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Spatial-frequency and orientation tuning in psychophysical end-stopping

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Abstract

A psychophysical analog to cortical receptive-field end-stopping has been demonstrated previously in spatial filters tuned to a wide range of spatial frequencies (Yu & Levi, 1997*a*). The current study investigated tuning characteristics in psychophysical spatial filter end-stopping. When a D6 (the sixth derivative of a Gaussian) target is masked by a center mask (placed in the putative spatial filter center), two end-zone masks (placed in the filter end-zones) reduce thresholds. This "end-stopping" effect (the reduction of masking induced by end-zone masks) was measured at various spatial frequencies and orientations of end-zone masks. End-stopping reached its maximal strength when the spatial frequency and/or orientation of the end-zone masks matched the spatial frequency and/or orientation of the target and center mask, showing spatial-frequency tuning and orientation tuning. The bandwidths of spatial-frequency and orientation tuning functions decreased with increasing target spatial frequency. At larger orientation differences, however, end-zone masks induced a secondary facilitation effect, which was maximal when the spatial frequency of end-zone masks equated the target spatial frequency. This facilitation effect might be related to certain types of contour and texture perception, such as perceptual pop-out.

Keywords: End-stopping, Psychophysics, Spatial-frequency tuning, Orientation tuning, Spatial filter, Pop-out perception

Introduction

Cells with end-zones in their receptive fields were first identified by Hubel and Wiesel (1965, 1968) in the cat and monkey visual cortex. These hypercomplex or end-stopped cells constitute a significant portion of simple and complex cells (Dreher, 1972; Schiller et al., 1976; Murphy & Sillito, 1987), and are tuned to not only the stimulus width, but also the stimulus length. In psychophysical and computational theories, however, end-stopping is rarely considered and pattern perception is often assumed to be realized by simple-cell like spatial filters or channels (e.g. Watson, 1983; Wilson & Gelb, 1984).

Evidence for end-stopping in psychophysical spatial filters has recently been suggested by a length Westheimer effect (Yu & Essock, 1996*a*) and by masking experiments (Yu & Levi, 1997*a*). For a small line target superimposed on a rectangular background, increment thresholds first increase (desensitization), then decrease (sensitization), with increasing background length (Yu & Essock, 1996*a*). The desensitization effect caused by the elongated background can be easily understood as increased masking due to area summation within the center of a perceptive field or spatial filter responding to the target line. However, the antagonistic sensitization effect produced by further increases of background length resembles the end-stopping effect in cortical end-stopped receptive fields. Both physiological and psychophysical end-stopping take place beyond line ends, and both have an antagonistic effect on the activity of the receptive-field center. Therefore, desensitization and sensitization are taken as analogs of central length summation and end-stopping, respectively, in psychophysical perceptive fields or spatial filters.

Accumulating evidence supports the link between psychophysical and physiological end-stopping. A cortical origin of psychophysical end-stopping was demonstrated by its steep spatial scaling function (Yu & Essock, 1996*b*), which resembles the cortical magnification function, and by its dichoptic transfer (Yu & Levi, 1997*b*). Psychophysical end-stopping is relatively unaffected by the background polarity (Yu & Levi, 1998), analogous to the phase insensitivity of physiological end-stopping (DeAngelis et al., 1994). It is nearly abolished in humans with naturally occurring amblyopia (Yu & Levi, 1997*b*), which might reflect the general vulnerability of end-stopping to abnormal postnatal visual conditions. Similar vulnerability of end-stopped neurons was found in the visual cortex areas 17 and 18 of cats reared in stroboscopic light (Kennedy & Orban, 1983). The proportion of end-stopped cells in these cats decreased from the normal level of 27–30% to 6–7%.

Psychophysical evidence for end-stopping in spatial filters was detailed in the spatial-frequency domain by masking experiments (Yu & Levi, 1997*a*). For a wide range of spatial frequencies, when

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a D6 (the sixth derivative of a Gaussian function, Swanson & Wilson, 1985) grating target is masked by another D6 mask of the same spatial frequency but variable length, masking is maximal when the mask is approximately 5–6 arcmin longer than the target, regardless of the spatial frequency, suggesting central summation in spatial filters. Masking is then reduced by further lengthening the mask, showing end-stopping. Unlike central summation, psychophysical end-stopping is unaffected by the spatial phase of the mask placed in the putative end-zones, consistent with the phase insensitivity of physiological end-stopping (DeAngelis et al., 1994). These data clearly demonstrate the necessity of integrating end-stopping in the modeling of spatial filters and pattern perception.

The current study investigated the tuning properties of psychophysical end-stopping in spatial filters. Our results show that psychophysical end-stopping reaches its maximal strength when the spatial frequency and orientation of the end-zone masks match those of the target, suggesting that psychophysical end-stopping is tuned to target spatial frequency and orientation, similar to physiological end-stopping (DeAngelis et al., 1994). Our results also suggest that the bandwidths of spatial-frequency and orientation tuning functions decrease with increasing target spatial frequency. Results concerning orientation tuning in psychophysical end-stopping also reveal an interesting and unexpected phenomenon, in that end-zone masks at larger orientation differences can induce a secondary facilitation effect after producing peak thresholds at certain orientation deviations. This facilitation effect is also tuned to the target spatial frequency, and may be related to certain types of contour and texture perception, such as orientation-related perceptual pop-out.

Methods

Observers

Four observers (two males, CU and YC, and two females, LY and QL, aged 19–32 years) participated in this study. All had normal or corrected-to-normal vision. LY, QL, and YC were experienced in psychophysical observations and served as principle observers. CU had no previous experience, and substituted for QL in Experiment 3. 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., Durham, NH) and presented on a U.S. Pixel Px19 monochrome monitor. The resolution of the monitor was 1024 × 512 pixels, with the size of each pixel being 0.28 mm horizontal × 0.41 mm vertical. The frame rate of the monitor was 117 Hz. Luminance of the monitor was made linear by means of a fifteen-bit look-up table. The mean luminance of the monitor screen was 62 cd/m^2. Experiments were run in a dimly lit room, with a low-Watt light on the back of the monitor.

