times 3'$ squares placed side-by-side with the target line [Fig. 1(b)]. Previous work (Yu & Essock, 1996a) indicated a width Westheimer function for a $1' \times 5'$ line which peaked at a background width of $6'$ and started to level off at 14 – $16'$. From the view of an end-stopped filter theory of spatial facilitation, such a function should predict a facilitation effect starting at a center-to-center inducer separation of about $6'$ and ending around 17 – $19'$. Clear evidence of spatial facilitation is shown in Fig. 5, indicating facilitation starting around 6 – $10'$ and ending around 16 – $22'$ across observers, with the mean at about $8'$ and $19'$, respectively. The prediction is again quite reasonable. Therefore, it can be concluded that it is the antagonistic surround of the spatial filter, rather than collinearity, that really matters in spatial facilitation. The role of collinearity is only to place the

inducers into the end-zones, which is a sufficient, but not a necessary, condition for spatial facilitation.

Polat and Sagi (1994) found that spatial facilitation was weaker for a vertical Gabor patch when the two vertical inducing Gabor patches were placed side-by-side with it (global orientation = local orientation + 90 deg) than when the inducers were placed end-to-end (collinearly) with it (global orientation = local orientation). Since these stimulus conditions were similar to our length and width-inducing conditions, the mean data from length and width-inducing experiments were compared (Fig. 6) and showed basically no difference between two conditions except for a small shift along the separation axis. The weaker facilitation in Polat and Sagi's side-by-side condition could be attributed to the Gabor patches they used, which had at least one full cycle and thus should have excited the center as well as the flanks of the spatial filter, but not the end-zones. Thus, inducers placed within the flanks would have less impact than those placed within the end-zones.

EXPERIMENT 3: SPATIAL FACILITATION BY INDUCERS WITH THE OPPOSITE POLARITY

Dresp (1993) reported that an inducing line with the opposite polarity (dark line), unlike a bright line, had no

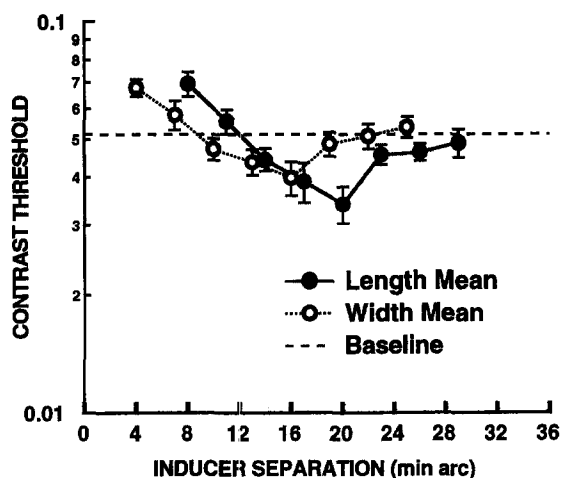


FIGURE 6. A comparison of spatial interaction effects between end-to-end inducing (collinear) and side-by-side inducing (non-collinear).

facilitation effect on the detection of a dot target, implying that spatial facilitation is specific to information from ON or OFF channels. This result provided evidence for the pedestal model, which is based on linear spatial filters [some individual difference was actually shown in Morgan and Dresp's (1995) study, in which one of three observers showed slight facilitation when a dark inducer was used]. On the other hand, receptive field end-stopping has been shown to be phase independent (DeAngelis *et al.*, 1994), suggesting that ON and OFF inputs have been rectified to their absolute values before being processed by end-zones. The same full-wave rectification is also present in psychophysical end-stopping measured with a masking paradigm (Yu & Levi, 1997b), in that end-stopping can be produced by the lengthened mask covering end-zones, regardless of the phase of the mask covering end-zones. Accordingly, inducers with the opposite polarity placed within end-zones should be able to produce facilitation if our end-stopping theory is correct.

We studied this issue by measuring the inducing effects of two dark inducers ($3' \times 3'$ squares at 0 cd/m^2) on the contrast thresholds for a $1' \times 5'$ bright line. Inducers were arranged end-to-end with the target line [Fig. 1(c)]. The whole scenario was the same as in Experiment 1, except for the opposite polarity of the inducers. In contrast to Dresp's report, clear evidence of facilitation was obtained [Fig. 7, filled circles; data in this figure were normalized by the baseline (no inducer) values to allow comparison]. However, compared with the effects of bright inducers (Fig. 7, open circles, from Fig. 3), the facilitation region in at least two observers' results (TH and YC) shifted to larger inducer separations, suggesting the possible involvement of a larger spatial filter or some additional mechanisms when inducers with the opposite polarity are used. This shift is also suggested by Zenger and Sagi (1996) who studied the effects of opposite phase Gabor patches on facilitation, and may explain why no facilitation was observed in Dresp's study, since her measurement only used one fixed separation ($4.5'$ in terms of gap distance).

