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Rectification nonlinearity in cortical end-stopped perceptive fields

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Abstract

End-stopped perceptive fields associated with line targets were demonstrated previously with length and width Westheimer functions. In this study we investigated rectifying non-linearity in these perceptive fields to examine whether they directly reflect the organization of cortical receptive fields. Specifically, we reversed the polarity of parts of the background field associated with a specific perceptive field sub-region and examined threshold changes in corresponding length or width Westheimer functions. Results showed full-wave rectification in end-stopping and half-wave rectification in center summation and flank-inhibition preceding linear summation in end-stopped perceptive fields. Half-wave rectification in center summation and surround-inhibition preceding linear summation was also found in circular perceptive fields associated with spot targets. These results are inconsistent with direct links between perceptive fields and cortical receptive fields. Rather they suggest that these perceptive fields are likely the second-order fields formed by pooled non-linearly rectified outputs from cortical receptive fields. © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: Perceptive field; Rectification nonlinearity; Second-order; End-stopping; Westheimer function

1. Introduction

Evidence for psychophysical end-stopped perceptive fields resembling cortical end-stopped simple cell receptive fields has been reported recently [1–3]. Using a variation of the Westheimer paradigm [4,5], Yu and Essock [1] measured increment thresholds for a small line target centered on a rectangular background of various lengths or widths. The increment thresholds were first elevated (desensitization), then lowered (sensitization), with increasing background width or length, showing inverted-V shapes typical of the Westheimer function. The desensitization and sensitization branches of the length Westheimer function obtained under the variable-length background condition are taken as suggesting central length summation and end-stopping, respectively, and those of the width Westheimer function obtained under the variable-width background condition are taken as suggesting central width summation and flank-inhibition, respectively, in end-stopped psychophysical perceptive fields. These perceptive fields are composed of a summation center, antagonistic flanks, and end-zones, analogous to cortical end-stopped simple cell receptive fields. A cortical locus of these end-stopped perceptive fields has been suggested by several lines of evidence, including steep spatial scaling of end-zones and flanks resembling cortical magnification, severe degradation of end-stopping and flank-inhibition by amblyopia, and dichoptic transfer of desensitization and sensitization in length and width Westheimer functions [2,3].

In this study we attempt to address the question: What is the nature of these end-stopped perceptive fields? A simple and attractive assumption is that end-stopped perceptive fields are the direct perceptual reflection of neural end-stopped simple cell receptive fields. This assumption is similar to traditional retinal receptive field explanations of the Westheimer function [4], except that the locus of the functions is moved up to the visual cortex and the functions are based on cortical cell receptive fields. Indeed our previous data have shown that these end-stopped perceptive fields not only resemble end-stopped simple cell receptive fields in terms of the geographic organization of the fields (i.e. end-zones, flanks, centers), they also share many critical properties. Taking psychophysical end-stopping as an example, there is evidence showing that it is relatively

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unaffected by mask phase [6], analogous to the phase insensitivity of receptive field end-stopping [7]. It also has similar spatial frequency and orientation tuning to receptive field end-stopping [8]. Psychophysical end-stopping is nearly abolished in humans with naturally occurring amblyopia [3], which might reflect the general vulnerability of end-stopping to abnormal post-natal visual conditions. Similar vulnerability of end-stopped neurons was found in the visual cortex areas 17 and 18 of cats reared in stroboscopic light by Kennedy and Orban [9] who reported that the proportion of end-stopped cells in these cats decreased from the normal level of 27–30 to 6–7%.

However, this naive assumption about the neural basis of end-stopped perceptive fields could be over-simplified. A wide range of spatial vision tasks, from line and edge encoding to texture segregation, appear to depend on second-order non-Fourier mechanisms [10–13], rather than by directly first-order Fourier mechanisms at the beginning stage of cortical visual processing (i.e. V1 cells). These second-order mechanisms pool outputs from first-order mechanisms after these outputs are rectified or normalized by some non-linear processes, and form the basis for many psychophysical judgments. Therefore, there is a possibility that end-stopped perceptive fields suggested by length and width Westheimer functions could be second-order composite fields contributed by a number of first-order visual neurons within a local neural network.

Several properties of first- and second-order mechanisms can help distinguish whether psychophysical perceptive fields are first- or second-order. It is known that cortical simple cells are linear filters followed by half-wave rectification [14,15]. They are said to be linear because light is linearly summed within the excitatory subregions and then subtracted by light linearly summed within the inhibitory subregions of the receptive fields [16], at least over a limited contrast range. Therefore, if perceptive fields are first-order, these rules of linear summation have to be obeyed. At the simple cell level, the ON and OFF pathways are segregated and ON- and OFF-center simple cells respond to ON and OFF signals respectively. Unlike truly linear filters which can produce both positive and negative responses to light increments and decrements, simple cell responses are half-wave rectified beyond the linear stage. Thus the second-order mechanisms would receive half-wave rectified inputs. This rectification property should be evident in perceptive fields if the latter are second-order.

On the other hand, physiological studies show that receptive field end-stopping is at least partly generated by interlaminar influences in the visual cortex [17–20], and can be disabled pharmacologically without disturbing other receptive field properties [19]. This process occurs at a later stage than the generation of other receptive field properties, probably after the convergence of ON and OFF pathways. There is evidence that end-stopping in neurons in cat striate cortex is little affected by the phase of grating stimuli [7]. Such phase insensitivity is also shown in psychophysical end-stopping revealed in masking experiments [6]. Thus end-stopping is determined by the absolute strength of stimuli and full-wave rectified. Since this nonlinear property occurs as early as in first-order V1 simple cells (many of these first-order units if end-stopped are thus actually not purely first-order because of the non-linear nature of end-stopping), the full-wave rectification should be evident in end-stopped perceptive fields, regardless of whether the latter are first- or second-order.

On the basis of these properties of first- and second-order mechanisms, we designed a series of straightforward experiments to examine the first- or second-order nature of psychophysical end-stopped perceptive fields. We reversed the polarity of part(s) of the background field associated with a specific perceptive field subregion and examined threshold changes in corresponding length or width Westheimer functions. If end-stopped perceptive fields are the direct perceptual reflection of end-stopped simple cell receptive fields, the rules of linear summation and subtraction should be obeyed in the perceptive field center and flanks. On the other hand, reversing the polarity of the end-zone background should not affect the end-stopping effect since the latter is full-wave rectified before acting on central summation. Our results did reveal full-wave rectification in psychophysical end-stopping, consistent with full-wave rectification in receptive field end-stopping. However, results also revealed nonlinear half-wave rectification preceding linear summation in central summation and linear subtraction between central summation and flank (surround) inhibition. These results in general are inconsistent with direct links between perceptive fields and cortical receptive fields, but rather they suggest that these perceptive fields are likely the second-order composite fields formed by pooled nonlinearly rectified outputs from first-order receptive fields.

2. Methods

2.1. Observers

Four observers (two males, VP and YC, and two females, LY and QL, aged 20–32) served in most experiments in this study. The fifth observer (DK, male, aged 24) completed a few control conditions. All had normal or corrected-to-normal vision. DK, LY and YC were experienced. QL and VP were new to psychophysical experiments and received many hours of training prior to data collection. Only YC was aware of the purpose of the study.