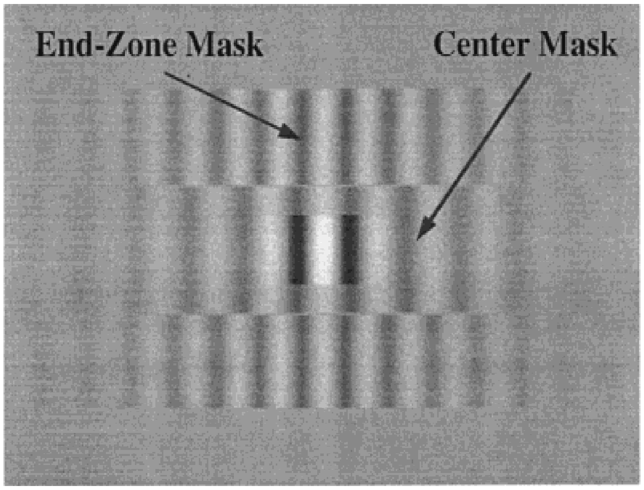


Fig. 1. Stimulus configuration used to study the spatial-frequency tuning in psychophysical end-stopping. The target is a 10-arcmin-long D6 grating centered on a composite masking background. The composite masking background was composed of a 18-arcmin-long sinusoidal grating "center mask" and two 11-arcmin-long sinusoidal grating "end-zone masks."

The basic stimulus configuration consisted of a spatially localized vertical D6 target centered on, and simultaneously masked by, a composite masking background (Figs. 1 and 3). The D6 target, at a (window) length of 10 arcmin, had a 1.0-octave spatial-frequency bandwidth, and was presented on the center of the 3.8 deg × 3.0 deg monitor screen. The composite masking background consisted of a central sinusoidal grating which masked the center of the spatial filters (center mask), and two abutting sinusoidal gratings which masked the end-zones (end-zone masks). The center and end-zone masks were blurred by a Gaussian window along the width dimension ($\sigma = 0.75$ deg). The center mask shared the same spatial frequency and orientation as the D6 target. Either the spatial frequency or the orientation of the end-zone masks was varied as an independent variable in the experiments, with other dimensions the same as those of the center mask and target. To generate the stimuli, the target and mask were actually presented in separate frames which were interlaced to produce the required configuration. In this way, the frame rate for the stimuli (58.5 Hz) was actually half of the monitor frame rate, but was still fast enough to avoid any perceptible flicker. Both the center mask and end-zone masks were presented at a contrast of 40%. The contrast of the D6 target was varied according to a staircase procedure. Viewing was monocular by the dominant eye (right eyes for all observers), at a viewing distance of 5.64 m.

Procedure

A successive two-alternative forced-choice staircase procedure was used. The mask was presented in each of the two stimulus intervals (300 ms each) separated by a 550-ms interstimulus interval. In one of the two intervals the target was also presented for the same duration. Each trial was preceded by a 6.3 arcmin × 6.3 arcmin fixation cross in the center of the screen which disappeared 100 ms 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 of the target was usually set at 20% but sometimes higher. The step size in practice reversals was set at 0.75% and in experimental reversals at 0.25%. Each correct response lowered target contrast by one step and each incorrect response raised target contrast by three steps, which resulted in a 75% convergence level of the staircase. The mean of the six experimental reversals was taken as the contrast threshold. An experimental session usually consisted of 9–10 randomly presented conditions, and lasted for about 35 min. Each datum represents the mean of 4–6 replications for each condition, and the error bars represent ±1 standard error of the mean.

Experiment 1: Spatial-frequency tuning in psychophysical end-stopping

It has been reported that the spatial-frequency tuning of cortical receptive-field end-stopping is a bandpass function, the peak of which coincides with the peak of the receptive-field center spatial-frequency tuning (Tanaka et al., 1987; DeAngelis et al., 1994). This experiment investigated spatial-frequency tuning in psychophysical spatial filter end-stopping.

Contrast thresholds for a 10-arcmin-long D6 target centered on a composite masking background (Fig. 1) were measured. The composite masking background was composed of a sinusoidal grating "center mask" and two sinusoidal grating "end-zone masks" (see Methods). The center mask, which shared the spatial frequency of the target, had a window length of 18 arcmin. For a 10-arcmin-long D6 target, a mask at this specific length can produce the maximal contrast threshold and thus may have fully masked the length extent of the underlying spatial filter center (Yu & Levi, 1997*a*). Two abutting end-zone masks each had a window length of 11 arcmin, which allowed these masks to fully cover the end-zones of the underlying spatial filter (Yu & Levi, 1997*a*). As a baseline measure, contrast thresholds were also measured under "center-mask only" conditions producing peak contrast thresholds in previous experiments, so that end-stopping could be represented as facilitation as compared to the baseline. The experiment was conducted at four target spatial frequencies from 1.7 cpd to 16.0 cpd. Under each target spatial-frequency condition, the spatial frequency of the end-zone masks was varied to examine its effects on facilitation (end-stopping), within a range of about ±1 octave from the target spatial frequency (except for the 16 cpd target frequency condition in which the range was -1 to 0.65 octaves).

Fig. 2 shows contrast thresholds as a function of the end-zone mask spatial frequency. Individual functions at each target spatial-frequency condition are presented in Fig. 2a and the mean results are summarized in Fig. 2b. For all individual and mean functions, the strongest facilitation occurs consistently when the spatial frequency of end-zone masks is equal or very close to the spatial frequency of the target. Facilitation decreases towards the baseline with increasing spatial-frequency difference between the target and the end-zone masks. Thus, like single-cell receptive-field end-stopping, psychophysical end-stopping is also spatial frequency tuned.

