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Spatial Scaling of End-stopped Perceptive Fields: Differences in Neural Bases of End-zones, Flanks and Centers

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Length and width spatial interactions associated with a small test line centered on a rectangular background were measured at 0, 5 and 10 deg retinal eccentricities. Results indicated an elongated central region of summation with antagonistic flanks and end-zones comparable to earlier results [Yu, C. & Essock, E. A. (1996). *Vision Research 36*, 2883-2896]. The extent of the end-zones, flanks and centers (length and width) exhibited significantly different spatial scaling, which was steepest for the end-zones (£$_2$ = 0.45 deg), less steep for the flanks (*E*$_2$ = 0.77 deg) and least steep for the centers (*E*$_2$ = 2.05 deg). Perceptive fields measured with concentric circular stimuli showed center and surround scaling equivalent to center and flank scaling, respectively, in line target experiments. These results suggest that: (1) psychophysical end-stopping and flank-inhibition reflect different underlying cortical neural processes; and (2) the spatial interactions apparent on the conventional Westheimer paradigm are partly governed by cortical factors. Copyright © 1996 Elsevier Science Ltd.

End-stopping Flank-inhibition Perceptive field Spatial scaling Westheimer paradigm

INTRODUCTION

Simple, complex and hypercomplex cells were first distinguished by Hubel and Wiesel (1962,1965,1968) in cat and monkey striate cortex. Subsequent studies (e.g. Dreher, 1972; Schiller *et al.*, 1976; Gilbert, 1977; Murphy & Sillito, 1987) showed that end-stopping, the defining characteristic of hypercomplex cells, is present also in many simple and complex cells. Hypercomplex cells are now viewed as subsets of simple and complex cells and are referred to as end-stopped or end-inhibited cells (e.g. Bolz & Gilbert, 1986; Murphy & Sillito, 1987). A typical end-stopped simple cell receptive field includes both inhibitory flanks and end-zones and is thus not only phase-sensitive, but also length-tuned.

Psychophysical end-stopping and flank-inhibition associated with line targets were demonstrated in increment threshold tasks with a modified Westheimer paradigm (Essock & Krebs, 1992; Essock *et al.*, 1997; Yu & Essock, 1993,1996). For a small target line centered on a rectangular background, the detection threshold is first elevated, then lowered, as the background size is increased in either width or length. This classic pattern of desensitization followed by sensitization is taken to reflect local spatial interactions corresponding to a central region of summation surrounded by a region of antagonistic influence (Westheimer, 1965, 1967). Thus, with a line target, the desensitization and sensitization branches of the function obtained under the variable-length condition suggest central length summation and end-stopping, respectively, and those obtained under the variable-width condition suggest central width summation and flank-inhibition, respectively. Taken together, these end-zone, flank and central summation regions form an elongated end-stopped perceptive field which resembles a typical end-stopped simple cell receptive field. We have proposed that cortical end-stopped receptive fields may be the neural basis of these psychophysical expressions (Yu & Essock, 1996). This assumption is supported by the oblique effect of stronger psychophysical flank-inhibition (Essock & Krebs, 1992; Essock *et al*, 1997) and end-stopping (Yu & Essock, 1996) observed at horizontal or vertical target orientations. This orientation bias suggests the involvement of cortical mechanisms (Mansfield, 1974; Essock, 1980).

In this psychophysical paradigm, end-stopping and flank-inhibition are functionally comparable, differing only in the locations (end-zones or sides) where they occur. On the other hand, compared to flank antagonism, receptive field end-stopping has been shown to be

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generated by distinct neural circuits, such as intracortical inhibition from cells with spatially offset receptive fields (e.g. Hubel & Wiesel, 1965; Bolz & Gilbert, 1986). Bolz and Gilbert (1986) demonstrated the disassociation of end-zone and flank-inhibition by pharmacologically abolishing end-inhibition while preserving flank properties. Accordingly, if psychophysical end-stopping and flank-inhibition are truly the behavioral expressions of receptive field properties, they would have different underlying neural mechanisms and therefore might exhibit distinct features under appropriate psychophysical test circumstances. Thus, the psychophysical disassociation of end-stopping from flank-inhibition, as well as from central summation, would be an important criterion to evaluate the validity of our assumption.