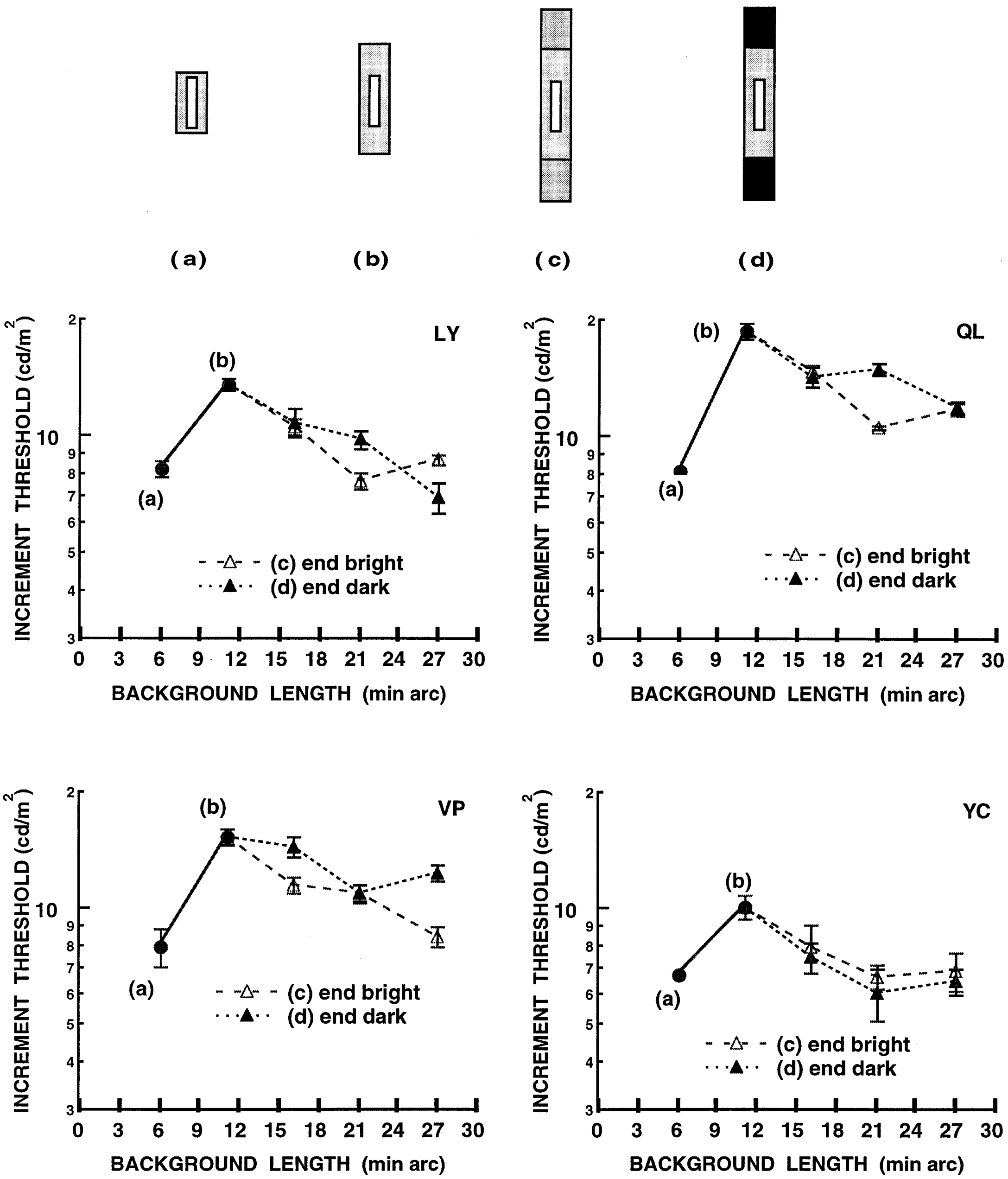

Fig. 1. The effects of polarity reversal on psychophysical end-stopping. The top row shows stimuli: a 1′ × 5′ line target centered on a 3′ wide bright background which was (a) 6′ long, (b) 11′ long covering maximal length summation, (c) 11′ long plus two bright background regions covering end-zones with length varying from 2.5 to 8′, and (d) 11′ long plus two dark background regions covering end-zones with length also varying from 2.5 to 8′. The overall background length in (c) and (d) varied from 16 to 27′. The bottom two rows show psychophysical end-stopping presented as after-peak threshold change, which is similar under the same and opposite polarity conditions.

2.2. Apparatus and stimuli

The stimuli were generated by a Vision Works computer graphics system (Vision Research Graphics) 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 arcmin at the viewing distance of 5.64 m). The frame rate was 117 Hz. Luminance of the monitor was made linear by means of a 15-bit look-up table. 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 1′ × 5′ foveal line target centered on a rectangular background of variable length or width, or a 1′ foveal spot target centered on a circular background of variable diameter. The rectangular background field consisted of three subregions with the same length or width while the other dimension was variable, including a rectangular central bright region containing the target and two rectangular distal regions whose polarity was either positive (bright) or negative (dark) (Figs. 1–4). The circular background field consisted of two subregions, a central bright region containing the target and one surrounding bright or dark annulus (Figs. 7 and 8). Further details are given later along with the specific experiments. The luminance of the screen, bright background, and dark background was 25, 50, and 0 cd/m^2, respectively. Viewing was monocular by the dominant eye (right eye for all observers).

2.3. Procedure

A successive two-alternative forced-choice staircase procedure was used. The background field was presented in each of the two intervals (400 msec) separated by a 380 msec inter-stimulus interval. In one of the two intervals the target was also presented for 400 msec. The screen luminance remained constant both throughout and between trials. Each trial was preceded by a 6.3′ × 6.3′ 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.

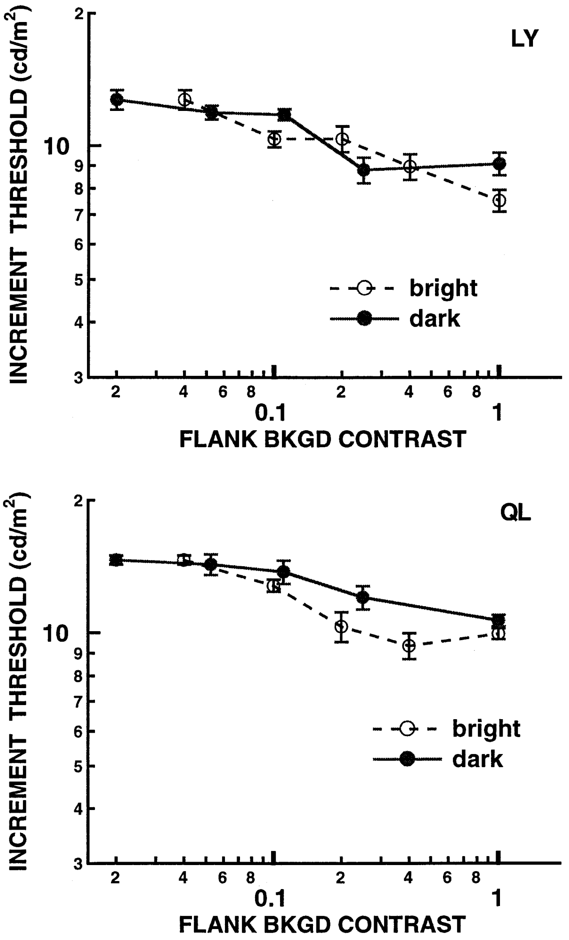

Fig. 2. Psychophysical end-stopping as a function of the Weber contrast of end-zone background regions under the same and opposite polarity conditions.

Each staircase consisted of four practice reversals and six experimental reversals. Each correct response lowered target luminance by one step and each incorrect response raised target luminance by three steps, resulting in a 75% convergence rate of the staircase. The step size was 2.7 cd/m^2 at the first pair of practice reversals and 1.35 cd/m^2 at the second pair. It was 0.45 cd/m^2 throughout the experimental phase. The mean of the six experimental reversals was used to estimate the increment threshold. An experimental session usually consisted of 9–10 stimulus conditions presented in a random order, and lasted for about 50 min. Each datum represents the mean of five replications for each condition, and the error bars represent ± 1 S.E.M.

3. Experiments

For a 1′ × 5′ target line, increment thresholds in length Westheimer functions peak at a background length of about 11′, and then decrease until reaching a plateau at a background length of about 23′ [1], suggesting an 11′ long summation center and two 6′ long end-zones, for a total length of 23′. Width Westheimer functions for the same target line peak at a background width of 6′ and start to level off at 14–16′, suggesting a 6′ wide summation center and two 4–5′ wide flanks, with a total width of 14–16′. Assuming symmetry, these data describe end-stopped perceptive fields composed of a 6′ wide and 11′ long summation center, two 4–5′ wide flanks, and two 6′ long end-zones. On the basis of these quantitative descriptions, the following experiments examine the effects of background polarity reversal on length and width Westheimer functions associated with the same 1′ × 5′ line target. The effects of background polarity reversal on the conventional Westheimer function measured with a 1′ spot target were also investigated.