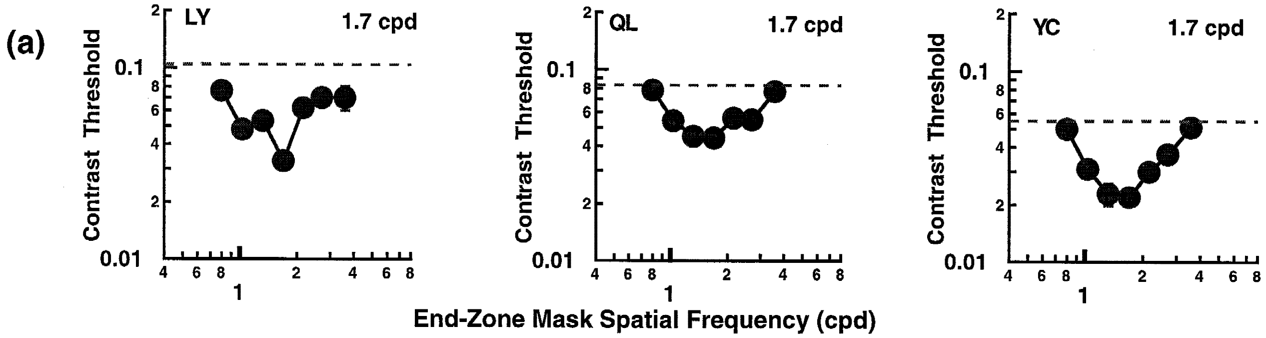
For functions measured at higher target spatial frequencies (8.0 and 16.0 cpd), when the spatial frequencies of end-zone masks are significantly lower than the target spatial frequency, end-zone masks produce suppression (thresholds higher than the baseline, Fig 2a, bottom two panels). This effect is very strong and consistent at 16 cpd, though a little weaker and present only in two of three observers at 8 cpd. We believe that this suppression effect can be at least in part attributed to the fact that the high visibility of the (lower frequency) end-zone masks deploys the observer's attention from the target to the masks. For example, the 8 cpd end-zone mask is much more salient than the (equal physical contrast) 16 cpd center mask, and our observers report that it is difficult to attend to the target (even after extensive practice). It is plausible that the deployment of attention toward the more salient end-zone masks may be related to the distinct responses of the magnocellular and parvocellular pathways and their cortical afferents. For example, in the LGN, M cells have much higher contrast sensitivity than P cells, but they also have poorer spatial resolution (e.g. Derrington & Lennie, 1984). Thus, in the current case, M cells could be sensitive to the lower spatial-frequency end-zone masks, but much less sensitive to the high spatial-frequency target, which is mainly detected by P cells (though the sensitivity of these P cells could be much lower than that of M cells responding to end-zone masks). This large difference in sensitivity could lead to the short latency M pathway inhibiting the P pathway, and/or a rapid shift of attention to the end-zone masks from the target (thus elevating contrast thresholds). The possibility of an attention shift due to M and P cell sensitivity differences has been discussed by Lennie (1993). At low target spatial frequencies, there is no large difference in the visibility of the center mask and end-zone mask, and M cells would be sensitive to both the target and end-zone masks, so no attention shift occurs.

To obtain further insights about the spatial-frequency tuning of psychophysical end-stopping, the tuning function at each target spatial-frequency condition was fitted with a Gaussian function (dotted lines in Fig. 2b). The full bandwidth of each function at half height is plotted as a function of the target spatial frequency (Fig. 2c), and shows a slow decrease in bandwidth from 1.6 octaves to 1.37 octaves as the target spatial frequency increases from 1.7 cpd to 8 cpd, and then a rapid decrease from 1.37 octaves to 0.71 octaves as the target spatial frequency further increases from 8 cpd to 16 cpd. The slow bandwidth decrease (in terms of octaves) at lower target spatial frequencies might suggest that spatial filters tuned to these spatial frequencies scale their size in the width dimension with spatial frequency, such that filters' shapes across the subregions remain relatively constant (i.e. the number of ON/OFF subregions remains relatively constant). Note that for the 16 cpd target spatial-frequency condition, the Gaussian fitting is based on the baseline (no mask) level instead of the suppression level in order to reduce bandwidth biases caused by suppression—possibly originating from processes unrelated to end-stopping (see above). However, this fitting might have made the estimated bandwidth narrower than its actual value because the pure effects of end-zone masking at low spatial frequencies are unavailable. Fitting the data relative to the suppression level results in a wider bandwidth, comparable to that obtained at 4 and 8 cpd. In general, the pattern of bandwidth change with spatial frequency in end-stopping is consistent with that in spatial filter spatial-frequency tuning estimated by Wilson et al. (1983). However, since their study used a very long target and a full-field mask, it is not clear whether end-stopping contributed to their tuning functions. It is interesting to note that in cat primary visual cortex, the inhibitory spatial-frequency tuning bandwidths associated with end-stopping are narrower than the excitatory bandwidths of the same neurons (DeAngelis et al., 1994).

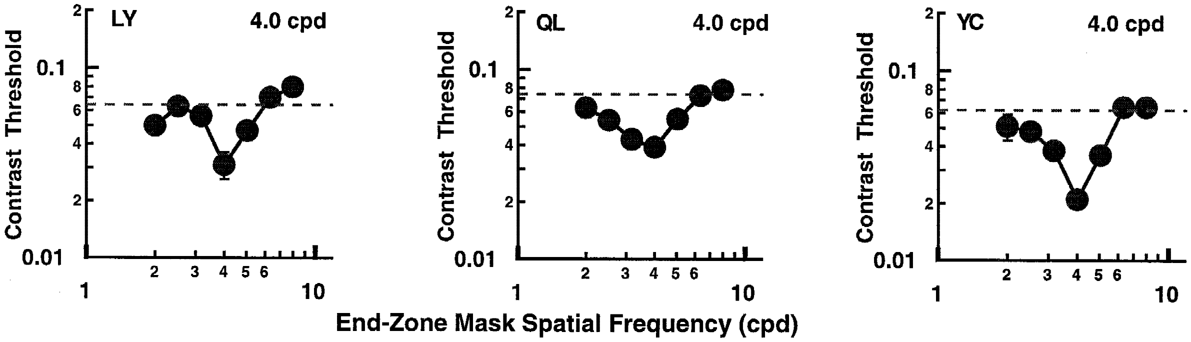
Experiment 2: Orientation tuning in psychophysical end-stopping

Orientation tuning in single-cell receptive-field end-stopping was first reported by Hubel and Wiesel in their original paper on hypercomplex cells (Hubel & Wiesel, 1965), and confirmed by later studies (Nelson & Frost, 1978; Orban et al., 1979; DeAngelis et al., 1994), in that end-stopping is the strongest at approximately the same orientation which causes maximal center excitation. In this experiment, we studied orientation tuning in psychophysical end-stopping by examining the facilitation effects of end-zone masks at various orientations. The stimulus configurations and procedures were identical to that used in Experiment 1, except that it was the orientation of the end-zone masks, rather than their spatial frequency, that was manipulated (Fig. 3). The spatial frequency of the end-zone masks was always the same as the target spatial