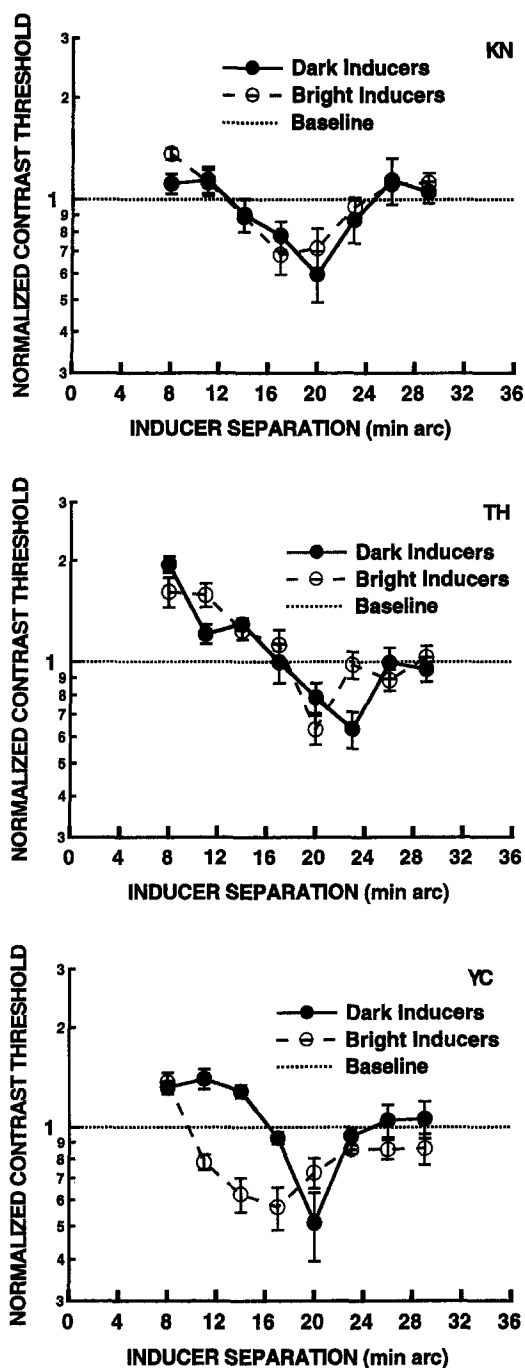


FIGURE 7. The effects of polarity on spatial facilitation: contrast threshold for a $1' \times 5'$ line as a function of the center-to-center separation between two dark square inducers (filled circles). Functions measured with bright inducers from Fig. 3 are also shown for comparison (open circles). Results in this figure are normalized.

Our results suggest that spatial facilitation caused by inducers with the opposite polarity located in the end-zones of the spatial filter is a second-order process, consistent with a full-wave rectifying nonlinearity in physiological and psychophysical end-stopping. These results again cause serious problems for the pedestal model, which is based on half-wave rectified linear spatial filters and would have predicted zero facilitation by inducers with the opposite polarity.