Measuring the scale change of the extent of a spatial property across various retinal eccentricities can provide information about whether the processing is limited by retinal or cortical factors (Levi *et al.,* 1985; Wilson *et al.,* 1990; Drasdo, 1991). This spatial scaling is often characterized by the value E_2 defined by $F = 1 + E/E_2$, where F is the scaling factor indicating how a spatial property or performance varies, E is the retinal eccentricity, and E_2 is the eccentricity at which the measured value is equal to twice the foveal value. Levi *et al* (1985) and Wilson *et al* (1990) suggested that the spatial scaling across eccentricity of a variety of visual tasks falls into two categories. Spatial scaling functions for tasks such as hyperacuity and spatial interaction have an E_2 value in the range 0.3—0.9 deg, which matches the E_2 values of cortical magnification in human (Cowey & Rolls, 1974) and monkey (Dow *et al.,* 1981). It is assumed that spatial abilities having E_2 values comparable to that for cortical magnification *(c.* 0.8 deg) are limited by cortical factors (e.g. Wilson *et al,* 1990). On

monitor. The resolution of the monitor was 1024 x 512 pixels. Pixel size was 0.28 mm horizontal x 0.41 mm vertical. The frame rate was 117 Hz. Luminance of the monitor was made linear by means of an eight-bit look-up table (LUT). Viewing distance was varied for testing at the three retinal eccentricities to fit both fixation cross and stimuli on the screen, yet maximize the resolution of stimuli. Subjects were positioned by means of a chin rest at 5.64 m from the screen for foveal viewing, half of the foveal viewing distance (2.82 m) for 5 deg retinal eccentricity viewing and a quarter of the foveal distance (1.41 m) for 10 deg retinal eccentricity viewing. Viewing was monocular by the dominant eye (right eyes for both subjects) with a white translucent diffuser positioned before the other eye.

An increment test field and a background field were presented on the center of the monitor screen for foveal viewing or at the 5 deg and 10 deg retinal eccentricities on the temporal side of the horizontal meridian in the visual field for peripheral viewing. The test field was a target line centered on a rectangular background. In a given experiment, only one dimension (e.g. length or width) of the background field was varied and the other dimension was fixed. The sides of the rectangular background were parallel to the sides of the target line in all experiments. The test line and background were oriented vertically, except as noted below. The luminance of the monitor screen was constant (6.85 cd/m^2) throughout all experiments, as was the luminance of the rectangular background (30 cd/m^2). The luminance of the target line was varied by a staircase procedure as the dependent measure. Additional details are given in corresponding sections.

Procedure

A successive two-alternative forced-choice (2AFC) procedure was used. The background was presented in each of the two intervals (1.1 sec each). In one of the two intervals, the target line was also presented, starting 420 msec after the onset of the background, lasting for 420 msec, and disappearing 260 msec before the background offset. There was no interruption between two intervals. In foveal viewing each trial was preceded by a fixation cross which disappeared 100 msec before the beginning of the trial. For peripheral viewing, the fixation cross was present throughout testing. Intervals were marked by tones with different frequencies. Another tone gave feedback on incorrect responses.

Each staircase consisted of four "practice" reversals and six experimental reversals. Each correct response lowered test field luminance by one step and each incorrect response raised test luminance by three steps. Step size was 3.6 cd/m^2 at the first pair of practice reversals and 1.8 cd/m^2 at the second pair. It was 0.6 cd/m^2 throughout the experimental phase. The mean of six experimental reversals was used to estimate the increment threshold which was defined as the difference of target luminance at threshold and background luminance on a log scale [log ($\Delta L + L$) - log$L$].

Besides the practice at the beginning of the study, each observer also had two to three sessions of practice before each peripheral experiment. One experimental session usually consisted of 9-13 background conditions presented in a random order and lasted for 50 to 60 min. Each data point was the mean of the thresholds from five to six replication sessions, and the error bars represent ± 1 SEM.