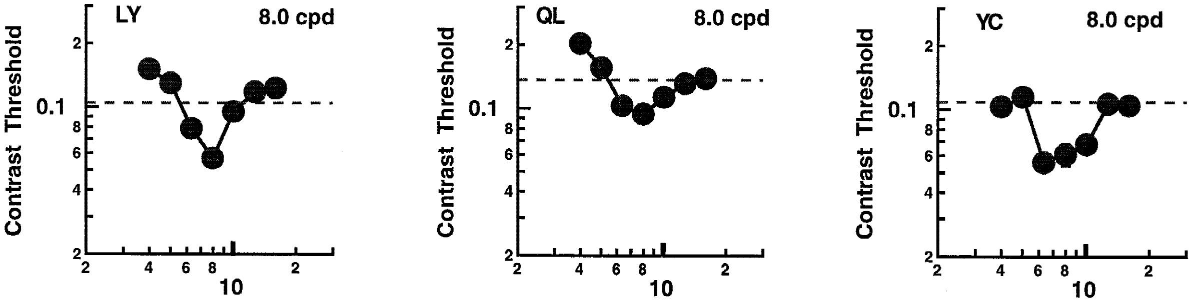
target spatial frequency = 1.7 cpd



target spatial frequency = 4.0 cpd



target spatial frequency = 8.0 cpd



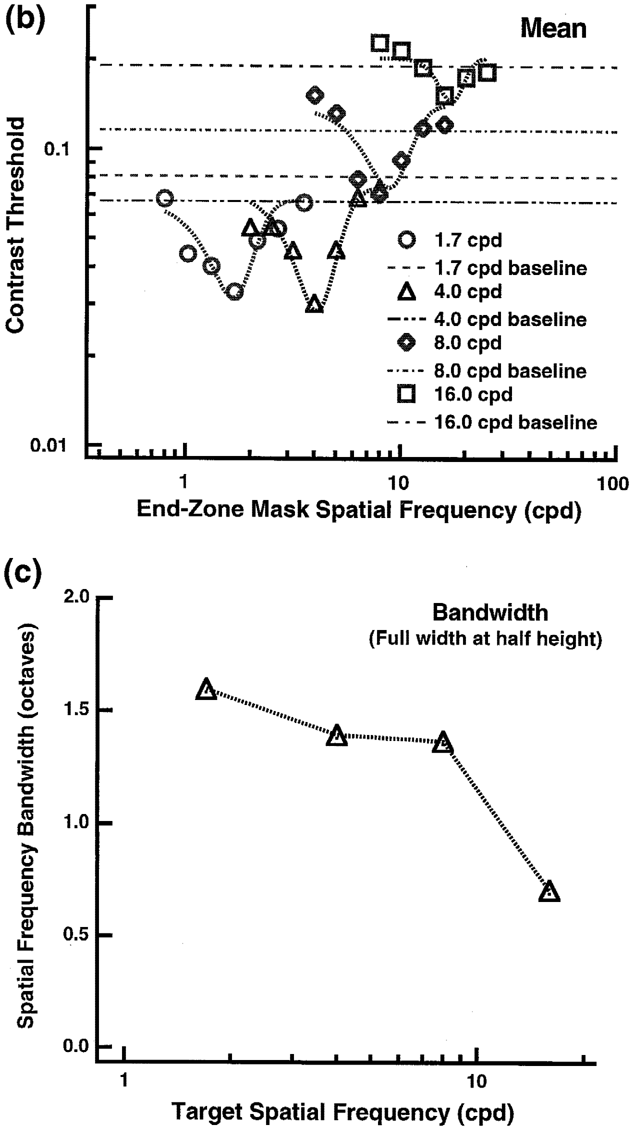


Fig. 2. (*Continued*.) (b) Mean tuning functions (dotted lines show Gaussians fitted to the tuning functions). (c) Bandwidth of spatial-frequency tuning functions (derived from the Gaussian fits) at each target spatial frequency.

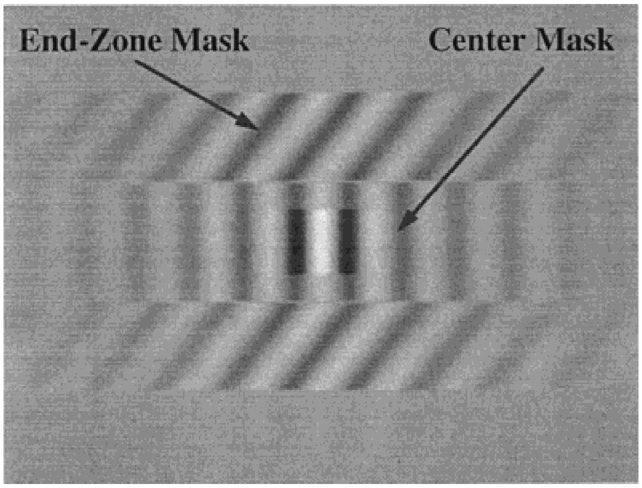


Fig. 3. Stimulus configuration used to study the orientation tuning in psychophysical end-stopping. It is identical to the stimulus configuration in Fig. 1 except that the orientation of end-zone masks is varied in the experiments.

frequency. Tests were conducted at three target spatial frequencies, at 1.7, 4.0, and 8.0 cpd.

Individual results are presented in Fig. 4a and mean results are summarized in Fig. 4b. Each function can be divided into two components. The first component is a desensitization process which suggests orientation tuning in psychophysical end-stopping. The second component is a secondary facilitation (in contrast to facilitation or end-stopping induced by end-zone masks at zero or small orientation deviations) at large orientation deviations.

When the end-zone mask orientation is the same as the target orientation, contrast thresholds are well below the baseline, suggesting that end-zone masks induce a strong facilitation or end-stopping effect, consistent with our previous results. This facilitation effect diminishes, as indicated by elevated contrast thresholds with increasing orientation difference between the end-zone masks and the target. Therefore, psychophysical end-stopping is a bandpass function of orientation, and is tuned to the target orientation. At a certain orientation deviation, contrast thresholds reach a peak which is about equal to the baseline contrast threshold. Thus end-stopping induced by end-zone masks ends at this point. This deviation is approximately 15 deg, 30 deg, and 55 deg, respectively, for functions at target spatial frequencies of 8.0 cpd, 4.0 cpd, and 1.7 cpd.