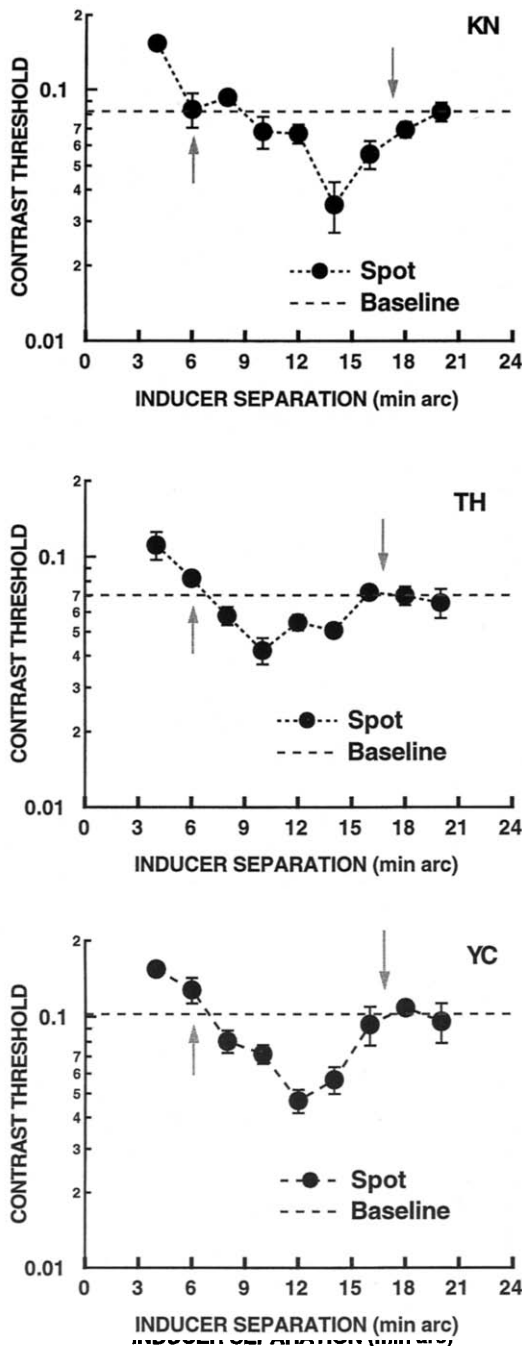


FIGURE 8. The inducing effect for non-orientational target and inducers: contrast threshold for a 1'-diameter spot target as a function of the center-to-center separation between two 2'-diameter spot inducers. The arrows indicate predicted start and end of spatial facilitation.

EXPERIMENT 4: SPATIAL FACILITATION WITH CIRCULAR TARGET AND INDUCERS

It has been reported that contrast thresholds for a circular target can also be facilitated by a line inducer (Dresp, 1993) or a dot inducer (Morgan & Dresp, 1995). Earlier we demonstrated that what matters in spatial facilitation is the antagonism surrounding the filter. A circular center-surround spatial interaction area for a spot target has long been established by Westheimer (1965, 1967). Although this classic phenomenon has often been

interpreted as reflecting the center-surround organization of retinal cells, recent evidence from spatial scaling, dichoptic, and amblyopic experiments (Yu & Essock, 1996b; Yu & Levi, 1997c) suggests that it is mainly a cortical process [see also Lennie and Macleod (1973) and others], and the center-surround antagonism may equate to the center-flank antagonism in a wide Westheimer function associated with a line target (Yu & Essock, 1996b; Yu & Levi, 1997c). Thus, the antagonistic surround in a cortical spatial filter could provide the basis for spatial facilitation for a spot target.

Generally, for a 1'-diameter spot target, a classical Westheimer function reaches its peak at about 6' and levels off at about 14-16', which would predict in an inducing paradigm a facilitation effect starting at an inducer separation of 6' and ending at 16-18', when two 2'-diameter spot inducers are used. We measured the inducing effects of two such spot inducers on the contrast thresholds for a 1'-diameter spot target [Fig. 1(d)]. Results (Fig. 8) show that facilitation starts at about an inducer separation of 7' and returns to baseline at about 16' for observers TH and YC, closely matching the prediction. Results for KN are not quite as good, although still fair, with facilitation starting at around 6-8' and finishing at 20'. Therefore, spatial facilitation for a spot target can be satisfyingly predicted by the conventional Westheimer function.

EXPERIMENT 5: EXAMINING THE TARGET-INDUCER ADDITIVITY

One important line of evidence Morgan and Dresp (1995) used to support their pedestal theory was the finding that inducers function additively with the pedestal. In other words, when inducers causing facilitation are used together with a high contrast pedestal, they suppress detection, but when inducers are used with a near-threshold contrast pedestal, they enhance facilitation. We examined this additivity by performing similar experiments in three observers, two of whom (LY & QL) had not participated in the earlier experiments. A 1' x 5' target was superimposed on a same-sized pedestal at contrasts of 2.5, 5, 10 and 20%. The near-threshold contrast for the target was approximately 5%, the average of the baseline values in Fig. 3. Two 3' x 3' inducers at a contrast of 33% were placed either in the summation center of the spatial filters (center-to-center inducer separation = 8', see Experiment 1) or in the end-zones (separation = 20'), end-to-end to the target line. Thresholds were also measured with no inducers.