3.1. The effects of background polarity reversal on psychophysical end-stopping and central length summation

As indicated above, a length function associated with a 1′ × 5′ target line typically peaks at 11′ and levels off at 23′. To examine the effects of background polarity reversal on psychophysical end-stopping, a 1′ × 5′ line target was centered on a 3′ wide bright background (Fig. 1, top row) which was (a) 6′ long covering a small area within the perceptive field center, (b) 11′ long covering the whole length of the perceptive field center, (c) 11′ long plus two bright end-zone background subregions varying from 2.5 to 8′ in length, covering part

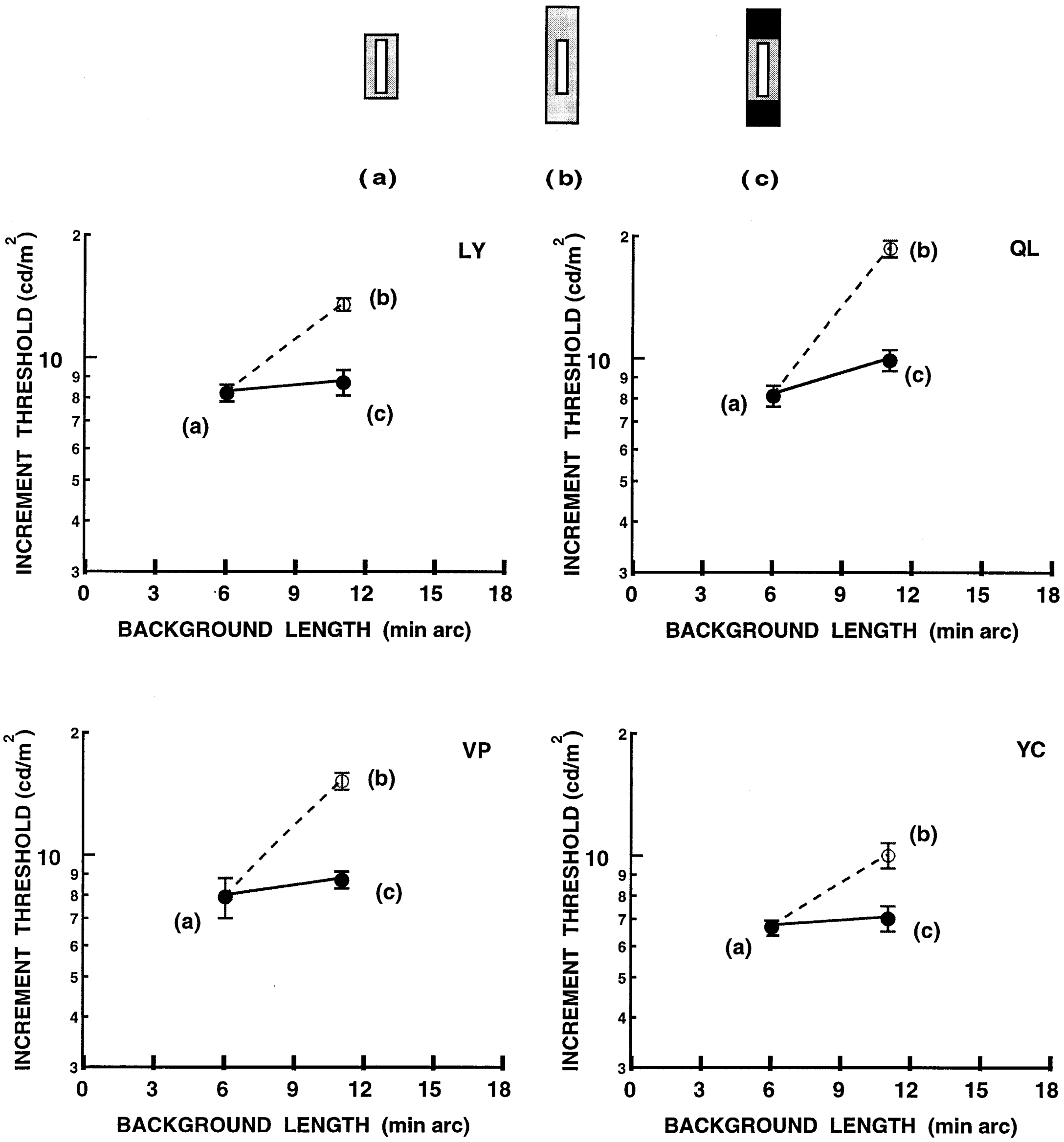

Fig. 3. The effects of polarity reversal on central length summation. The top row shows stimuli as a 1′ × 5′ target line centered on (a) a 3′ × 6′ background, (b) a 3′ × 6′ central region plus two 3′ × 2.5′ outer regions of the same polarity (actually a 3′ × 11′ background covering maximal central length summation), (c) a 3′ × 6′ central region plus two 3′ × 2.5′ outer regions of the opposite polarity. The bottom two rows show the polarity effects on central length summation, which indicate half-wave rectification.

or all of the length of the end-zones, and (d) 11′ long plus two dark end-zone background subregions also varying from 2.5 to 8′ in length. The overall background length in (c) and (d) varied from 16 to 27′. If psychophysical end-stopping, like its neural counterpart, presents full-wave rectifying non-linearity, bright end-zone background subfields (c) and end-zone background subfields (d) should produce the same sensitization effect, which is exactly what the results show! After being raised to the peak at condition (b), the increment thresholds were reduced by extended end-zone background subfields of both polarities (Fig. 1, bottom two rows). There is no systematic and significant difference between the effects of (c) and (d). Thus, psychophysical end-stopping is insensitive to the background polarity and therefore full-wave rectified, consistent with full-wave rectifying nonlinearity in receptive field end-stopping.

To examine the relationship between full-wave rectification in end-stopping and background contrast, thresholds were measured in two observers (LY and QL) for the same target line centered on a 3′ × 11′ central summation background subregions plus two 3′ × 5′ end-zone background subregions. The total length of the background was 21′. The two end-zone background subregions had either positive or negative polarity (examples of conditions (c) and (d) in Fig. 1), and the luminance was set to be 0, ± 10, ± 20, ± 40,