Beyond this peak point, contrast thresholds decrease with further increasing orientation difference. For the 8 cpd target spatial frequency, this secondary facilitation effect starts from the peak orientation deviation of 15 deg and reaches a plateau at an orientation deviation of about 30 deg—a range of about 15 deg (Fig. 4a, bottom panel). The range of the secondary facilitation effect appears to be larger at lower target spatial frequencies (Fig. 4a, top two panels), though a precise estimation cannot be made because the threshold reductions have not reached a plateau at the largest orientation deviations we used. This facilitation effect is unexpected, but it resembles Sillito et al.'s findings of cortical cells detecting focal orientation discontinuities (Sillito et al., 1995). They reported that stimulating a surround field at a significantly different orientation can enhance a cell's response to a target located within the classical receptive field. This effect was further studied in Experiment 3.

To determine the bandwidth change in the orientation tuning functions of psychophysical end-stopping, the desensitization component of each mean function was fitted by a half-Gaussian function (dotted lines in Fig. 4b). The bandwidth of the orientation tuning functions decreases with increasing target spatial frequency (Fig. 4c), consistent with the bandwidth properties of orientation tuning in spatial filters (Phillips & Wilson, 1984). Similar results were found in end-stopped neurons in cat's primary visual cortex by DeAngelis et al. (1994), in that the optimal orientation for end-stopping corresponds to the optimal orientation for center excitation, and the orientation bandwidth of end-stopping, though broader, is positively correlated with that of center excitation. Compared to the bandwidth change of spatial-frequency tuning in psychophysical end-stopping (Fig. 2c), the orientation bandwidth decreases much more rapidly. Since the longer the receptive fields, the narrower the orientation tuning, this rapid bandwidth decrease implies that the length dimension of the underlying spatial filters

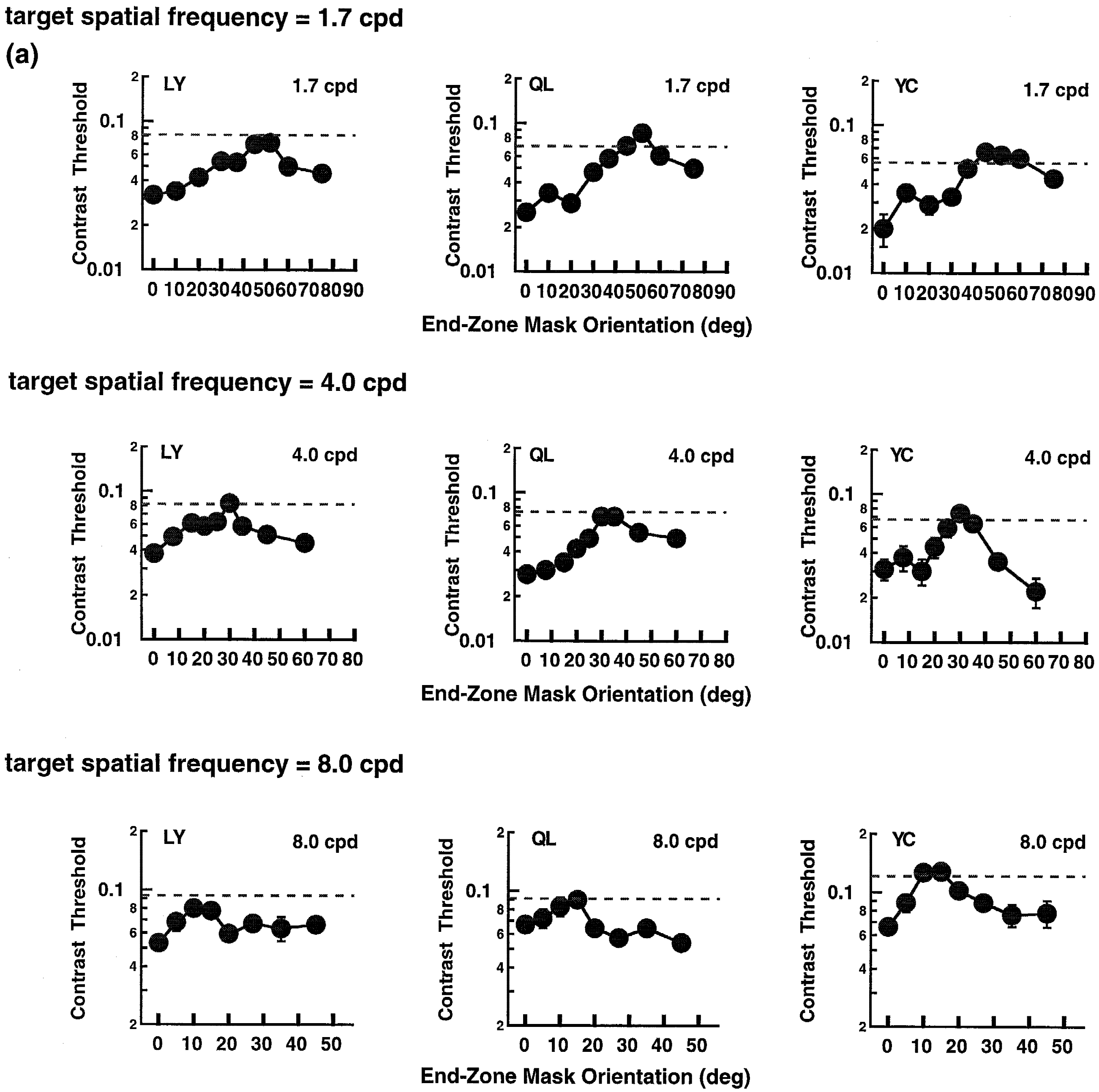


Fig. 4. Orientation tuning functions of psychophysical end-stopping. (a) Individual tuning functions at each target spatial frequency. (*Figure continues on facing page.*)

does not scale with the spatial frequency; instead the filter shapes are more elongated at high spatial frequencies. It has been suggested that end-stopped cells play a role in curvature perception (Hubel & Wiesel, 1965; Dobbins et al., 1987). These long, end-stopped spatial filters with very fine orientation tuning are especially suitable for fine curvature detection.

Experiment 3: Spatial-frequency tuning in secondary facilitation induced by end-zone masks at large orientation differences

The results of Experiment 2 showed surprising secondary facilitation induced by end-zone masks at large orientation differences. An interesting question is how this effect is influenced by the spatial frequency of significantly oriented end-zone masks. At two target spatial frequencies, 4.0 cpd and 8.0 cpd, we measured the impact of end-zone mask spatial frequency on secondary facilitation when the end-zone mask orientation was set at a point where strong facilitation occurred in Experiment 2, i.e. at 60 deg at a target spatial frequency of 4.0 cpd and 35 deg at a target spatial frequency of 8.0 cpd. The spatial frequency of end-zone masks was varied ±1 octave from the target spatial frequency.