EXPERIMENT 1: MEASUREMENT OF LOCAL SCALING FACTORS

Since visual spatial sensitivity declines with increasing retinal eccentricity due to reduced neural sampling (e.g. Rovamo & Virsu, 1979), it was desirable to equate the visibility of peripheral and foveal targets before we compared the perceptive fields at different retinal eccentricities. It has been shown also that spatial processing can be homogeneous across the visual field if the stimuli are appropriately scaled (Rovamo *et al.*, 1978; Koenderink *et al.*, 1978). Although estimating the scaling

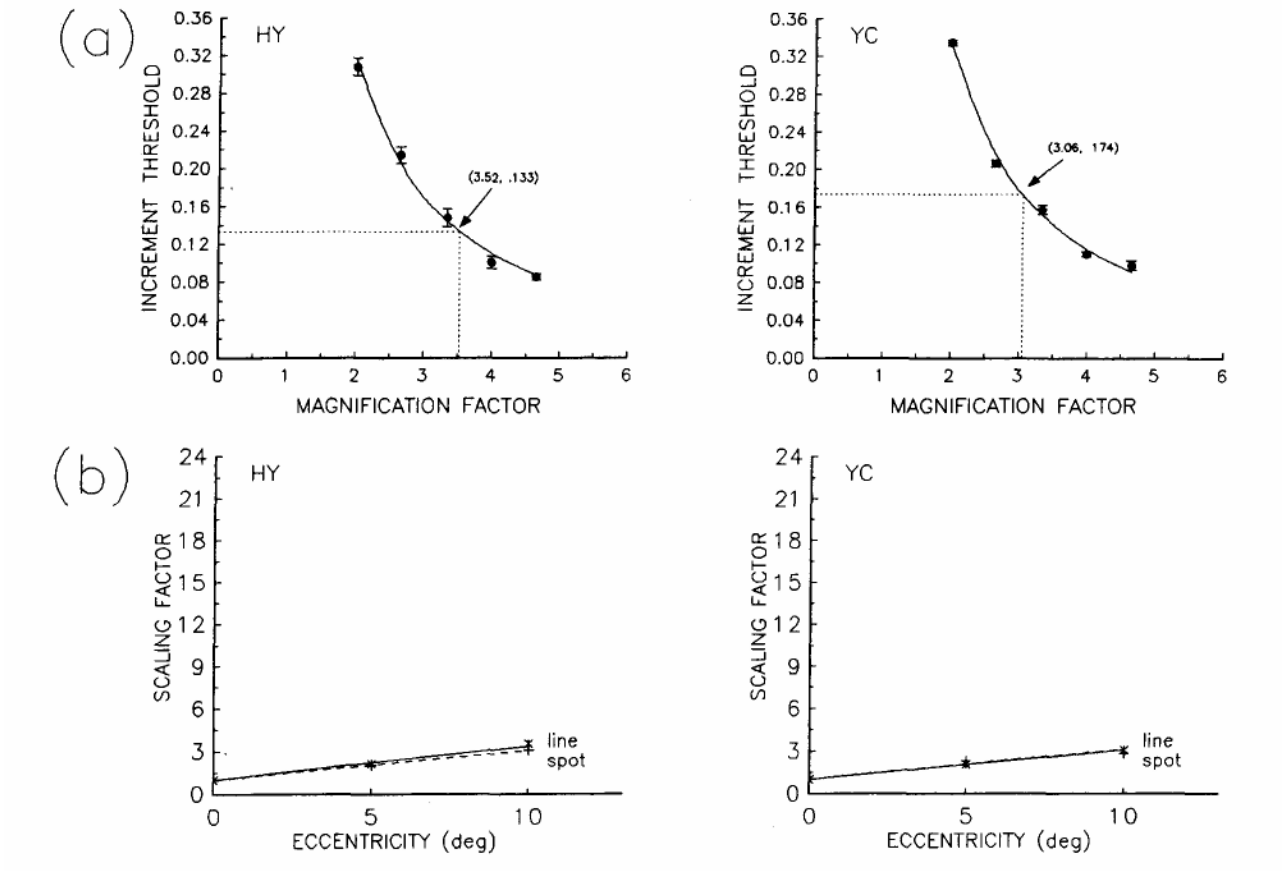

FIGURE 1. Local scaling factors used to magnify the sizes of peripheral stimuli for equal retinal sampling across retinal eccentricity, (a) An example of data fitting and local scaling factor derivation. Data were measured at the 10 deg retinal eccentricit y for the line target. The raw data (filled circles) are first fitted by an exponential equation (see text). The fitted data (solid curve) are then matched with foveal threshold (indicated by the dotted horizontal line). The *x* value of the intersection point of the dotted horizontal line (foveal threshold) and solid curve (fitted data) is taken as the local scaling factor (indicated by the dotted vertical line), (b) Local scaling factors [as obtained in (a)] plotted as a function of the retinal eccentricity. Least-squares regression lines are plotted for line-only (x) and spot-only (+) targets.