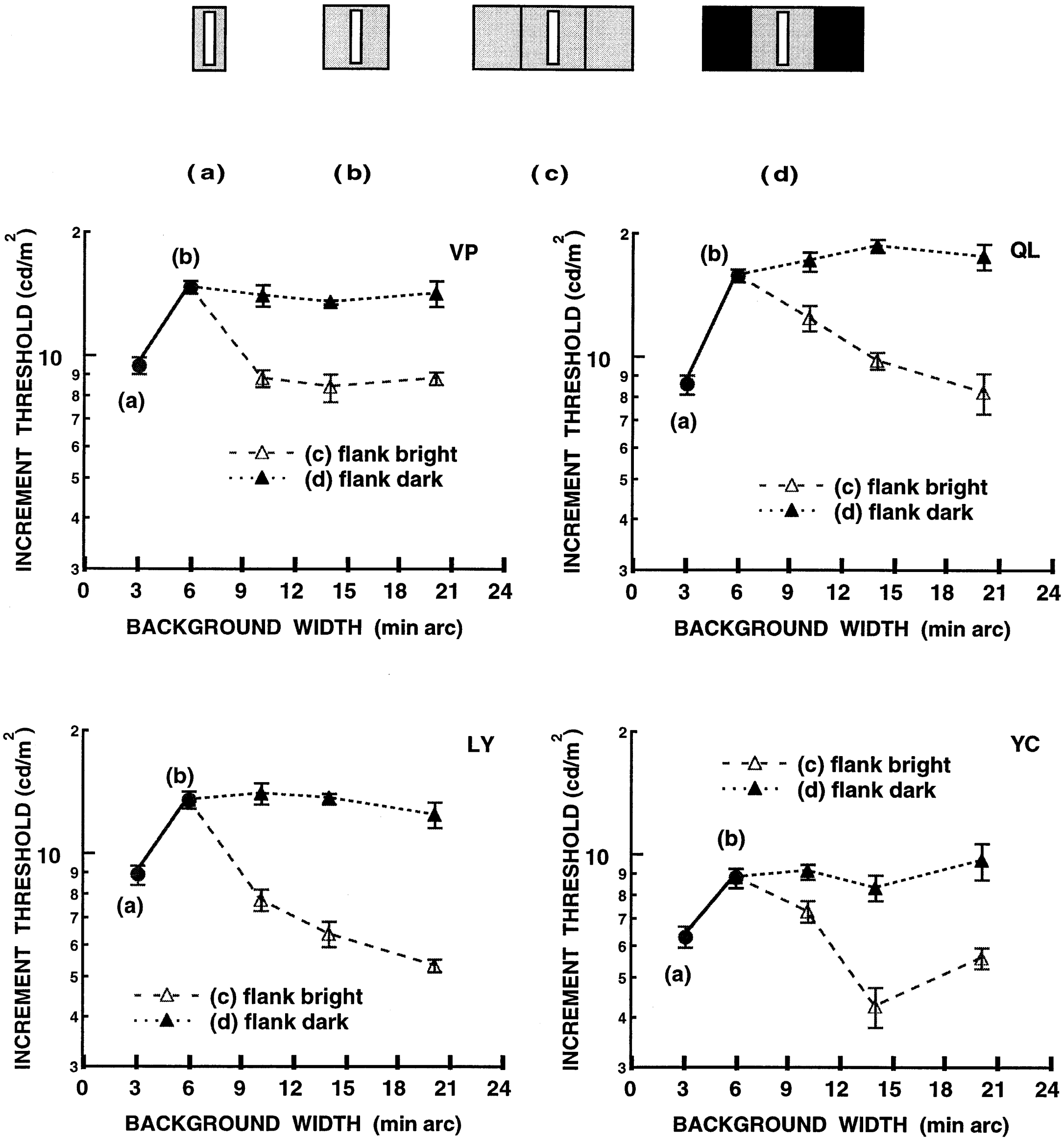

Fig. 4. The effects of polarity reversal on psychophysical flank-inhibition. The top row shows stimuli composed of a 1′ × 5′ line target centered on a 6′ long background which was (a) 3′ wide, (b) 6′ wide covering maximal width summation, (c) 6′ wide flanked by a pair of the same sign background regions with width varying from 2 to 7′ covering inhibitory flanks, or (d) 6′ wide flanked by a pair of the opposite sign background regions with width also varying from 2 to 7′. The overall background widths in (c) and (d) varied from 10 to 20′. The bottom two rows show psychophysical flank-inhibition indicated by after-peak threshold change. No inhibition is evident under the opposite polarity conditions.

and ± 100% different from the screen luminance (25 cd/m^2). When the luminance was ± 100% different from the screen luminance, end-zone background subregions were as bright (50 cd/m^2) or dark (0 cd/m^2) as those in conditions (c) or (d) in Fig. 1. Data are shown in Fig. 2 in which the threshold is plotted against the Weber contrast of end-zone background subregions. The strength of end-stopping (amplitude of threshold reduction) is clearly contrast dependent, regardless of the polarity of end-zone background subregions.

Experiments then focused on the effects of background polarity reversal on length summation of the perceptive field center. Thresholds for the same target line centered on three background conditions (Fig. 3, top row) were measured. When the background lengthened from condition (a), a 3′ × 6′ background, to condition (b), a 3′ × 11′ background, the threshold was elevated due to maximally increased central length summation (Fig. 3, bottom two rows). This threshold elevation is consistent with linear summation within the center of the cortical receptive fields. However, compared to condition (a), reversing the polarity of two end parts of the 11′ long background (two 3′ × 2.5′ subregions beyond the central 3′ × 6′ subregion) in condition (c) had little effect on thresholds, rather than causing threshold reduction as a simple cell receptive field would predict, suggesting that opposite-sign signals were not linearly summed within the central summation zone, but were half-wave rectified. It appears that, in the perceptive field center, linear light summation occurs after nonlinear half-wave rectification, which is contradictory to the known property of linear summation preceding nonlinear half-wave rectification in simple cell receptive field center (this point will be addressed later in Section 4).

3.2. The effects of background polarity reversal on psychophysical flank-inhibition and central width summation

The effects of background polarity reversal on flank-inhibition and central width summation were investigated in a manner similar to that used in the length function experiments described above. Both length and width experiments were actually run during the same period in a counterbalanced order. Based on earlier results [1] which showed a width function composed of 6′ wide central summation and 8–10′ wide flank-inhibition, thresholds were measured for a 1′ × 5′ target line centered on a 6′ long rectangular background (Fig. 4, top row) which was (a) 3′ wide covering a small area within the perceptive field center, (b) 6′ wide covering the whole width of the perceptive field center, (c) 6′ wide flanked by a pair of the same sign background subregions whose width varied from 2 to 7′, covering part or all of the width of antagonistic flanks, or (d) 6′ wide flanked by a pair of opposite sign background subregions whose width also varied from 2 to 7′. The overall background widths in (c) and (d) ranged from 10 to 20′. Thresholds measured from conditions (a) to (c) formed regular width Westheimer functions, as shown in Fig. 4, bottom two rows. Condition (c) reduced thresholds by subtracting the center summation of light as a simple cell receptive field model would predict. What is interesting is the effect of reversed polarity in background subregions covering the antagonistic flanks of the perceptive field (condition (d)). Unlike the full-wave rectification in psychophysical end-stopping, the dark parts of the background in condition (d), though covering the inhibitory flanks, had little effect on thresholds at all, regardless of the width of those dark regions. This behavior, however, is also inconsistent with a simple cell model, which would predict further threshold elevation. It appears that signals summed within the inhibitory flanks of the perceptive fields are half-wave rectified before they subtract the signals summed within the perceptive field center. Thus, like the perceptive field center, perceptive field flanks are unlikely a direct reflection of simple cell receptive field flanks.

We performed a control experiment to see whether the interesting anisotropy of full-wave and half-wave rectification between psychophysical end-stopping and flank-inhibition changes with the orientation change of the target line. Increment thresholds for stimulus conditions the same as those in Figs. 1 and 4 were measured, except that all stimuli were oriented horizontally. Fig. 5(a and b) show results of length and width measurements from two observers respectively. Clearly the anisotropy between psychophysical end-stopping and flank-inhibition is not affected by the target orientation, providing strong supports for the cortical nature of mechanisms underlying the length and width Westheimer functions.

The relationship between half-wave rectification in flank-inhibition and contrast was also examined in the same two observers (LY and QL) as in the length function contrast experiment (Fig. 2). The length function contrast experiment and the current one were run together in a counterbalanced order. The luminance of two 4′ wide background subregions covering flanks was also set to be 0, ± 10, ± 20, ± 40, and ± 100% different from the screen luminance (25 cd/m^2). Because opposite sign signals are ignored in half-wave rectification, the thresholds should not be affected by the contrast of dark background subregions, which is consistent with the results shown in Fig. 6. Although the thresholds decreased with increasing contrast of the bright flank background subregions, the thresholds remained unchanged under the dark flank background conditions, regardless of the contrast.

Previous studies have suggested that central length and width summation are homogeneous in nature, both of which are identically scaled across the periphery and affected by amblyopia [2,3]. This conclusion is also supported by the same rectifying nonlinearity in central length and width summation. The effects of background polarity reversal on central width summation were studied in three conditions (Fig. 7, top row): (a) a 3′ wide background, (b) a 3′ wide background subregion flanked by two 1.5′ wide background subregions of the same sign (actually a 6′ wide background covering the whole width of the perceptive field center), (c) a 3′ wide background subregion flanked by two 1.5′ wide background subregions of the opposite sign. As compared to thresholds measured under condition (a), increasing the background area in (b) increased the threshold due to maximally increased summation as shown in regular width functions, but adding the same sized dark areas had little effect on thresholds (Fig. 7, bottom two rows). These results indicate that, as in central length summation, opposite sign signals in central width summation also appear to be half-wave rectified, inconsistent with the linear summation properties of simple cell receptive field center.

