End stopping and length tuning in psychophysical spatial filters

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Psychophysical spatial filters or channels are usually modeled after simple-cell receptive fields, although many cortical cells are end stopped and length tuned. Using psychophysical masking, we demonstrate an analog to receptive field end stopping and length tuning in psychophysical spatial filters tuned to a wide range of spatial frequencies. Specifically, masking is maximal when the mask is approximately 5–6 arcmin longer than the target but is reduced when the mask exceeds this length, consistent with the properties of end-stopped cells. The strength and the extent of psychophysical end stopping appear to be determined by the filter's spatial-frequency tuning, but length tuning varies with target length. The latter implies that spatial filters tuned to the same spatial frequency could have different length tuning and that there is no fixed length-to-width ratio of filter size. Phase effects suggest linear length summation but nonlinear psychophysical end stopping, which suggests that both first- and second-order visual processing is involved in end-stopped spatial filters.

1. INTRODUCTION

Contemporary theories of spatial vision regard pattern perception as being constructed by spatial filters or channels.[1,2] These psychophysical functional units, each tuned to a limited range of spatial frequencies and orientations, are usually modeled after typical cortical simple-cell receptive fields.[3,4] The resulting symmetric and asymmetric organization of ON and OFF regions enable these filters to provide width and edge information of stimuli. However, because of the lack of length tuning in simple-cell receptive fields and in spatial filters modeled after them, additional second-order filters in orthogonal orientations have to be used to compute length information.[5] Physiologically, however, length tuning is realized by hypercomplex cells or end-stopped simple and complex cells.[6–9] These cells, characterized by inhibitory end zones at the ends of their elongated receptive field centers, are tuned to both width and length. They are excited by line segments but are inhibited by extended lines entering the end zones. It has been suggested that end stopping may play an important role in a variety of visual processes, such as curvature, corner and line terminator detection, illusory contour perception, orientation discontinuity, and facilitatory spatial interactions.[6,10–13]

Psychophysical evidence for end stopping[14] has been suggested recently by spatial interactions near the line ends demonstrated with a modified Westheimer paradigm.[15,16] Yu and Essock[14] measured detection thresholds for a small line superimposed on a rectangular background of variable length or width. Detection thresholds were first elevated and then lowered, with increasing background width or length, showing inverted-V shapes typical of the Westheimer function. The desensitization and the sensitization branches of the length function obtained under the variable-length background condition were taken as suggesting central length summation and end stopping, respectively, and those obtained under the variable-width background condition were taken as suggesting central width summation and flank inhibition, respectively. Length and width functions together revealed end-stopped spatial interaction areas or perceptive fields resembling cortical end-stopped receptive fields. Later experiments[17,18] further demonstrated the cortical origin of these spatial interactions, supporting the links between end-stopped perceptive fields and end-stopped cortical receptive fields.

Both the psychophysical evidence discussed above and the cortical physiology strongly point to the possibility that psychophysical spatial filters might also be end stopped, rather than non-end-stopped as commonly assumed. In this study we use psychophysical masking, a common method used in spatial filter studies, to investigate length effects in pattern masking. Our results show that the masking effect is maximal when the mask is approximately 5–6 arcmin longer than the target but is reduced when the mask exceeds this length, consistent with the properties of cortical end-stopped cells. Varying the target length mainly affects length tuning but not psychophysical end stopping, although the extent and the strength of the latter are determined by the filter's spatial-frequency tuning. Varying the phase of the mask indicates that psychophysical end stopping is independent of mask phase and is thus nonlinear, but length summation (a combination of length summation in center and flanks) is phase sensitive and linear, suggesting both first- and second-order visual processing in end-stopped spatial filters. These results suggest that psychophysical spatial filters revealed by masking may not be simple but end stopped instead.

2. METHODS

A. Observers

Five observers (one male, YC; and four females, CN, KN, LY, and RP; age 19–32) served in this study. All had normal or corrected-to-normal vision. Observers CN, KN, RP, and YC were experienced; others were new to psychophysical experiments and received many hours of training. Only YC was aware of the purpose of the study.

B. Apparatus and Stimuli

The stimuli were generated by a Vision Works computer graphics system (Vision Research Graphics, Inc.) and were presented on a U.S. Pixel Px19 monochrome monitor. The resolution of the monitor was 1024 $\times$ 512 pixels, with the size of each pixel being 0.28 mm horizontal $\times$ 0.41 mm vertical. The frame rate of the monitor was 117 Hz. Luminance of the monitor was made linear by means of an 8-bit lookup 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.

The basic stimulus configuration consisted of a spatially localized vertical D6 [the sixth derivative of a Gaussian (DOG) function[19]] target centered on, and so simultaneously masked by, a D6 mask of the same peak spatial frequency (Fig. 1; simultaneous masking was used to ensure that the spatially localized target was precisely centered on the mask and was not affected by eye movements). Both the target and the mask had a 1.0-octave spatial-frequency bandwidth and were presented on the center of the 3.8 deg $\times$ 3.0 deg monitor screen. The D6 target was partially blurred by a Gaussian window along its long axis (σ = 1.8 arcmin when the target length was 5 arcmin) and was truncated at the target length, but the D6 mask was not blurred. Some variations of the mask were used and are detailed in experiment 3. To generate the stimuli, the target and the mask were actually presented in separate frames that were interlaced to produce the required configuration. In this way the frame rate for the stimuli (58.5 Hz) was actually half the monitor frame rate but was still fast enough to avoid any flicker perception. Under certain conditions the D6 mask was replaced by a spatially more extended D20 mask. The D6 or the D20 mask was presented at 40% contrast. The contrast of the D6 target was varied according to a staircase procedure. Viewing was monocular by the dominant eye (right eyes except for observer CN), at a viewing distance of 5.64 m.