scaling factors. Examples of this procedure are shown in Fig. l(a). The E_2 values in this and later experiments were calculated from the equation $F = 1 + E/E_2$ given earlier. As seen from this function, E_2 is actually the inverse of the slope of the eccentricity function, and thus is independent of any specific eccentricity. Local scaling factors plotted as a function of retinal eccentricity are shown in Fig. l(b). For subject HY, the local scaling factor for the line target is 2.11 (E_2 = 4.51 deg) at the 5 deg retinal eccentricity and 3.52 (E_2 = 3.97 deg) at the 10 deg retinal eccentricity, and for the spot target is 2.02 (E_2 = 4.90 deg) at the 5deg retinal eccentricity and 3.06 (E_2 = 4.85 deg) at the 10 deg retinal eccentricity. For subject YC, the local scaling factor for the line target is 2.06 (E_2 = 4.72 deg) at the 5 deg retinal eccentricity and 3.06 (E_2 = 4.85 deg) at the 10 deg retinal eccentricity, and for the spot target is 2.32 (E_2 = 3.79 deg) at the 5 deg retinal eccentricity and 2.82 (E_2 = 5.49 deg) at the 10 deg retinal eccentricity. As Fig. l(b) indicates, each subject's spatial scaling functions for line and spot targets are linear and essentially identical. The E_2 values from the two subjects fall into a range 3.79-5.49 deg, with an overall mean value of 4.64 deg (the overall slope of the psychometric functions is about 0.22). These E_2 values are about equal to Watson's (1987) estimation of local spatial scale in a contrast sensitivity function measurement using a similar procedure (E_2 = 4.17 deg, recalculated from Watson, 1987).

EXPERIMENT 2: LENGTH SUMMATION AND END-STOPPING ACROSS RETINAL ECCENTRICITY

Length summation and end-stopping were measured first at the 0 deg retinal eccentricity for a 1 x 5' line superimposed on a 3'-wide rectangular background of various lengths. This was a replication of an earlier experiment (Experiment 2, Yu & Essock, 1996) and served as the baseline for later 5 and 10 deg retinal eccentricity length experiments. Because data collected from seven subjects in the earlier measurement had been very consistent, only five-six critical background length conditions were selected. Increment threshold as a function of background length is shown in Fig. 2(a). The length of central summation region (i.e. background length at which the peak threshold occurs) is about 11'