As indicated in Fig. 9, when the inducers are placed in the summation center, strong suppression is shown at all pedestal contrasts except 2.5%, where a significant effect is only evident for QL. This masking effect is predicted by the end-stopping theory, as well as by the pedestal theory (as long as inducers are close to the target). However, because the length of spatial filters is limited owing to end-stopping, inducers placed within the filter center are always close to the target. Thus, it is unlikely that these inducers can be placed far away but still within

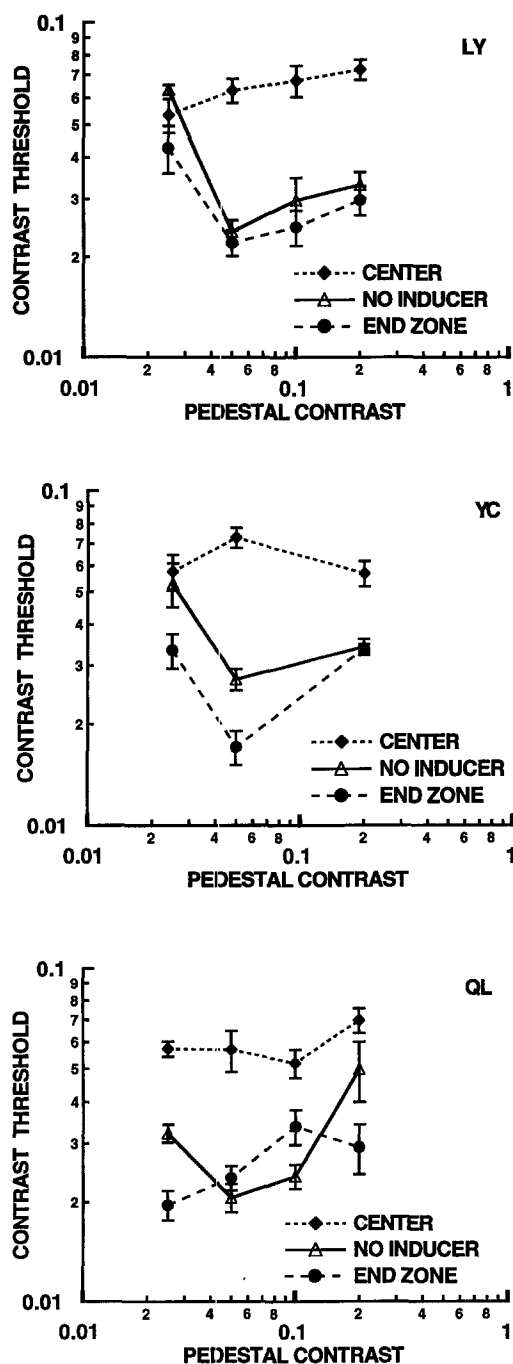


FIGURE 9. Inducing effects measured when the target was superimposed on a same-sized pedestal at near-threshold contrast (5%) and at supra-threshold contrast (20%). Inducers were placed either within the center of the spatial filter or within end-zones.

the center to produce weak inputs for facilitation. When the inducers fall into end-zones, enhanced facilitation as compared to the no-inducer condition is evident at the 2.5% pedestal contrast for all three observers, but is only significant for YC at the 5% pedestal contrast, to some degree consistent with the prediction of additivity.

However, at supra-threshold pedestal contrasts (10 and 20%), results fail to show consistent suppression but present large individual differences. Suppression and facilitation are evident for QL at 10 and 20% pedestal

contrasts, respectively. Slight facilitation at both pedestal contrasts is shown for LY. And no effect is found for YC at the 20% pedestal contrast (the 10% pedestal contrast was not measured). This large individual difference among three observers, as well as between our study and Morgan and Dresch's study, may be attributed to the complex nature of interactions between the supra-threshold inducer and supra-threshold pedestal, in a way similar to the interactions between supra-threshold center and surround patches studied by Cannon and Fullenkamp (1993), who found that the contrast induction of the surround patch to the center patch could be either suppressive or facilitatory for different observers. Therefore, if the apparent contrast of the supra-threshold pedestal in the current experiments is either reduced or enhanced for a particular observer, rather than a purely additive effect, it is unlikely that any simple lateral shift would superimpose the end-zone inducer function and the no-inducer function.

GENERAL DISCUSSION

The present results favor our hypothesis that spatial facilitation mainly results from surround antagonism in end-stopped spatial filters. The latter may increase the gain of the spatial filter through subtractive interactions with divisive suppression caused by pooled inputs from other filters. In most cases where inducers are collinear with the target, it is end-stopping which plays a central role. These results do not require the involvement of long-range interactions from spatially non-overlapped channels or filters, nor do they support a simple pedestal effect explanation of spatial facilitation.