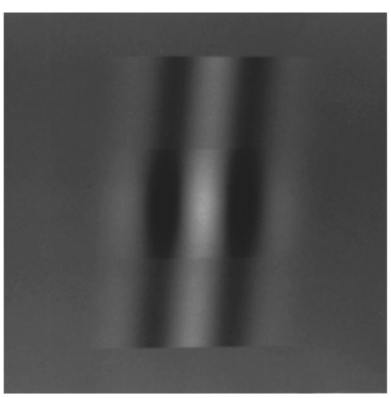


Fig. 1. Typical stimulus pattern used in many experiments. It consisted of a vertical D6 target partially blurred by a Gaussian window along its long axis and centered on a D6 mask of the same peak spatial frequency but not blurred. The D6 mask was presented at 40% contrast.

C. Procedure

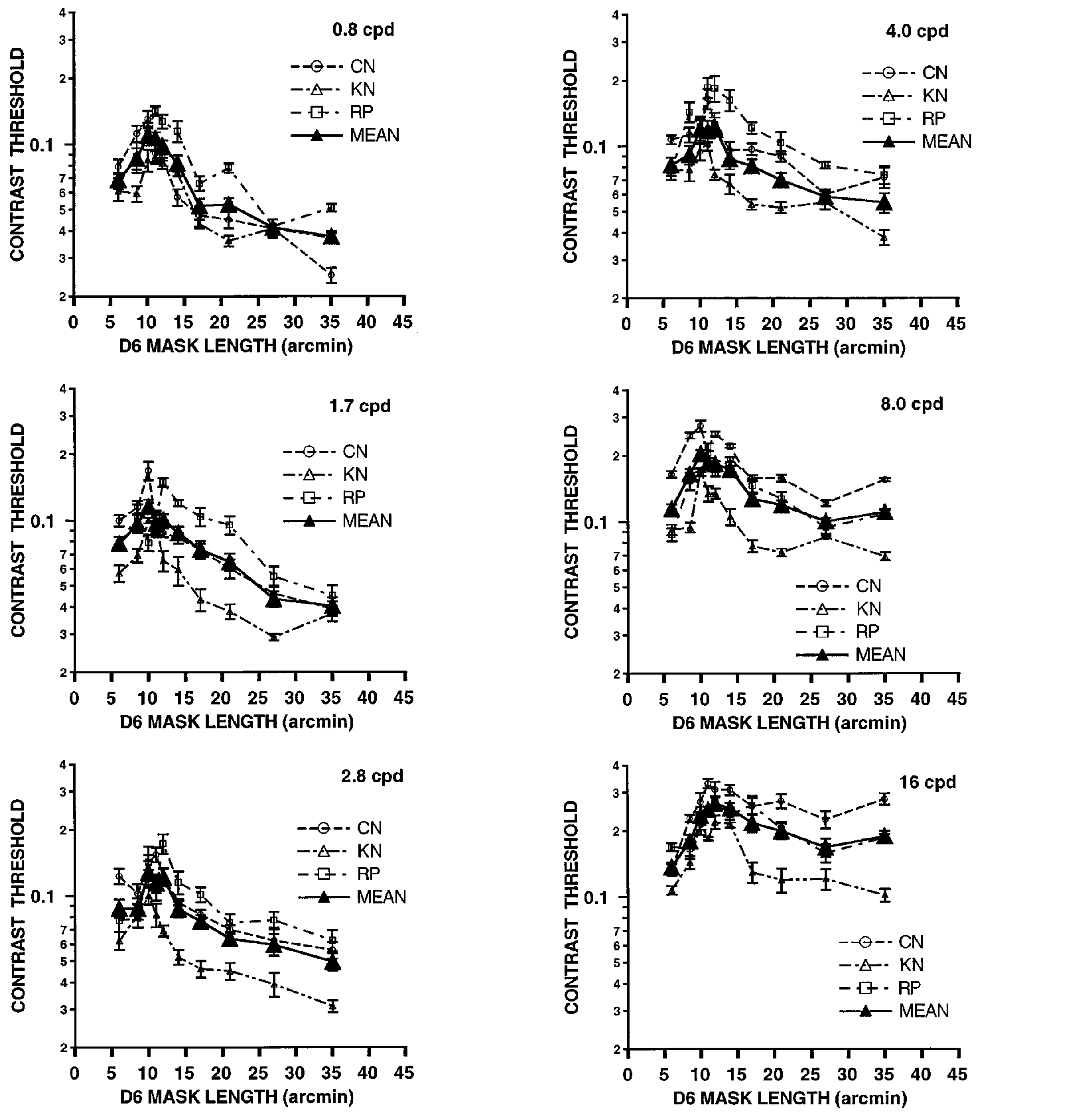
A successive two-alternative forced-choice staircase procedure with a convergence rate of 75% was used. The mask was presented in each of the two stimulus intervals (300 ms each) separated by a 550-ms interstimulus interval. In one of the two intervals the target was also presented for the same duration. Each trial was preceded by a 6.3 arcmin $\times$ 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 it was set higher. The step size in practice reversals was set at 0.75%; in experimental reversals, at 0.25%. 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 approximately 35 min. Each datum represents the mean of 4–6 replications for each condition, and the error bars represent $\pm$1 standard error of the mean.