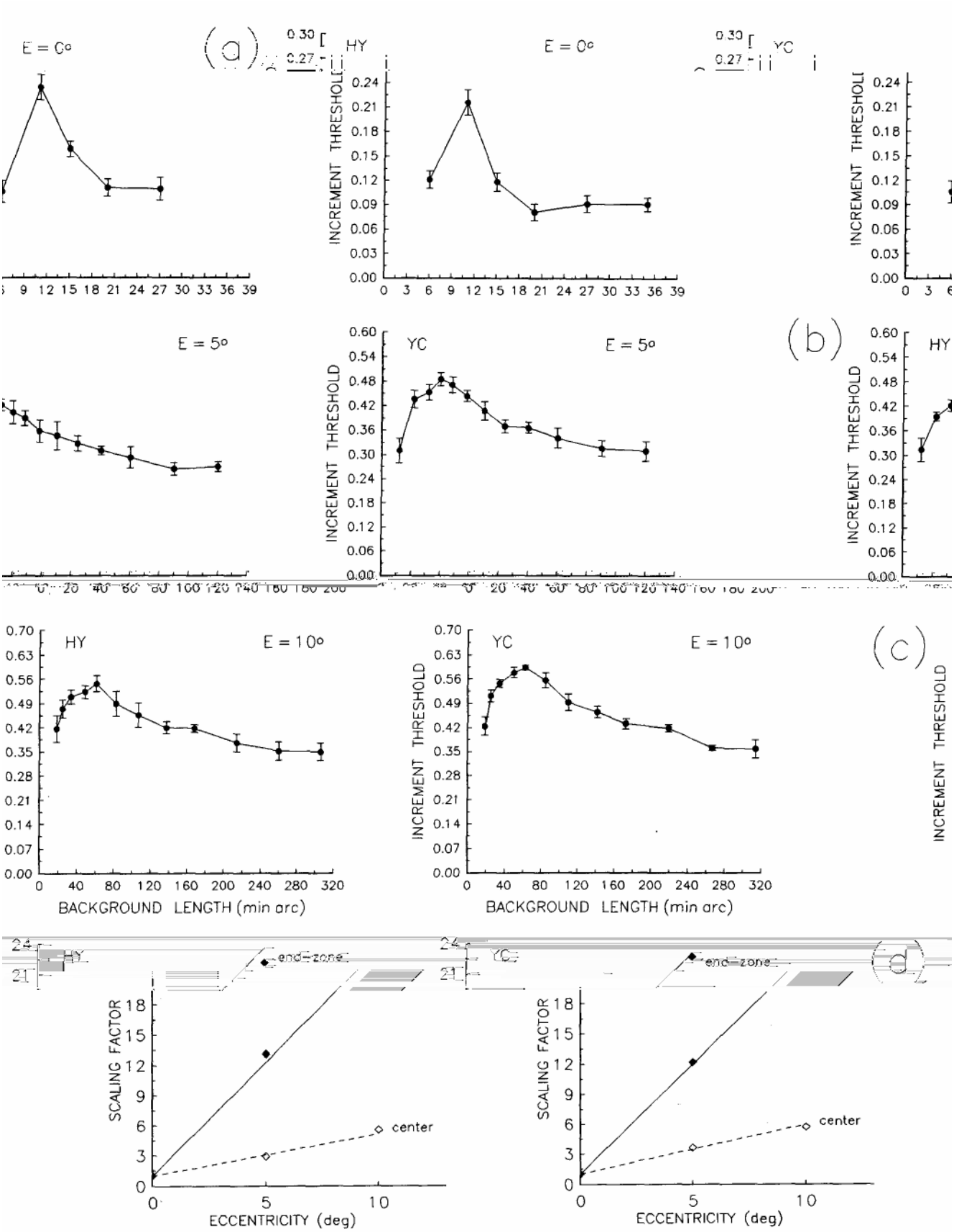

FIGURE 2. (a)-(c) Increment threshold plotted as a function of the length of the background field at 0, 5 and 10 deg retinal eccentricities. The rising portion of the function is taken to reflect length summation, and the declining portion reflects end-stopping. Note the scale of* and *y* abscissas are different among figures (also in Figs 3 and 4). (d) Spatial scaling factors (ratio of peripheral data: foveal data) for the lengths of the center region and end-zone region of the perceptive field plotted as a function of the retinal eccentricity.