Results from the 4.0 and 8.0 cpd target spatial-frequency conditions are presented in Figs. 5a and 5b, respectively. The left column of each figure shows the three baselines, i.e. contrast thresholds at end-zone mask orientations: (1) equal to the target orien-

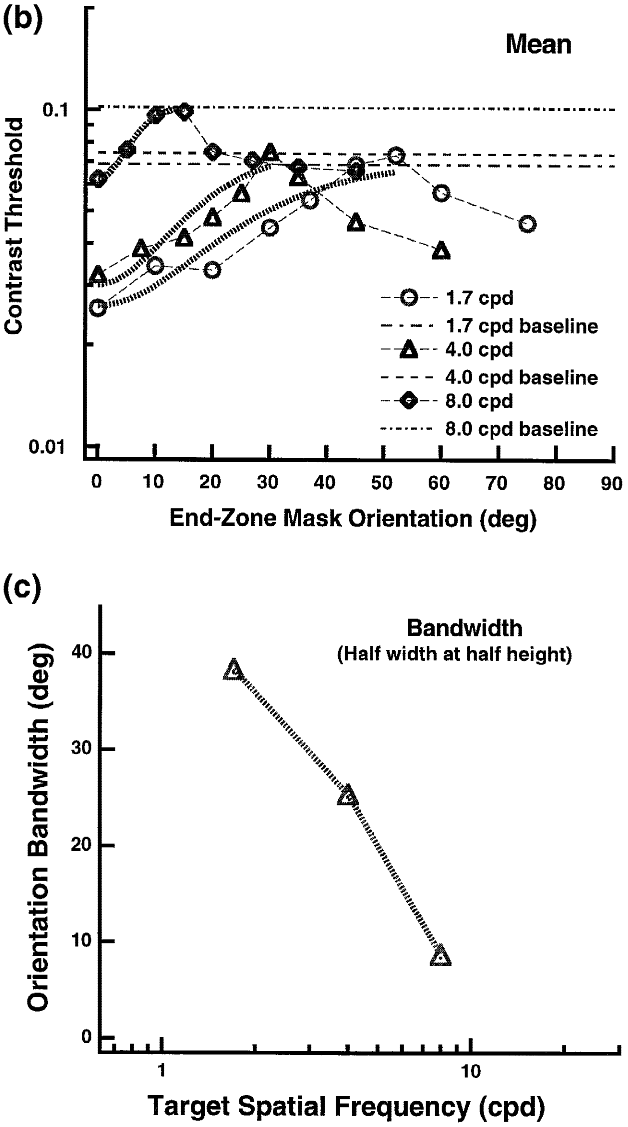


Fig. 4. (*Continued*.) (b) Mean tuning functions (dotted lines show half Gaussian functions fitted to the desensitization portion of the tuning functions). (c) Bandwidth of orientation tuning functions (derived from the half-Gaussian fits) at each target spatial frequency.

tation (0 deg), (2) producing peak contrast threshold (30 deg at 4.0 cpd target frequency and 15 deg at 8.0 cpd target frequency), and (3) producing secondary facilitation (60 deg at 4.0 cpd target frequency and 35 deg at 8.0 cpd target frequency). Thus, these baseline functions are simplified replications of the functions in Fig. 4. The spatial frequency of end-zone masks at these orientations was the same as the target spatial frequency. The contrast threshold under the "center-mask only" condition was also measured and used as the primary baseline for all other conditions. These functions confirm the finding of secondary facilitation in Experiment 2.

The right column shows contrast thresholds as a function of the spatial frequency of end-zone masks oriented 60 deg (Fig. 5a, 4.0 cpd target frequency condition) or 35 deg (Fig. 5b, 8.0 cpd target frequency condition) from the target. Evidently, at both target spatial frequencies, secondary facilitation is maximal when the end-zone mask spatial frequency closely matches the target frequency [except for LY's results in Fig. 5a which have a dip at a slightly higher end-zone mask spatial frequency (5 cpd)]. Therefore, secondary facilitation induced by end-zone masks at large orientation differences is also tuned to the target spatial frequency.

General discussion

Our results demonstrate spatial-frequency tuning and orientation tuning in psychophysical end-stopping. Maximal end-stopping effects are achieved when the spatial frequency and orientation of the end-zone masks matched those of the target. These tuning properties add to our knowledge of psychophysical end-stopping which already suggests that the latter is affected by the target spatial frequency, but is unaffected by target length, and is insensitive to the phase change of end-zone masks (Yu & Levi, 1997*a*). An unexpected result is that a secondary facilitation effect can be induced by end-zone masks at larger orientation deviations from the target. This facilitation effect is also tuned to the target spatial frequency.

As discussed in the Introduction, there is close agreement between many of the properties of psychophysical end-stopping described here and in our previous studies, and that of physiological end-stopping. For example, both have a cortical origin, are unaffected by the background polarity or phase, and are vulnerable to abnormal postnatal visual conditions. The present study shows that, like physiological end-stopping, psychophysical end-stopping is tuned to both orientation and spatial frequency, being maximal when the center and end-zone stimuli are matched. However, one clear apparent difference between physiological and psychophysical end-stopping is that physiological end-stopping is primarily inhibitory (DeAngelis et al., 1994), whereas the psychophysical marker for end-stopping is facilitation. Below we discuss a model which can reconcile this apparent contradiction.

Recent neurophysiological and psychophysical studies (Robson, 1988; Albrecht & Geisler, 1991; Ross & Speed, 1991; DeAngelis et al., 1992; Heeger, 1992; Wilson & Humanski, 1993; Foley, 1994) suggest that the response of striate neurons or spatial filters is in part determined by a nonlinear divisive suppression or normalization process. This suppressive effect is orientation nonspecific and originates from outputs of a pool of neurons. In a masking paradigm, adding a mask elevates the contrast threshold because of increased suppressive signals, which reduces the response of the filter to the target (Foley, 1994). This process explains peak contrast thresholds caused by the center mask which masks the spatial filter center and elicits maximal suppression. However, this divisive suppression process cannot account for end-stopping induced by end-zone masks which indicates a recovered response or sensitivity of the spatial filter.