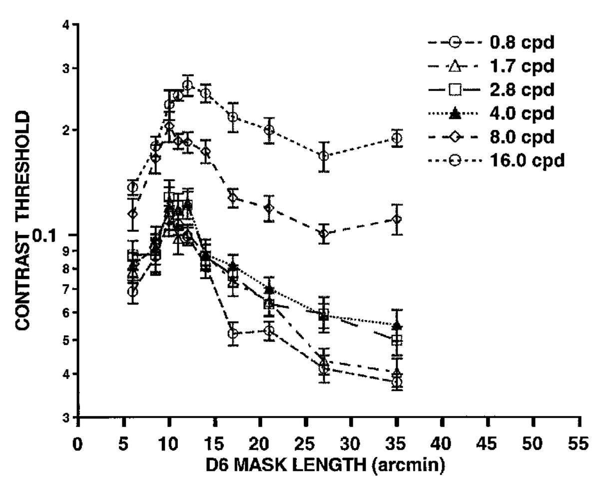
3. EXPERIMENT 1: LENGTH TUNING AND END STOPPING IN SPATIAL FILTERS TUNED TO DIFFERENT SPATIAL FREQUENCIES

In this experiment, length tuning and end stopping in spatial filters most sensitive to six spatial frequencies, 0.8, 1.7, 2.8, 4.0, 8.0, and 16 cycles per degree (cpd), were investigated in foveal vision. These six filters, covering much of the visible range of spatial frequency, can account for much of the variance of the human contrast sensitivity function.[3] At each spatial frequency tested, the contrast threshold was measured for a D6 target that was 5 arcmin long and masked by a second D6 grating of the same spatial frequency. The length of the D6 mask was varied from 6 to 35 arcmin in ten steps. The D6 mask was oriented slightly (5 deg) from the vertical as a precaution to minimize potential local cues.

Conventional simple-cell-receptive-field-based spatial filter theories would predict that, as the length of the D6 mask increases, the contrast threshold should first increase, because the mask covers more and more summation in the center and flanks, leading to stronger masking, until the mask reaches the limits of the receptive field center. Once the D6 mask is longer than the receptive field center, because there is no further activity beyond the conventional receptive field center along the length dimension, the masking effect should not be further affected, and the contrast threshold should reach a plateau. However, if there are inhibitory end zones beyond the receptive field center, the masking effect should be diminished or inhibited by antagonistic end-zone inhibition elicited by further lengthening of the mask, and the contrast thres-hold should decrease instead of forming a plateau,



(a)



(b)

Fig. 2. Length tuning and psychophysical end stopping in spatial filters. (a) Contrast thresholds for detecting a 5-arcmin-long D6 target as a function of mask length at each of the six spatial frequencies. (b) Mean curves for all six spatial frequencies.

until the mask reaches the outer limits of the end zones. This is precisely what our results show [Fig. 2(a)].

For all six spatial frequencies tested, contrast thresholds first increase until the D6 masks reach a length of approximately 10–12 arcmin, independent of spatial frequency, suggesting that the length extent of summation, or length tuning, in each filter is not affected by the filter's spatial-frequency tuning. Thresholds then decrease, showing psychophysical end stopping, consistent with the responses of end-stopped spatial filters. Averaged results [Fig. 2(b)] show that the decrease in percentage of after-peak threshold (the strength of end stopping) changes from 65.6% at 0.8 cpd to 37.4% at 16 cpd, suggesting weaker psychophysical end stopping in filters tuned to higher spatial frequencies. The full extent of psychophysical end stopping cannot be accurately determined from the functions at the four lower spatial frequencies, since the threshold decrease continues at the longest mask length used. However, functions at spatial frequencies of 8.0 and 16.0 cpd show that the threshold decrease stops before 30 arcmin of mask length, suggesting shorter end zones at higher spatial frequencies.

4. EXPERIMENT 2: EFFECTS OF TARGET LENGTH ON LENGTH TUNING OF SPATIAL FILTERS

Results described in experiment 1 suggest that the length tuning of spatial filters, at least in a certain range, is independent of their spatial-frequency tuning but is likely related to the target length. To further examine how length tuning is related to target length, we measured the masking effects of D6 masks for D6 targets at lengths of 7.5, 10, and 12.5 arcmin. The spatial frequency of the stimuli was fixed at 8 cpd. Other conditions were the same as those in experiment 1. Results [Fig. 3(a)] show that the peak of the masking function shifts to longer mask length as the target length increases. The peak mask lengths are approximately 14, 18, and 20 arcmin at target lengths of 7.5, 10, and 12.5 arcmin, respectively. Combined with results of the previous experiment in which a target length of 5 arcmin was used, the relationship between the peak mask length (PML) and the target length (TL) can be nicely described by a linear regression function $\mathrm{PML} = 1.24 \times \mathrm{TL} + 4.9$ arcmin [Fig. 3(b)]. These data suggest that a spatial filter tuned to a particular spatial frequency can be further divided into subunits with different length tuning and argue against the common assumption that there is a fixed length-to-width ratio of spatial filter size, though a limited range is likely.[20]