The key assumption in this paper is that surround antagonism activated by inducers reduces suppression in the spatial filter through subtractive interactions with divisive signals. In other words, when the spatial filter surround is stimulated, it facilitates sensitivity by disinhibiting the suppressive effects on the spatial filter. Neurophysiologically, sensitivity facilitation by activating the receptive field surround has been reported when the receptive field center is concurrently activated (Jones, 1970; Maffei & Fiorentini, 1976; Nelson & Frost, 1985; Gilbert & Wiesel, 1990; Toth *et al.*, 1996). For example, Maffei and Fiorentini (1976) reported facilitation in simple and complex cells in area 17 of the cat cortex when orientation-selective regions surrounding the receptive field center were stimulated. More recently, Toth *et al.* (1996) reported that, in cells in area 17 of the cat cortex, single-unit recording and optical imaging also showed surround facilitation when the receptive field center was simultaneously stimulated by a low contrast stimulus. This effect is especially interesting for psychophysical spatial facilitation, because the latter is revealed by threshold measurements in which the target is always at low contrast. Evidence for surround facilitation in cortical receptive fields may provide a neurophysiological foundation for psychophysical spatial facilitation, and is consistent with our explanation based on end-stopped spatial filters. It is important to

distinguish between situations in which an end-stopped cell or spatial filter is stimulated by a line stimulus covering *both* the center and end-zones, as in Hubel and Wiesel's (1965, 1968) classical experiments, and situations in which an end-stopped cell or spatial filter is concurrently stimulated by a stimulus on the center and different stimuli on the end-zones, as in the current paradigm. The former produces inhibition, but the latter may produce facilitation.

It could be argued that, in spatial facilitation experiments, inducers may enhance sensitivity by reducing spatial uncertainty of the target position (Pelli, 1985), a possibility not discussed above. However, we think that uncertainty reduction may not have a critical role in spatial facilitation, because these facilitatory effects are orientation and spatial-frequency specific (Polat & Sagi, 1993; Kapadia *et al.*, 1995), which is not consistent with the uncertainty explanation. In our experiments, spatial uncertainty of the target under no-inducer conditions was minimized by using a dark ring to help observers locate the stimulus (see Methods), so that the baseline threshold levels were relatively unaffected by spatial uncertainty. Therefore, thresholds below the baseline (facilitation) under certain inducing conditions are likely to be accounted for by other factors.

Spatial facilitation in this study was measured with non-periodic targets (lines and spots) identical to those used in earlier studies using the Westheimer paradigm (Westheimer, 1965, 1967; Yu & Essock, 1996a; Yu & Levi, 1997a). In this way we could quantitatively predict the inducing results on the basis of existing data. In general our results are similar to those measured with Gabor patches. Polat and Sagi reported that the peak position of spatial facilitation was not decided by absolute spatial separation, but by the wavelength of the Gabor patch (i.e., $2-3 \lambda$). In other words, spatial facilitation reaches a peak at longer spatial separations with lower spatial frequency, following a somewhat linear relationship. Although it could not be arrived at with the current stimulus patterns, this claim, when understood on the basis of our end-stopped spatial filter theory, is at least partially supported by evidence from masking experiments concerning the length tuning of spatial filters at different spatial frequencies (Yu & Levi, 1997b). In these experiments, the contrast threshold for a D6 (the sixth derivative of a gaussian function, Swanson and Wilson, 1985) target was measured as a function of the length of a D6 mask at the same spatial frequency. The resulting length tuning functions showed that end-zones of spatial filters tend to be shorter with higher spatial frequencies. However, these results did not reveal a clear linear relationship between the spatial frequency tuning of the spatial filters and the end-zone length. Note that Polat and Sagi's result, interactions scaling with filter size, is consistent with end-stopped filters, where end-zone size is proportional to filter size, but not necessarily consistent with long-range interactions, since there is no evidence that the latter scale with filter size.

Consistent with previous spatial facilitation studies, we

believe that the facilitatory spatial interactions play an important role in pattern perception. For a group of line segments, if each line segment is optimally placed within the end-zones of neighboring line segments, these line segments would facilitate each other and eventually stand out together as a salient pattern from other non-facilitated segments. Such a possibility of Gestalt formation is supported by Field *et al.* (1993). They reported that, at a certain spacing, Gabor patches arranged end-to-end had "good continuation" and stood out from other elements. The role of collinearity was also obeyed. The results were attributed to an "association field" near the ends of Gabor patches. Such an association field may be related to the end-zones of spatial filters. They also reported that the good continuation effect was degraded significantly when Gabor patches were arranged at the same spacing but side-to-side instead of end-to-end. This degradation might be because side-to-side facilitation requires narrower spacing than end-to-end spacing, as suggested by Fig. 6.

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