We have proposed previously that the increased sensitivity could be attributed to antagonistic end-stopping which might disinhibit the suppressive effect of pooled inputs (Yu & Levi, 1997*a*,*c*). This process can be expressed as $R = E/(DI - ES)^1$, where R is the response of the spatial filter, E is spatial filter excitation elicited by the target, DI is divisive inhibition or suppression, and ES is psychophysical end-stopping. Thus, in a masking paradigm masks have opposing roles on the sensitivity of spatial filters: on the center they decrease the sensitivity by increasing the divisive sup-

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[1] End-stopping might subtract from both the excitation and divisive inhibition [i.e. $R = E - ES/(DI - ES)$]; subtracting ES from both sides produces similar effects as long as the end-stopping is smaller than the divisive inhibition.

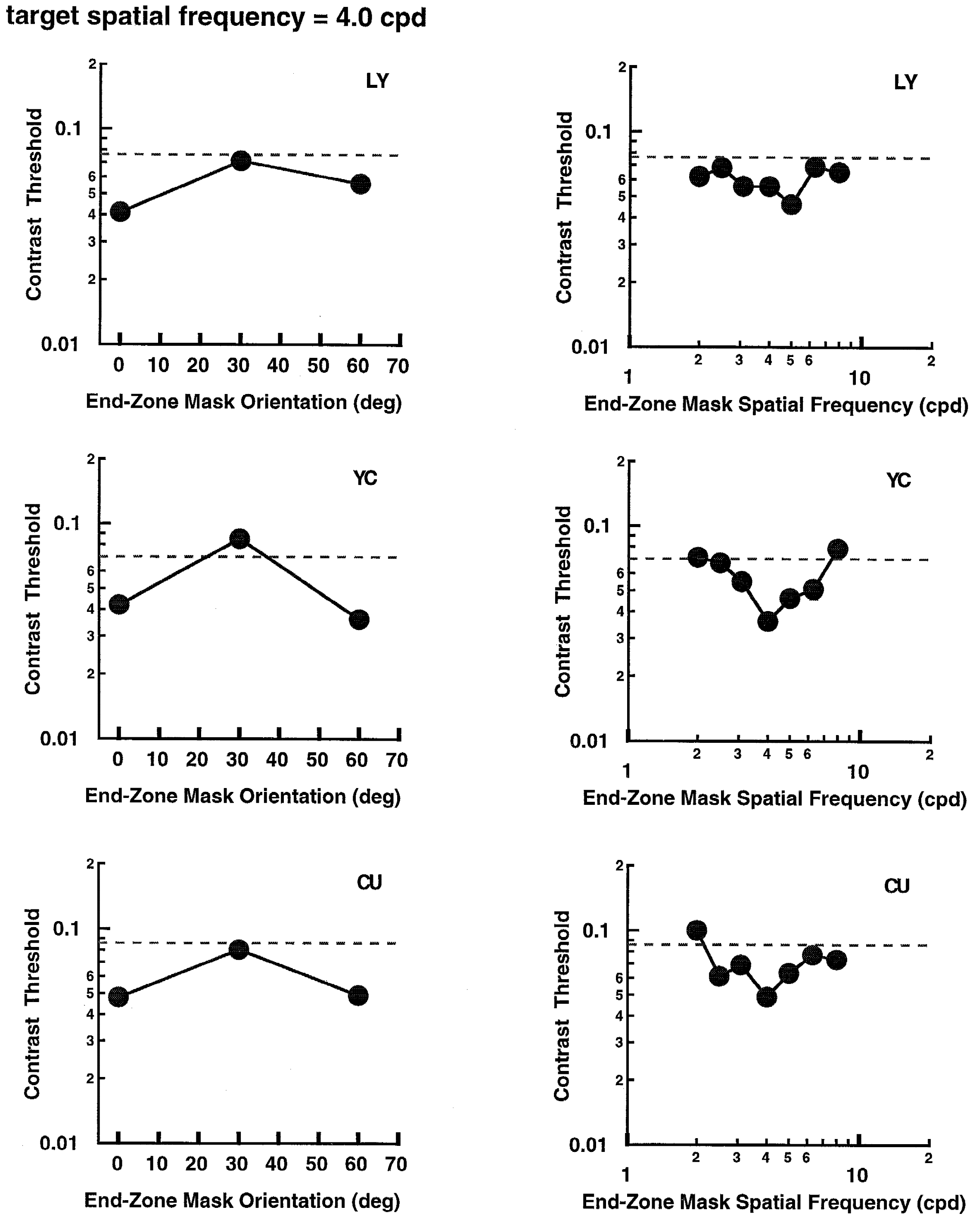

Fig. 5. The effect of end-zone mask spatial frequency on secondary facilitation. The *left* column of each figure is baselines, showing contrast thresholds at end-zone mask orientations: (1) equal to the target orientation (0 deg), (2) producing peak contrast threshold (30 deg and 15 deg at a target frequency of 4.0 and 8.0 cpd, respectively), and (3) producing secondary facilitation (60 deg and 35 deg at a target frequency of 4.0 and 8.0 cpd, respectively). (*Figure continues on facing page.*)

pression, and on end-zones they increase the sensitivity by decreasing the divisive suppression. This proposal derives some support from neurophysiological studies which show sensitivity facilitation by activating the receptive-field surround when the receptive-field center is concurrently activated (Jones, 1970; Maffei & Fiorentini, 1976; Nelson & Frost, 1985; Gilbert & Wiesel, 1990; Toth et al., 1996). Note that the formulation we are proposing is that end-stopping has a subtractive effect on the divisive inhibition. A potential alternative to this model is based on end-stopping acting through divisive rather than subtractive inhibition. In this formulation, the response of the spatial filter could be described as $R = E/(DI/ES)$. However, mathematically, this equation would