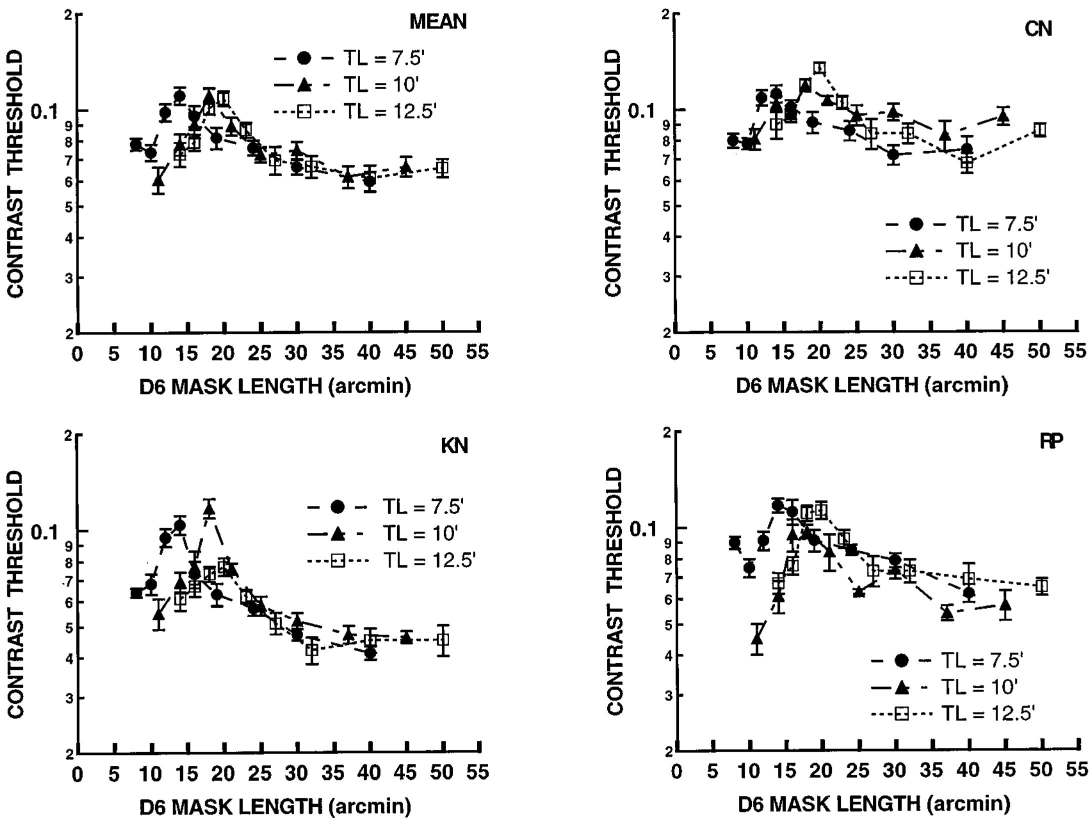
Although individual differences are present across the three observers' results, the strength of psychophysical end stopping does not appear to be systematically affected by the target length, as the amplitudes of after-peak threshold reduction, on the average, are approximately the same across three target length conditions. These results, combined with those of the previous experiment, suggest that the length tuning of spatial filters is indeed correlated with target length over the range tested but is independent of the spatial-frequency tuning of each spatial filter, while psychophysical end stopping is not affected by target length but is strongly related to the filter's spatial-frequency tuning.

5. EXPERIMENT 3: PHASE EFFECTS ON PSYCHOPHYSICAL END STOPPING AND LENGTH SUMMATION

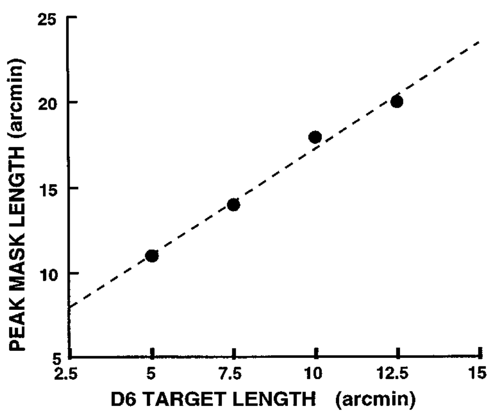
Although spatial filters are generally regarded as linear filters that are followed by a nonlinear processing stage,[3] recently Lawton and Tyler[21] and Zenger and Sagi[22] reported phase independence of masking, suggesting that these filters themselves might be nonlinear. In this experiment we investigated two issues: (1) phase effects on psychophysical end stopping; and (2) phase effects on length summation (a combination of summation in the filter center and flanks, or in the whole area of traditional non-end-stopped spatial filters). There is neurophysiological evidence that receptive field end stopping is nonlinear and phase independent.[23] Thus it is very likely that psychophysical endstopping is also a nonlinear process and is independent of mask phase. However, although results from Lawton and Tyler[21] and Zenger and Sagi[22] would predict that length summation might also be phase insensitive, these results could be questioned because changes of target luminance profile produced by mask phase shifts in these studies were not controlled.[24,25] Thus it is uncertain whether length summation in spatial filters is linear.