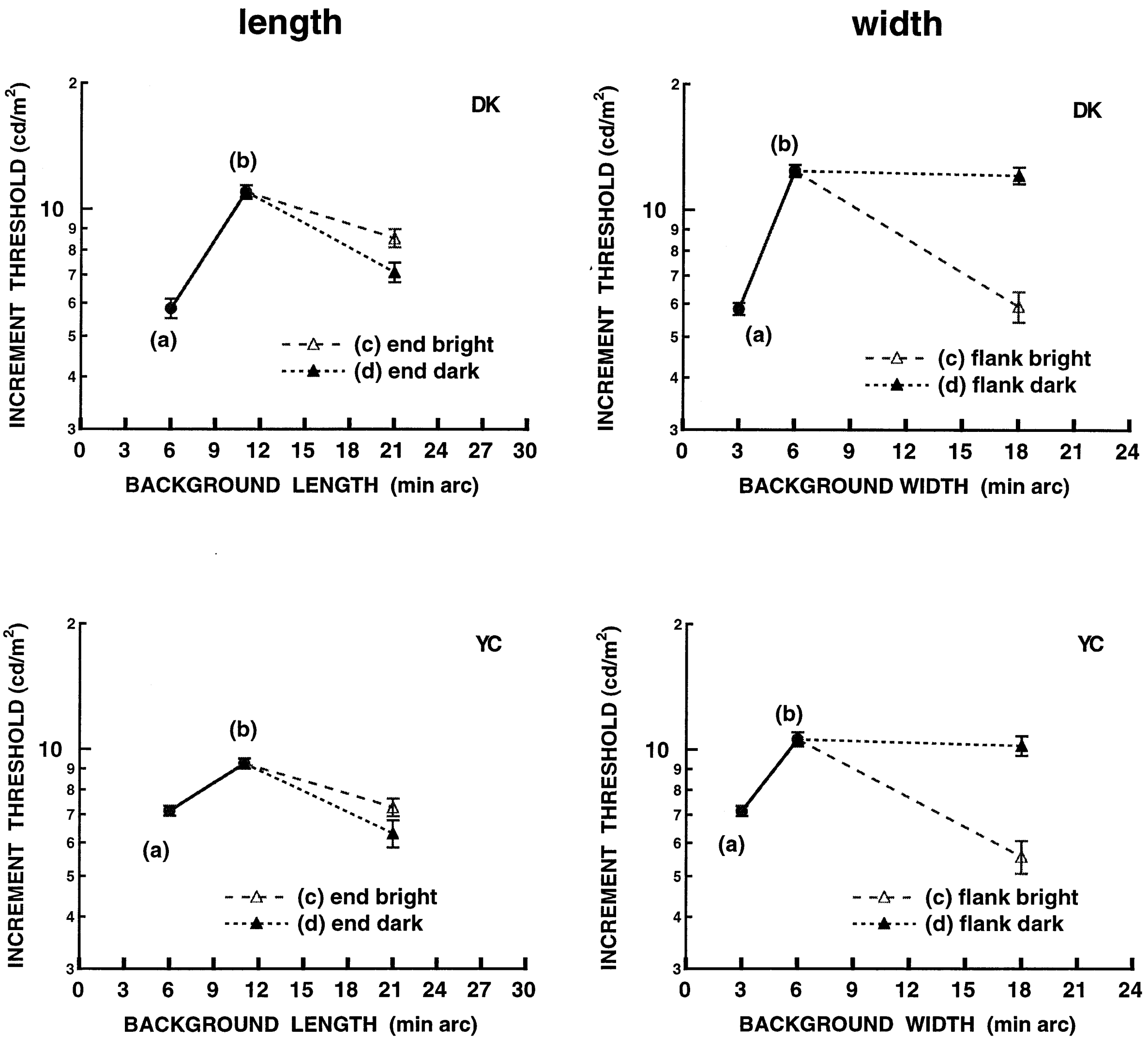

Fig. 5. The effects of polarity reversal on psychophysical end-stopping and flank-inhibition with horizontally oriented line targets. The stimuli are the same as those in Figs. 1 and 4 except at the horizontal orientation. Fig. 5(a and b) show results of length and width measurements from two observers respectively. Results indicate anisotropy of full-wave and half-wave rectification between psychophysical end-stopping and flank-inhibition which is unaffected by the target orientation.

3.3. The effects of background polarity reversal on the Westheimer function measured with circular stimuli

The conventional Westheimer function measured with spot targets has been often interpreted as mirroring the center-surround organization of retinal cell receptive fields [4,5,21,22], in that desensitization reflects center summation, and sensitization reflects surround inhibition of retinal receptive fields. This classic view, however, has been recently challenged and a cortical component of the Westheimer function has been suggested by evidence showing steep spatial scaling of sensitization resembling cortical magnification, alteration of sensitization by amblyopia, and dichoptic transfer of the Westheimer function [2,23]. Moreover, there is evidence suggesting that the conventional Westheimer function is similar to the width Westheimer function measured with a line target. Both functions show identical ranges of desensitization and sensitization [1], identical spatial scaling properties [2], and similar alteration of sensitization by amblyopia [3,23], suggesting that they are probably based on the same neural mechanisms. We further explored the nature of this classic version of the Westheimer function by examining the effects of background polarity reversal on its surround sensitization and central summation.

For a 1′ spot target, a Westheimer function typically reaches its peak at a background diameter of 6′ and starts to level off at approximately 14′ [5]. To investigate the effects of background polarity reversal on surround sensitization, thresholds were measured for four background conditions (Fig. 8, top row): (a) a 3′-diameter background covering a small area of the perceptive field center, (b) a 6′-diameter background covering the whole perceptive field center, (c) a 6′-diameter background surrounded by a 4′ thick annulus of the same sign covering the antagonistic surround (actually a 14′-diameter background), (d) a 6′-diameter background surrounded by a 4′ thick annulus of the opposite sign. Conditions (a) to (c) formed a regular Westheimer function (Fig. 8, bottom two rows), but reversing the polarity of the annulus (condition (d)) mainly had little effect on thresholds, showing half-wave rectification in surround sensitization, the same nonlinear rectification property shown in flank-inhibition.

The effects of background polarity reversal on central summation were investigated by comparing threshold changes when a 3′-diameter background (a) was added with a 1.5′ thick ring of the same sign (b) or with a 1.5′ thick ring of the opposite sign (c) (Fig. 9, top). Thresholds (Fig. 9, bottom two rows) were elevated in (b) because of maximally summed light. However, a consistent trend of threshold reduction was not shown as linear summation would predict. The thresholds in (c) were slightly reduced for LY and YC, unchanged for QL, and slightly elevated for VP. The average threshold reduction was 0.01 log units, which is negligible as compared to the 0.26 log unit average threshold elevation caused by condition (b), thus again showing half-wave rectification in central summation. Thus, rectifying nonlinearity in the original Westheimer function measured with circular stimuli is comparable to that in the width Westheimer function measured with rectilinear stimuli. However, neither the rule of linear summation within the receptive field center nor the rule of linear subtraction between receptive field center and surround is obeyed. In a similar experiment, Wyatt [24] found that, in scotopic vision, adding a dark annulus within the summation center raised the threshold. In our experiment, two novice observers QL and VP did show threshold elevation under condition (c) for the first few runs. But this threshold elevation quickly disappeared after practice. However, regardless of the difference between Wyatt's results and ours, neither study showed threshold reduction as might have been expected if the Westheimer function were directly based on first-order receptive fields.