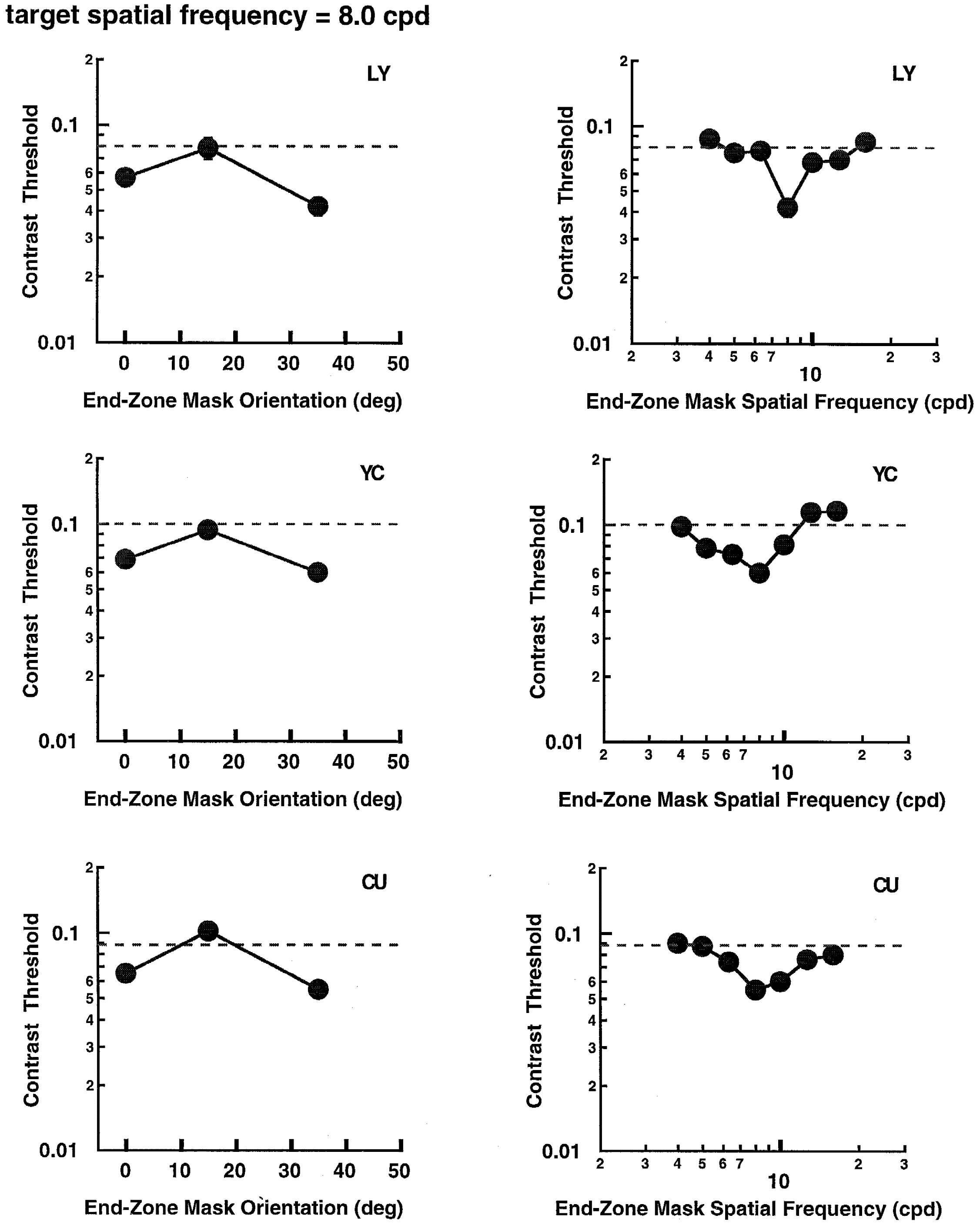

Fig. 5. (*Continued*.) Dashed lines represent contrast thresholds under the "center-mask only" conditions and serve as primary baselines for all other baseline conditions. The *right* column shows secondary facilitation as a function of the spatial frequency of end-zone masks which are oriented 60 deg and 35 deg from the target at a target frequency of 4.0 and 8.0 cpd, respectively. (a) Results from the 4.0-cpd target spatial-frequency condition. (b) Results from the 8.0-cpd target spatial-frequency condition.

produce facilitation only when $ES > 1$ but would produce suppression (i.e. increased masking) when $ES < 1$. The response of the filter would be unaffected when $ES = 1$ and completely suppressed when $ES = 0$. In addition when ES exceeds about half the value of DI, facilitation becomes implausibly large. These predictions are inconsistent with the experimental data, so we favor the subtractive model. Based on their physiological experiments, DeAngelis et al. (1994) suggest that end-stopping operates through divisive inhibition. Our proposal is that end-stopping modifies the strength of divisive inhibition through subtraction.

Results from the current study support and further enrich our model. Firstly, the orientation tuning in psychophysical end-stopping supports the separation between divisive inhibition and end-stopping, since one is orientation specific and one is not. Thus, the sensitivity of spatial filters is improved by psychophysical end-stopping counterbalancing the suppressive effects of pooled inputs from neighboring filters, not by the direct reduction of pooled inputs. Secondly, although previous results suggest that end-stopping is unaffected by the mask phase, current results show that the sensitivity of masked spatial filters can only be restored when the spatial frequency and orientation of the end-zone masks closely match those of the target frequency. These constraints help refine our previous descriptions about the interactions between divisive inhibition and end-stopping.

However, the model described above does not account for secondary facilitation induced by end-zone masks at large orientation deviations from the target. We presume that end-stopping does not operate with large orientation differences. The effects of large orientation differences on spatial filter sensitivity can be described by substituting the role of end-stopping with secondary facilitation, since both factors function exclusively and produce similar effects. Thus under these circumstances, the response of spatial filters (R) is determined by $E/(DI - SF)$, where SF stands for secondary facilitation. Like psychophysical end-stopping, secondary facilitation is also constrained by the spatial frequency, and reaches its maximum when the spatial frequency of the masks matches the spatial frequency of the target.

The secondary facilitation effect induced by end-zone masks at large orientation deviations is novel and unexpected. Objects with large orientation differences have been reported to have little or no spatial interaction in previous psychophysical studies (e.g. Cannon & Fullenkamp, 1991). As noted earlier, this effect closely resembles Sillito et al.'s findings of cortical cells detecting focal orientation discontinuities (Sillito et al., 1995). Sillito et al. suggested that this type of neural processing might be responsible for detecting the change in contour orientation associated with junctions or corners. Indeed, during the experiments, we observed that these oriented end-zone masks not only induced secondary facilitation at the threshold level, but they also produced a very strong pop-out perception for the D6 target at the suprathreshold level (at the beginning of the staircase procedure for threshold measurements, the target was set at a suprathreshold contrast. See the Methods section). This observation is consistent with a role for secondary facilitation in highlighting orientation discontinuities, similar to that described by Sillito et al. Though formal experiments need to be done at suprathreshold levels, it appears that secondary facilitation in spatial filters may have a role in the low-level processing of texture and contour perception.

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