We first used the stimulus configuration illustrated in Fig. 4(a) to examine the effect of mask phase on psychophysical end stopping. The target was a 5-arcmin-long vertical D6 grating at a spatial frequency of 8 cpd. The mask had three components: a central 11-arcmin-long D6 grating with its spatial frequency, orientation, and phase identical to those of the target, exactly covering the length summation zones or center and flanks of the underlying spatial filter as suggested in Fig. 2; and two 5-arcmin-long D6 gratings abutting at the top and the bottom of the central D6 grating, masking the end zones of the underlying spatial filter. These two end-zone masks also had the same spatial frequency and orientation, but their phases were either the same as those of the target and the central mask (standard phase) or reversed. The contrast of the central mask was 40%, the same as that in previous experiments, but the end-zone masks were presented at contrasts of 0%, 10%, 20%, and 40%. The 0% contrast condition actually masked only the central length summation zones (including the center and flanks) of the filter and thus set the baseline for other end-zone mask conditions. Other experimental conditions were the same as in experiment 1.

Contrast thresholds as a function of end-zone mask contrast are shown in Fig. 4(b) under two end-zone mask phase conditions. As mask contrast increases, the threshold systematically decreases, illustrating the basic result of psychophysical end stopping where masks in the end zones reduce the effect of the central mask that overlays the target. Moreover, this effect is phase independent. The results from two observers show no systematic difference between the standard and the reversed phase conditions. Psychophysical end stopping becomes stronger as the contrast of end-zone masks increases, regard-



(a)



(b)

Fig. 3. Effects of the target length on spatial filter length tuning. (a) Contrast thresholds for detecting 7.5-, 10-, and 12.5-arcmin D6 targets are plotted as a function of the mask length. Both the target and the mask had a spatial frequency of 8 cpd. (b) The linear relationship between peak mask length (PML) and target length (TL) is described by a regression line PML = 1.24 × TL+ 4.9 arcmin.

less of the mask phase. The phase independence of end-zone masking suggests that psychophysical end stopping is a nonlinear process, consistent with previous neurophysiological findings.[23]

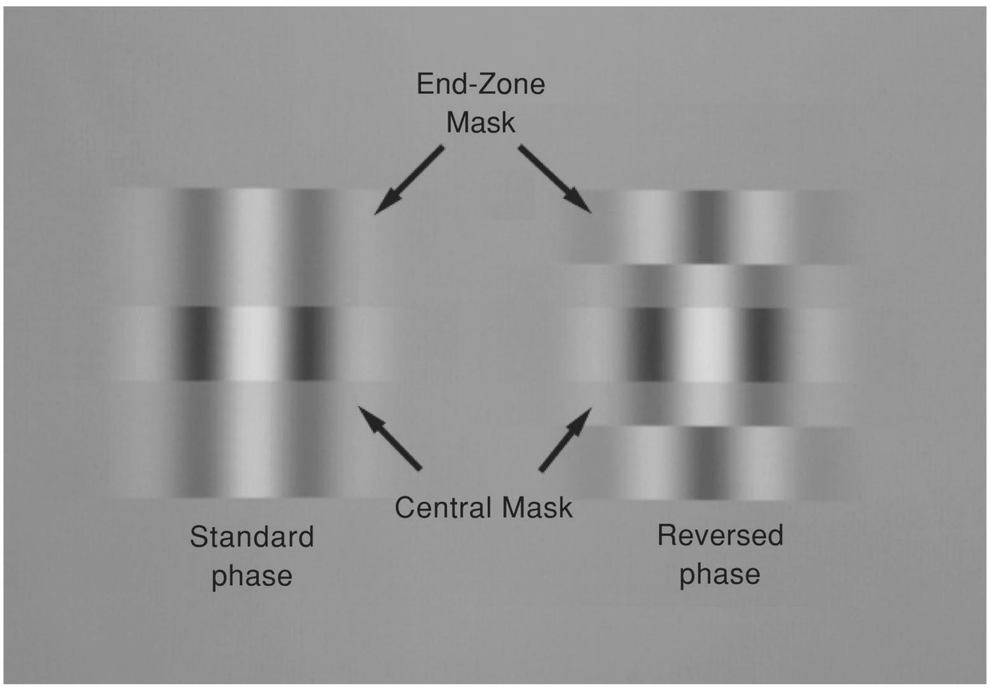
Next we examined the phase effect on length summation, using the stimulus configuration shown in Fig. 5(a). Because the D6 grating acts on both the center and the flanks of underlying spatial filters, the phase effect examined here is actually a combination of effects on the center and the flanks. The same D6 target was masked by another identical D6 grating at a contrast of 40%. Abutting at the top and the bottom of this mask were two additional 3-arcmin-long D6 masks (outer summation zone masks) of the same spatial frequency and orientation, but with either the same or reversed phase at contrasts of 0% or 40%. Together these masks formed an 11-arcmin-long region equal to the center and flanks of the underlying spatial filter. Other experimental conditions were the same as in experiment 1. Unlike the Lawton–Tyler[21] and the Zenger–Sagi[22] experiments, in which a phase shift was accompanied by uncontrolled target luminance profile changes, the current stimulus configuration allowed the luminance profile of the D6 target to be immune to phase change. Therefore a clean phase effect could be revealed by the contrast threshold changes under different phase conditions of outer summation-zone masks.