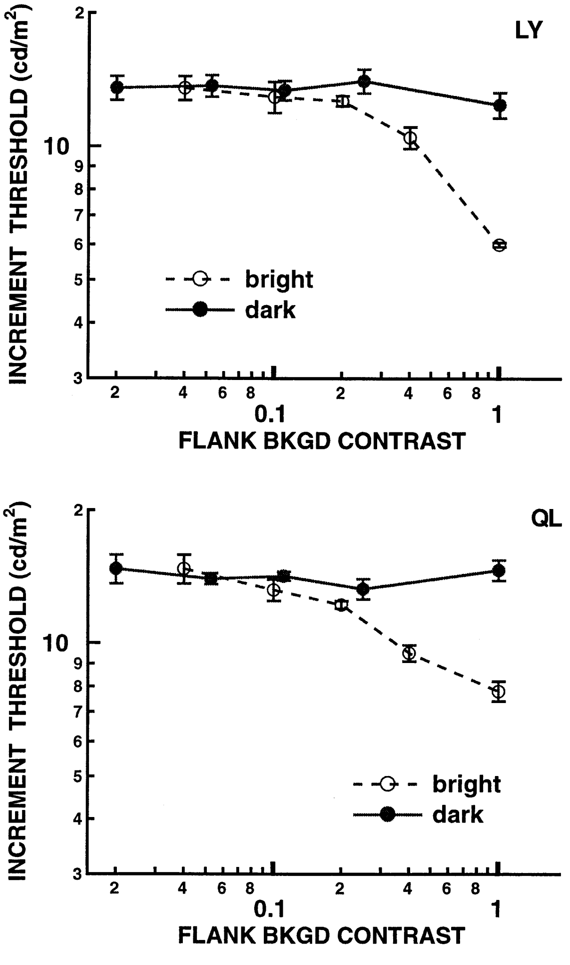

Fig. 6. Psychophysical flank-inhibition as a function of the contrast of flank background regions under the same and opposite polarity conditions.

4. Discussion

In this study we investigated the effects of background polarity reversal on the length and width Westheimer functions associated with line targets, as well as on the conventional Westheimer function associated with spot targets. Full-wave rectification was shown in psychophysical end-stopping, consistent with the property of rectification non-linearity of receptive field end-stopping. However, linear summation was not shown in central summation, nor was linear subtraction between antagonistic central summation and flank (surround) inhibition, as would have been predicted if the perceptive fields revealed by these Westheimer functions had directly mirrored the organization of single cell receptive fields. Instead the linear rules were only obeyed after a half-wave rectification process in the centers and flanks (surrounds) of perceptive fields. These results in general do not support the simple explanation that the Westheimer functions and the perceptive fields they suggest directly reflect the organization of cortical receptive fields. They however do provide further insights about the Westheimer function and its underlying neural mechanisms.

Our results of rectification nonlinearity preceding linear summation in the Westheimer functions are consistent with a second-order theory of the perceptive fields, in that outputs from individual first-order receptive fields are first rectified and then summed to form the second-order perceptive fields. Under stimulus conditions in which the whole background has the same polarity (bright) and excites one ON-center cell (in the

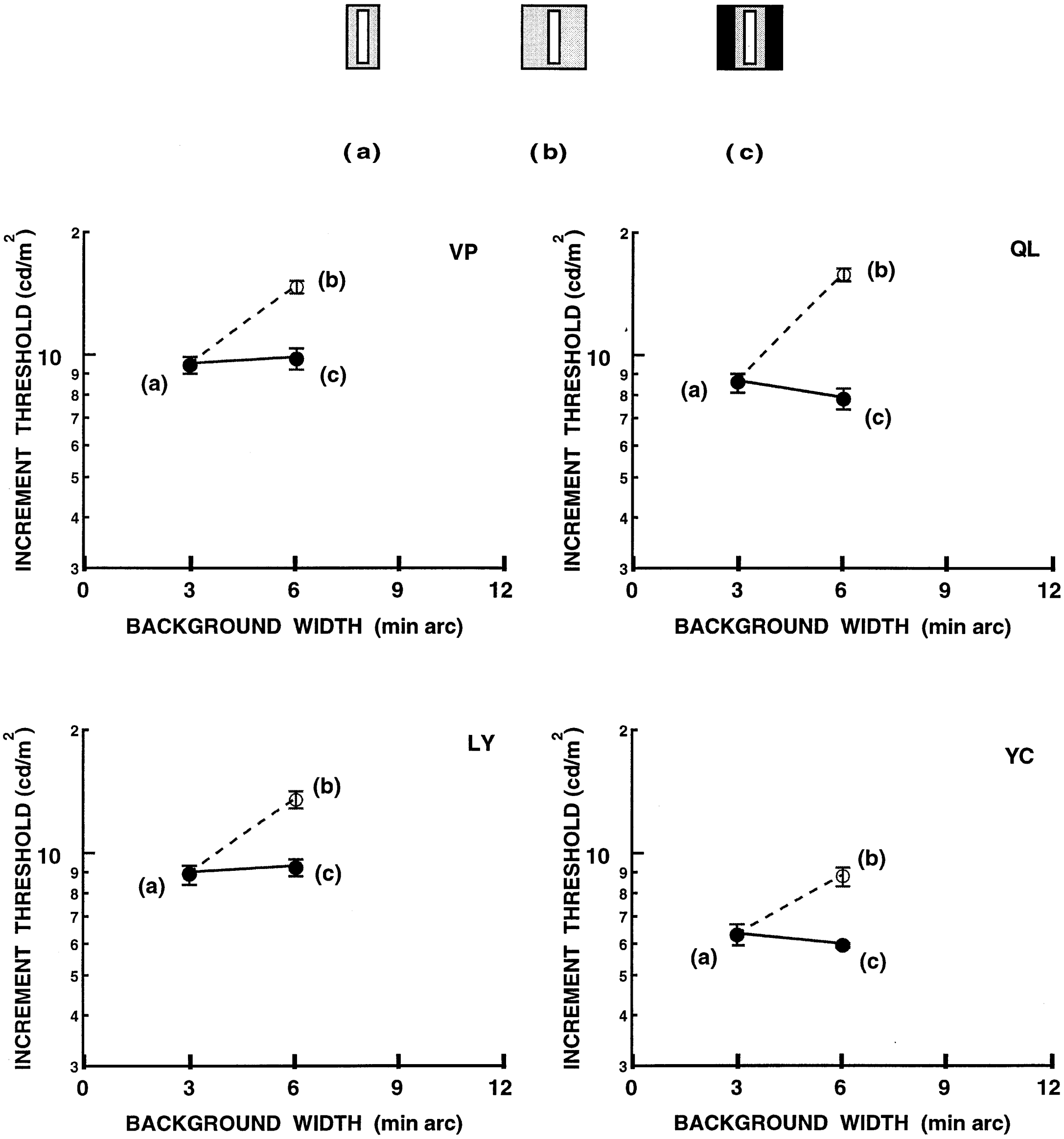

Fig. 7. The effects of polarity reversal on central width summation. The top row shows background conditions: (a) a 3′ wide background, (b) a 3′ wide background region flanked by two 1.5′ wide background regions of the same sign (actually a 6′ wide background covering maximal central width summation), (c) a 3′ wide background subregion flanked by two 1.5′ wide background regions of the opposite sign. The bottom two rows show the polarity effects on central width summation, which indicate half-wave rectification as in central length summation. (Fig. 3).

simplest case), the second-order perceptive field receives the inputs from first-order cells which are unchanged through the rectification stage. Therefore the responses of the second-order perceptive field are not different from those of the first-order receptive field and form a regular Westheimer function. However, when a bright background region is flanked by two dark regions, one ON-center cell and two-OFF center cells would be excited. These outputs are then half-wave rectified so that OFF signals are discounted and only ON signals remain. The effective inputs to the second-order perceptive field are equal to those from the bright-region-only condition, which could explain the nearly equal thresholds between conditions (a) and (c) in Fig. 3, (b) and (d) in Fig. 4, etc. This scheme of intermediate rectification nonlinearity in-between first-order single cells and second-order composite fields is similar to a number of models mentioned in the introduction which claim that the visual system doesn't have direct access to single cell based linear filters. Instead the outputs from these filters are normalized and combined to form non-Fourier second-order channels on which a great varieties of spatial vision tasks are based.