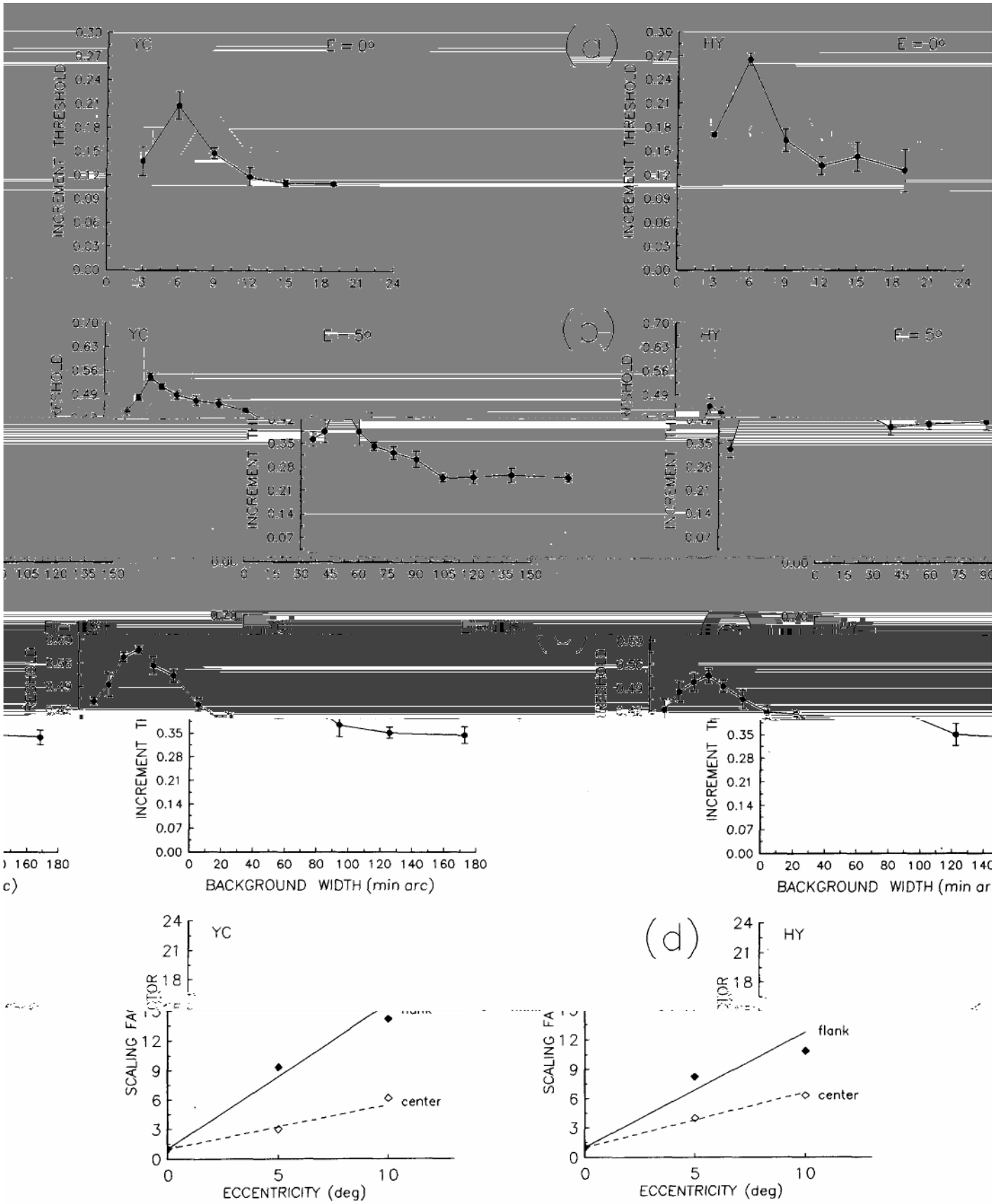

FIGURE 3. Spatial interaction functions and spatial scaling functions for a background of variable width plotted as in Fig. 2 for variable-length background. (a)-(c) Width summation and flank-inhibition at 0, 5 and 10 deg retinal eccentricities, (d) Spatial scaling factors for the width of the flank region and center region of the perceptive field plotted as a function of the retinal eccentricity.

long, and the length of the end-stopping region (half of the peak-to-plateau distance in terms of background length)* is about 4.5' long, respectively, for the two subjects. These data are comparable to those reported in earlier measurements (Yu & Essock, 1996).

This test was then performed at the 5 and 10 deg retinal eccentricities. For each subject, the width and length of the target line and the width of the rectangular background were magnified by his/her corresponding local scaling factors of the line target determined in Experiment 1. Therefore, the stimulus configuration at the 5 deg eccentricity was a 2.11 x 10.55' line centered on a 6.33' wide background for HY and a 2.06 x 10.3' line centered on a 6.18' wide background for YC. At the 10 deg retinal eccentricity, it was a 3.52 x 17.60' line on a 10.56' wide background for HY and a 3.06 x 15.30' line on a 9.18' wide background for YC. Data collected at the 5 deg retinal eccentricity are plotted in Fig. 2(b). The length of the central summation region is 32' *(F* = 2.91, E_2 = 2.62 deg) for HY and 40' *(F* = 3.64, E_2 = 1.90 deg) for YC (where *F is* the ratio of peripheral data to foveal data and E_2 is calculated from *F* based on the equation $F = 1 + El E_2$). The length of the end-stopping region is 59' (/"= 13.11, E_2 = 0.41 deg) for HY and 55' *(F = 12.22,* E_2 = 0.45 deg) for YC. Data collected at the 10 deg retinal eccentricity are plotted in Fig. 2(c). The length of the central summation region is 61' *(F* = 5.55, E_2 = 2.20 deg) for HY and 63' *(F* = 5.73, E_2 = 2.12 deg) for YC. The length of the end-stopping region is 100' *(F* = 22.11, E_2 = 0.47 deg) for HY and 102' *(F = 22.67,* E_2 = 0.46 deg) for YC.