Figure 5(b) demonstrates that masks with opposite phases have opposite masking effects on length summation. Compared with the 0% contrast condition of outer summation-zone masks (or no outer summation-zone masks), the outer summation-zone mask with standard phase at 40% contrast increases the masking effect, consistent with earlier results (experiment 1), but the outer summation-zone mask with reversed phase reduces the masking effect, showing facilitation. In general, masking on length summation is a linear effect of the central standard phase mask and the two outer summation-zone masks of either standard or reversed phase, which suggests that central length summation in the end-stopped spatial filters is a linear process.

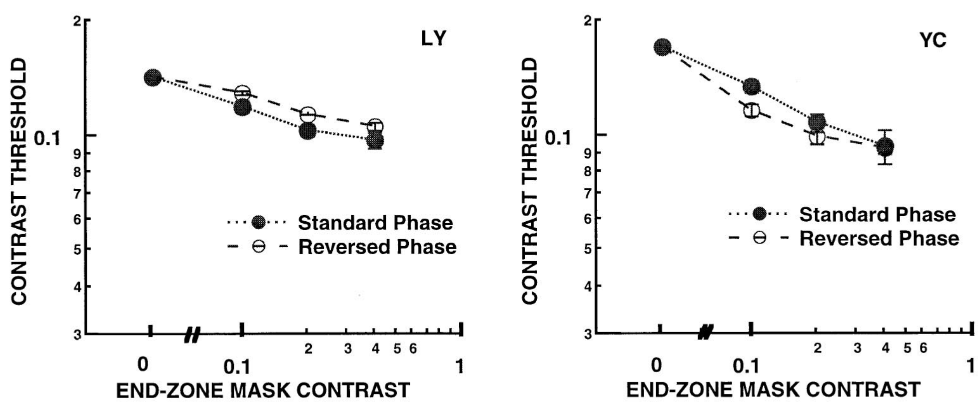
6. DISCUSSION

In this study we demonstrated length tuning and end stopping in psychophysical spatial filters, which are comparable with properties of cortical end-stopped receptive fields. Assuming symmetry, our results describe spatial filters composed of center and flanks abutted by inhibitory end zones that are tuned not only to spatial frequency but also to stimulus length. The phase dependence in length summation and the independence in end stopping suggest that both the first-order linear processing relative to stimulus luminance and the second-order nonlinear rectification relative to the absolute value of stimulus contrast are involved in end-stopped spatial filters. Thus spatial filters may not be simply labeled as linear or nonlinear units.

One concern with psychophysical end stopping is that it might actually reflect inhibition from large orthogonal filters that could also be excited by D6 masks. To examine this possibility, we measured masking effects of spatially more extended D20 masks on D6 targets at spatial frequencies of 1.7 and 8 cpd, with the D6 target and the D20



(a)



(b)

Fig. 4. Phase effects on end-zone masking. (a) Formation of the stimuli. A 5-arcmin-long D6 target is masked by an 11-arcmin-long D6 central mask abutted by two 5-arcmin-long D6 end-zone masks. The central mask excites central summation of the spatial filter, and end-zone masks activate end stopping. The phase of end-zone masks is either standard (in phase) or reversed (out of phase). The spatial frequency of the stimuli is fixed at 8 cpd. (b) Contrast thresholds for detecting a 5-arcmin-long D6 target under standard and reversed end-zone mask phase conditions are plotted as a function of end-zone mask contrast.