The full-wave rectification property of psychophysical end-stopping is consistent with our earlier finding in masking experiments which revealed that psychophysical end-stopping is not affected by phase change [6]. These results are consistent with the nonlinear property

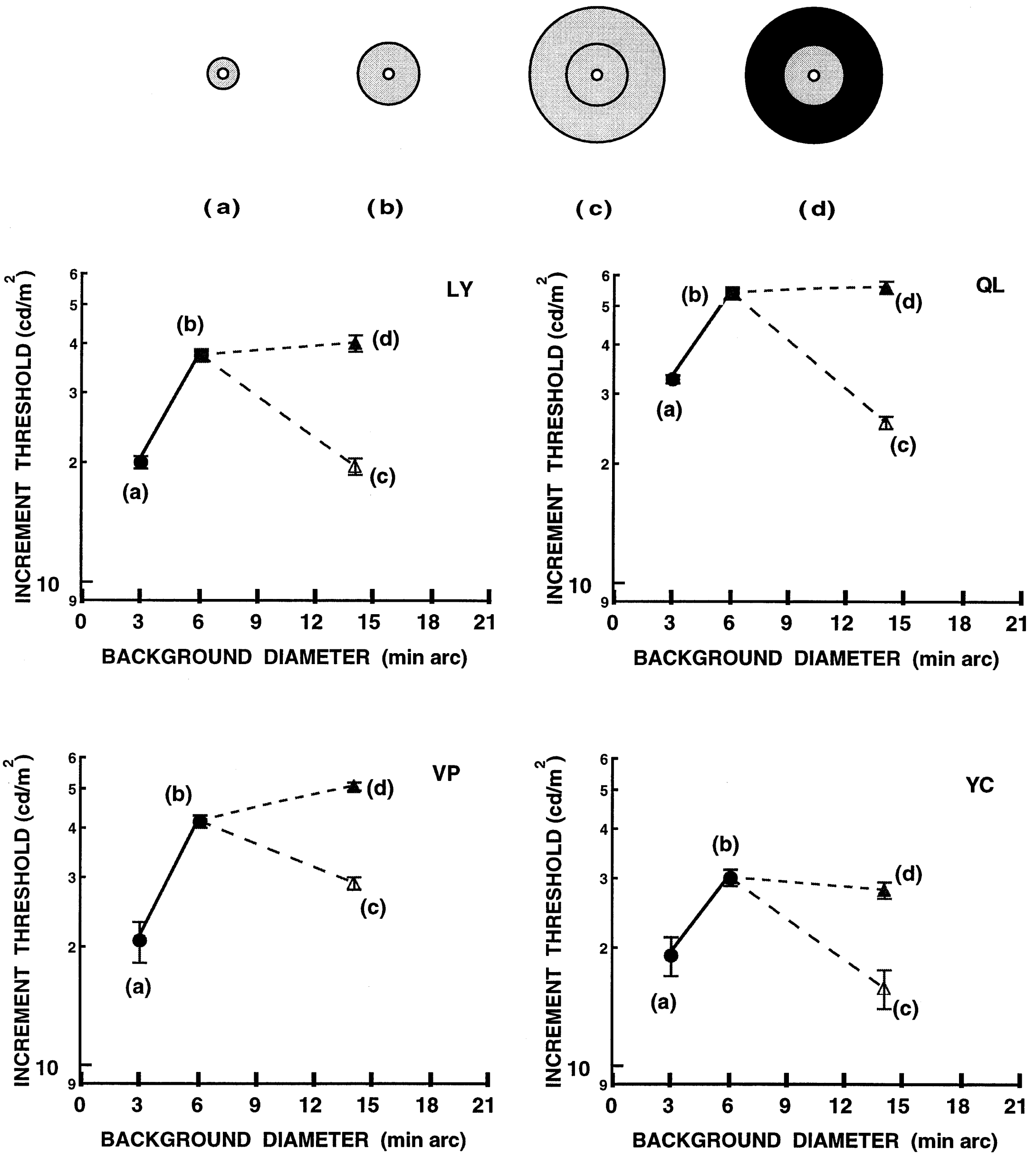

Fig. 8. The effects of polarity reversal on surround inhibition measured with the conventional Westheimer paradigm. The top row shows stimuli composed of a 1′ spot target centered on (a) a 3′-diameter background, (b) a 6′-diameter background covering maximal central summation, (c) a 6′-diameter background surrounded by a 4′ thick annulus of the same sign covering the inhibitory surround (actually a 14′ background), (d) a 6′-diameter background surrounded by a 4′ thick annulus of the opposite sign. The bottom two rows show the polarity effects on surround inhibition. No inhibition is shown under the opposite polarity conditions.

of receptive field end-stopping [7], providing further support for the link between psychophysical and receptive field end-stopping. The second-order nature of end-stopping in both single cells and perceptive fields indicates that it is not involved in the linear-nonlinear-linear process in the formation of second-order perceptive fields. Instead perceptive fields may receive direct inputs from high order visual neurons which form perceptive field end-stopping, and it is likely that there are feedback routes of end-stopping from second-order perceptive fields to first-order single cells. These possibilities are consistent with physiological evidence for intracortical feedback in the generation of end-stopping [17,18,20], which is independent of the generation of other receptive field properties [19].

Recently Makous [25] suggested that the Westheimer function measured with circular stimuli could be explained by considering the Fourier spectra of the stimuli at different background sizes, and that a theory of center-surround antagonism might not be necessary. For a 1′ spot target which has nearly equal amplitude at all spatial frequencies, increasing background diameter until 6′ increases the amplitude at all frequencies within the sensitive range, resulting in stronger masking at all

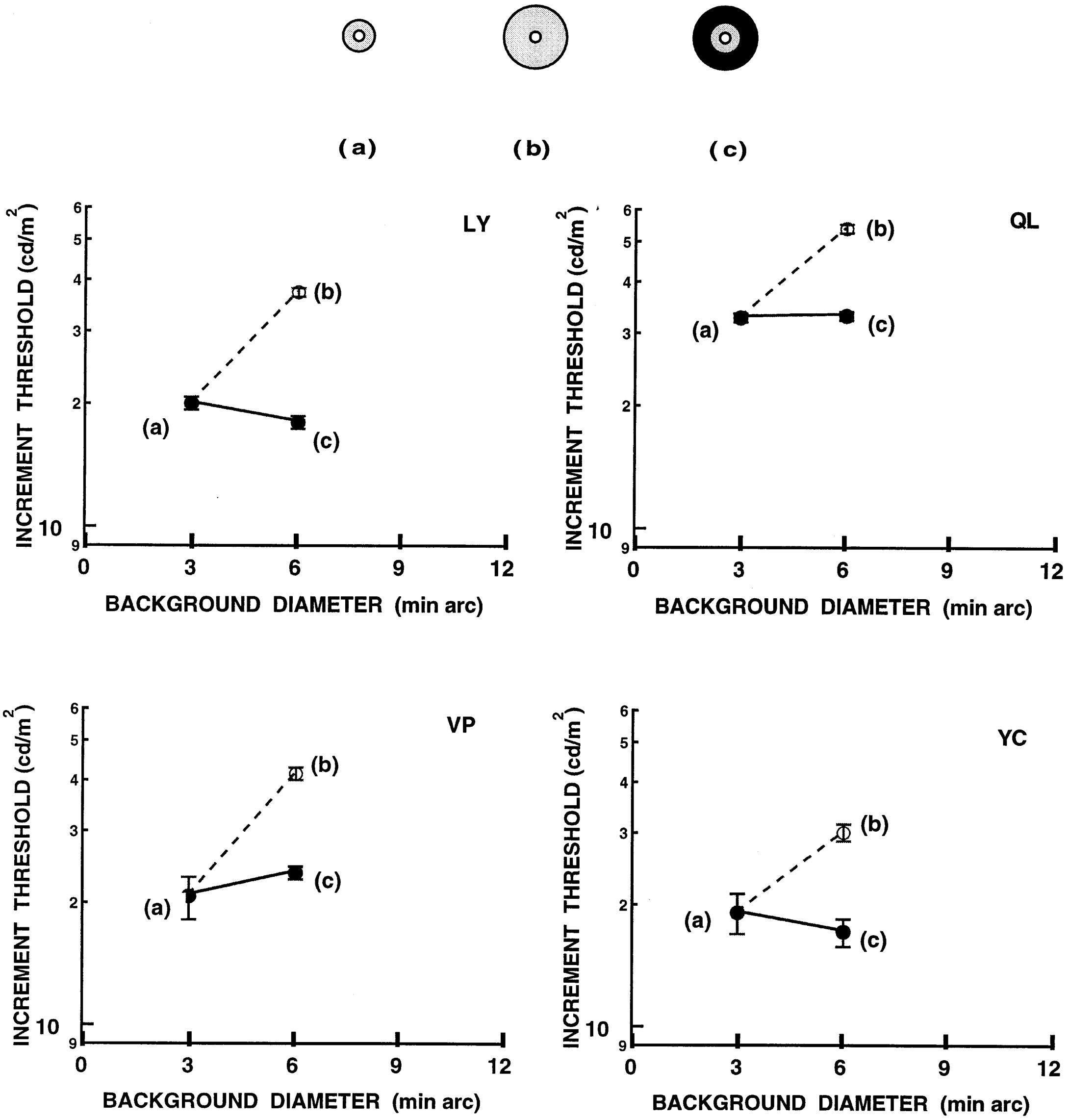

Fig. 9. The effects of polarity reversal on central summation measured with the conventional Westheimer paradigm. The top row shows background conditions: (a) a 3′-diameter background, (b) a 3′-diameter background added with a 1.5′ thick ring of the same sign, (c) a 3′-diameter background added with a 1.5′ thick ring of the opposite sign. The bottom two rows show the effects of polarity reversal on central summation, which are similar to those on central length and width summation (Figs. 3 and 7).