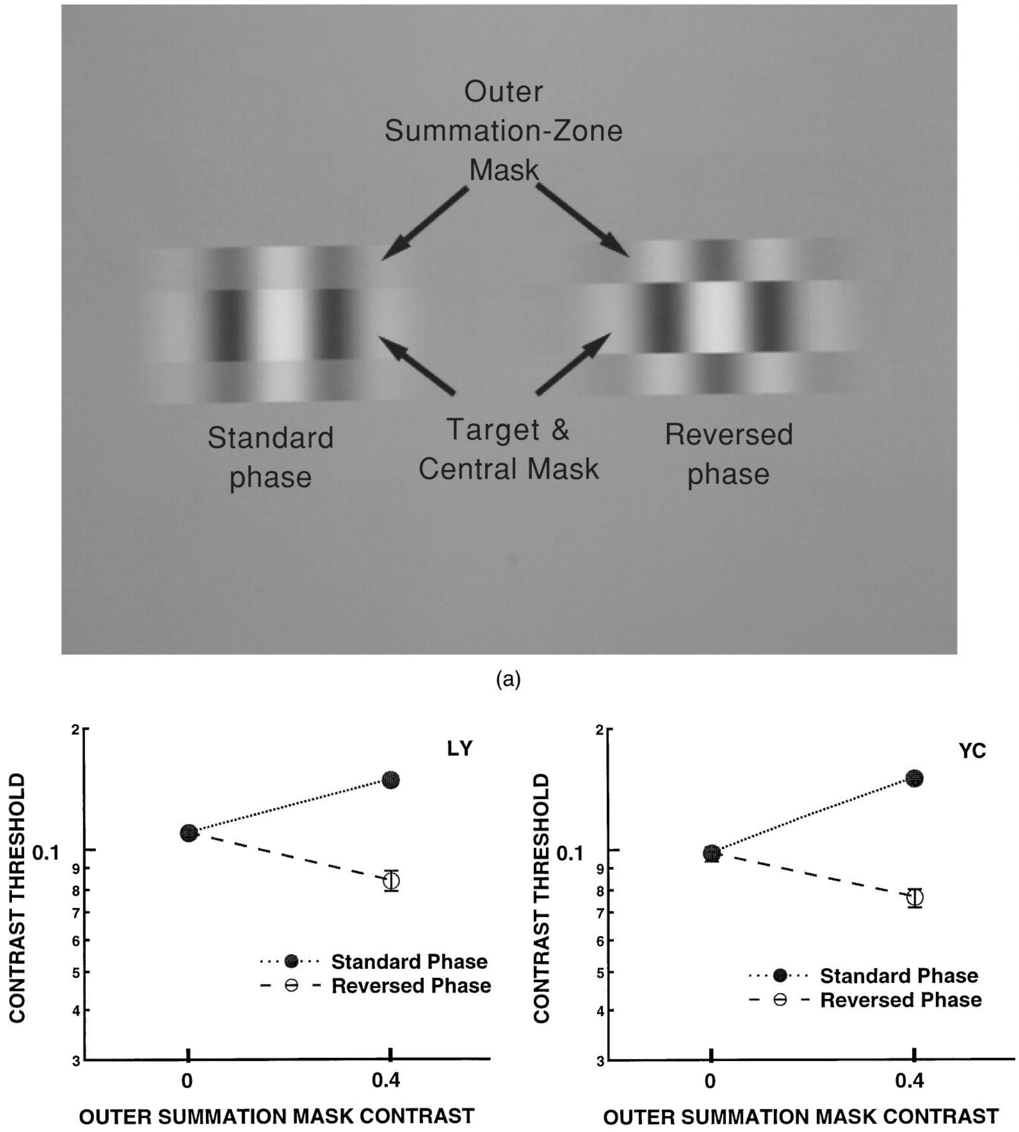


Fig. 5. Phase effects on central summation masking. (a) Formation of the stimuli. A 5-arcmin-long D6 target is masked by an identical D6 central mask abutted by two 3-arcmin-long D6 outer summation-zone masks. The central mask and outer summation-zone masks together cover the central summation zone of the spatial filter. The phase of outer summation-zone masks is either standard or reversed. The spatial frequency of the stimuli is fixed at 8 cpd. (b) Contrast thresholds for detecting a 5-arcmin-long D6 target under standard and reversed outer summation mask phase conditions are plotted as a function of outer summation mask contrast.

mask having the same peak spatial frequency. The D20 masks had three full cycles and therefore little likelihood of exciting filters tuned to the orthogonal orientation. The length of the D6 target was 5 arcmin at the 1.7-cpd spatial-frequency condition. At the 8-cpd condition the target length was 10 arcmin, and only the peak and the plateau background length conditions (18 and 45 arcmin; see Fig. 3) were used. Results (Fig. 6) show clear length tuning and end stopping at both spatial frequencies. Thus psychophysical end stopping cannot be attributed to the effects of large orthogonal spatial filters.

Recent literature[26–29] indicates that threshold elevation in masking is determined at least in part by divisive inhibition or normalization nonlinearity due to the total activity in a pool of filters. Thus the earlier contrast threshold elevation (length summation) in Fig. 2 could be attributed to the increased divisive inhibition that lowered the responses of spatial filters. The question is, Can the threshold reduction with increasing mask length (psychophysical end stopping) shown in Fig. 2 be attributed to reduced divisive inhibition? The answer could be “yes.” However, this reduced divisive inhibition may not be understood as the result of reduced inputs from the spatial filter pool; instead it is better understood if we consider that the effects of pooled inputs are reduced by antagonistic end stopping, because the pooled inputs are from other filters and usually nonspecifically suppressive, but end stopping is within the spatial filter and is specific to important stimulus parameters, such as spatial frequency and orientation, as suggested by neurophysiological and psychophysical studies. This distinction may provide a very interesting insight about the masking mechanism;

i.e., the divisive nonlinearity is determined not only by the effects of pooled inputs but also by the interactions of pooled inputs and antagonistic end stopping.

An alternative way to explain our masking results is that spatial filters with different length tuning might be excited by masks at different lengths, so that mask-excited spatial filters closest to target-excited spatial filters produce the strongest masking, while others have weaker effects as the difference increases. Consistent with our general conclusions, this explanation also implies length tuning and end stopping in spatial filters. However, it cannot account for the result that the strongest masking always occurs when the mask is a few minutes longer than the target, not when the mask and target have similar lengths (Fig. 3), since spatial filters in the latter situation are similar to each other and supposedly have the strongest masking.

Conventionally, the profile of spatial filters is often simulated with the product of a DOG function in the width dimension, which defines the center and flanks, and a Gaussian function in the length dimension, which limits the length extent of the spatial filter.[3] Yu and Essock[14] once suggested that, when spatial filter end stopping is considered, the Gaussian function could be replaced by a DOG function to simulate end stopping. The phase independence of psychophysical end stopping indicates that such a suggestion is not entirely appropriate, because it assumes linearity in psychophysical end stopping. However, one can include rectifying nonlinearity in end stopping in the DOG function by taking the absolute value of the inhibitory component, so that the DOG function in length is presented as $A_1 \exp(-y^2/\sigma_1^2) - \mathrm{abs}[A_2 \exp(-y^2/\sigma_2^2)]$. Another interesting question is, Can a conventional spatial filter with summation center and inhibitory flanks be accurately described only by a DOG or similar linear function in the width dimension? Implying filter nonlinearity, the Lawton–Tyler[21] and the Zenger–Sagi[22] results are not supportive, but those results are not entirely convincing either, as discussed above. However, combined linear summation in the center and flanks revealed in this study does suggest such a possibility, though linearity in the filter center and flanks has not been studied separately and such research is worth doing.

End-stopped spatial filters have an important advantage over conventional ones in that the processing of termination and corner information is one of their basic features and therefore does not require additional orthogonal second-order filters to compute length information. It may also provide an alternative explanation for recent findings of spatial facilitation effects.[22,30–32] These studies show that the sensitivity to a line or Gabor patch is enhanced by inducement of lines or Gabor patches located end to end with the target, but the facilitation effect is diminished when the inducer and the target have large gaps or are not collinear. Moreover, the facilitatory effects were reported to be independent of the phase or polarity of the inducer.[22,33] Although a long-range facilitation theory was introduced by Polat and Sagi,[32] the strongest facilitation often occurred when the inducer was close to or even overlapping the target and therefore was very likely placed within the same spatial filter.[13] When end stopping is considered in spatial filters, if the target is located on the filter center and inducers are located within the inhibitory end zones, these inducers, regardless of their polarity or phase, would elicit end-zone inhibition, which may reduce the divisive inhibition and thus enhance the sensitivity of the filter.[13] But if the target and the inducers are farther apart, or if the inducers are not collinear with the target, part or all of the inducers will be outside of the end zones, resulting in a weaker (or zero) effect on the sensitivity of the spatial filter. These predictions are consistent with results from our recent experiments.[13]

Although not strictly comparable, some of the results obtained with the masking paradigm are very similar to earlier results obtained with a modified Westheimer paradigm. Most notably, masking results show the peak mask length for a 5-arcmin-long D6 target being approximately 10–12 arcmin (Fig. 2), similar to the 10–11-arcmin background peak length for a 5-arcmin-long single line in the Westheimer paradigm.[14] A similar linear relationship between peak mask or background length and target length is also found within both paradigms. These results suggest that the Westheimer paradigm and masking paradigm may share similar mechanisms. Although the Westheimer function has a long history of being inter-

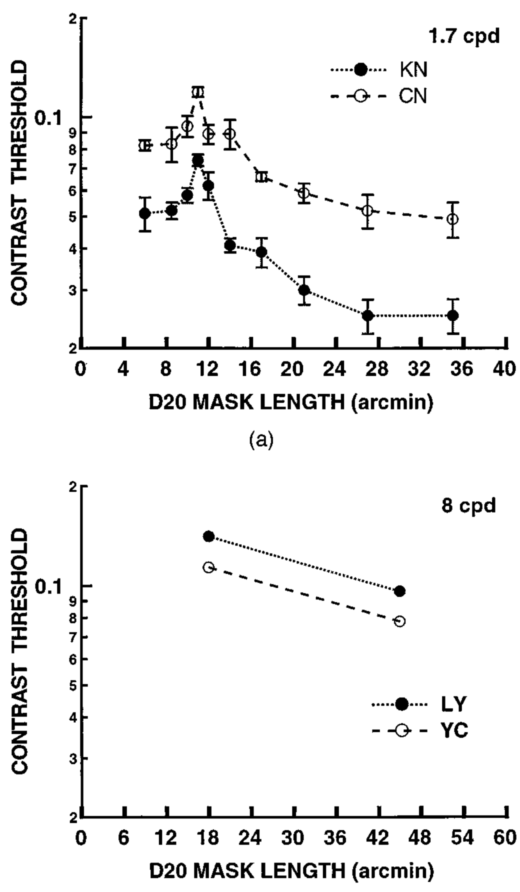


Fig. 6. Contrast thresholds for D6 targets masked by D20 masks at the same frequencies of (a) 1.7 and (b) 8 cpd, respectively. The target length was 5 arcmin at 1.7-cpd spatial frequency and 10 arcmin at 8-cpd spatial frequency.

preted as reflecting the behavior of retinal cell receptive fields,[16,34,35] the cortical locus of length and width spatial interactions revealed with the modified Westheimer paradigm using rectilinear stimuli has been supported by spatial scaling measurements[17] and by dichoptic and amblyopic measurements.[18] Furthermore, parallel studies also demonstrate that conventional Westheimer functions measured with circular stimuli may also be primarily cortical.[17,36] Thus the Westheimer function, like masking effects, may reflect the activities of cortical spatial filters.[36] Once the Westheimer paradigm is related to the masking paradigm, it is not surprising that desensitization and sensitization in the Westheimer function can be explained by the change of gain[26–29] in spatial filters caused by the change in background size. In other words, desensitization could occur because the enlarged background covering the central summation enhances the divisive inhibition by increasing the pooled inputs from other filters, a process that also elevates the contrast threshold in a masking paradigm. Similarly, sensitization could occur because further enlarged background elicits surround antagonism, which reduces the divisive inhibition by interfering with the effects of pooled inputs (see discussion above).

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