frequencies (desensitization). However, the Fourier spectra of larger backgrounds always have a dip within the sensitive range. The Fourier components of the target at these dips are not masked by the background, which leads to easy detection and sensitization. We wondered whether Makous's (linear) analysis could account for the length and width Westheimer functions and the related polarity reversal results. Fig. 10(a) shows the Fourier spectra of a 5′ long target line, a 6′ long background (condition (a) in Fig. 1), and an 11′ long background (condition (b) in Fig. 1) in the length dimension. The 11′ long background produced peak thresholds in our experiments (Fig. 1). However, Fig. 10(a) shows a dip between 5 to 6 cpd for the 11′ long background, which should have caused sensitization instead of desensitization as compared to the 6′ long background. Thus, the length Westheimer function is not simply explained on the basis of the Fourier spectrum changes. For the width Westheimer function, Fourier spectra in the width dimension of a 1′ wide target line, a 3′ width background (condition (a) in Fig. 4), a 6′ wide background (condition (b) in Fig. 4), and a 14′ wide background (condition(c) in Fig. 4) are plotted in Fig. 10(b). Though desensitization by a narrow background (3′) and sensitization by a wide background (14′) are predicted by Fourier spectra, the 6′ wide background is predicted to cause sensitization and might have no difference from the 14′ background, since it has a dip at 10 cpd, to which the visual system is surely sensitive. The peak of the width function

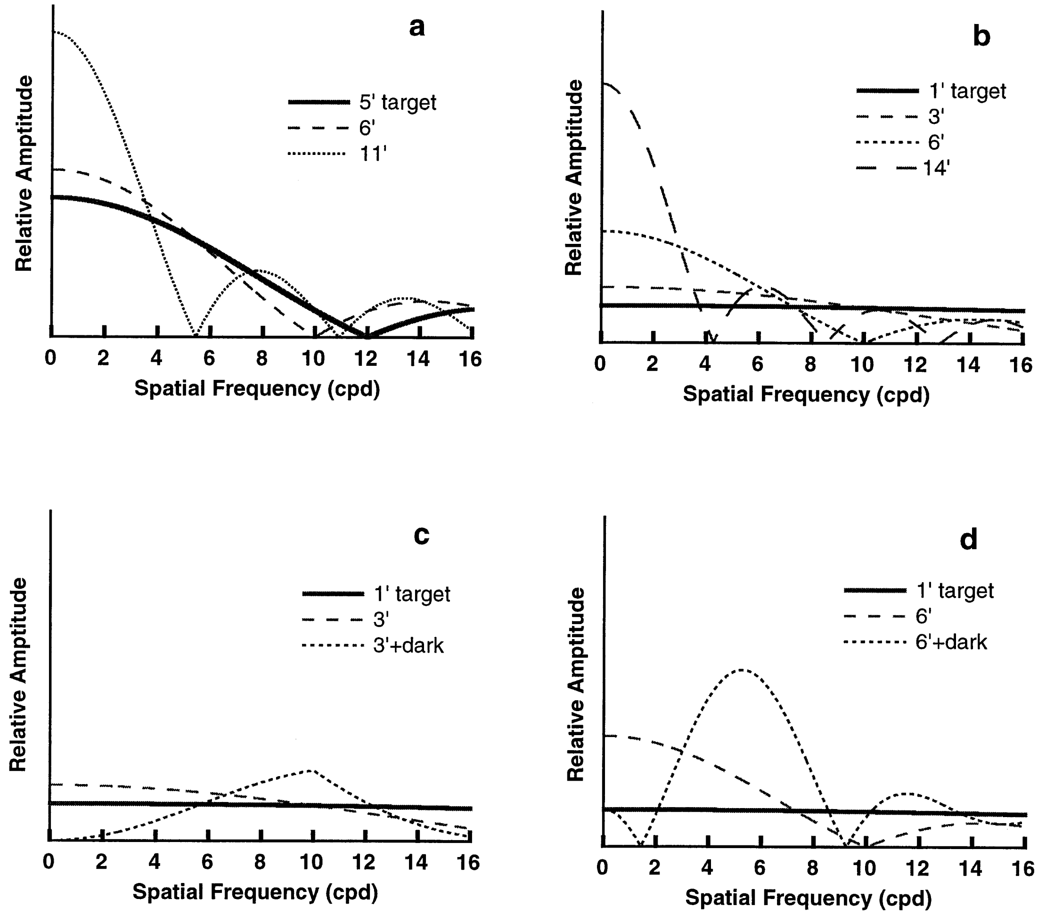

Fig. 10. Fourier spectra for a variety of background conditions. (a). Fourier spectra of a 5′ long target line, a 6′ long background, and an 11′ long background in the length dimension. (b). Fourier spectra of a 1′ wide target line, a 3′ width background, a 6′ wide background, and a 14′ wide background in the width dimension. (c). Fourier spectra of a 1′ wide target line, a 3′ wide background, and a 3′ wide region flanked by two 1.5′ dark regions. (d). Fourier spectra of a 1′ wide target line, a 6′ wide background, and a 6′ wide region flanked by two 4′ dark regions.

would be predicted to occur at a background width of about 4.5′. These predictions don't meet with the experimental data, suggesting that the change in the Fourier spectra is not responsible for the threshold change in the width Westheimer function either.

We also studied whether the change in the Fourier spectrum could account for the polarity reversal results. When the polarity of part of the background region is reversed, such as in Figs. 4 and 7, the background changes from lowpass to bandpass. Fig. 10(c) gives the Fourier spectra of a 1′ wide target line, a 3′ wide background (condition (a) in Fig. 7), and a 3′ wide region flanked by two 1.5′ dark regions (condition (c) in Fig. 7). Fig. 10(d) gives the Fourier spectra of a 1′ wide target line, a 6′ wide background (condition (b) in Fig. 4), and a 6′ wide region flanked by two 4′ dark regions (condition (d) in Fig. 4). Fig. 10(c) predicts lower thresholds when dark flanks are added to a 3′ wide background, because this composite stimulus losses its energy at low spatial frequencies as compared to the 3′ wide background only condition. In contrast to this prediction, our results show basically unchanged thresholds (Fig. 7). In Fig. 10(d), both background conditions have a dip at 9–10 cpd, thus the target at both background conditions should be easily detected. An additional low spatial frequency dip when two dark flanks are added would have made the threshold even lower. However, none of these linear system predictions are met by our results. It appears in general that additional Fourier cues due to the loss of energy at low spatial frequencies for bandpass background with added dark flanks are not helpful in reducing detection thresholds. This should also hold for results from polarity reversal experiment using circular stimuli (Figs. 8 and 9).

The above analyses suggest that a simple linear (Fourier) approach cannot easily explain all the complexities of the Westheimer function, which is further complicated by many distinct properties of psychophysical end-stopping. Our results are in general consistent with the center-surround antagonism theory in explaining this classic phenomenon, though the perceptive fields and accompanied center-surround antagonisms appear to be at a later stage of visual processing (second-order processing).

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