retinal eccentricity. Both subjects' data show the same trend. Spatial scaling factors for the end-zone and center both increase linearly 10.5 Tf -0.1665 Tc -0.2085 m subjects' data show, bu TD 0Tj ET 1 1 1 rg 51.75 372.75 243 11.25

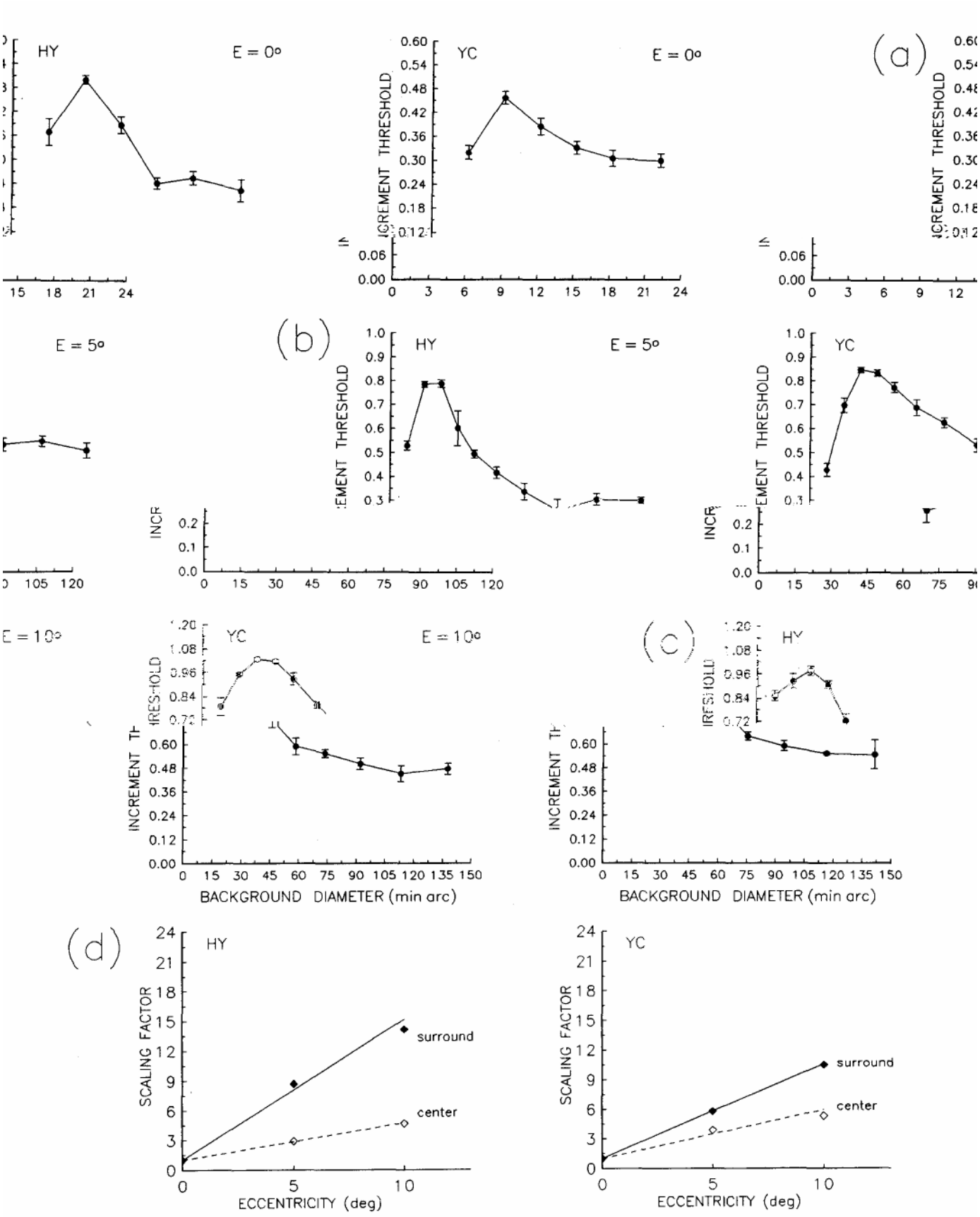

FIGURE 4. Spatial interaction functions and spatial scaling functions obtained for a circular spot target centered on a circular background of variable diameter. (a)-(c) Center/surround spatial interactions at 0,5 and 10 deg retinal eccentricities, (d) Spatial scaling factors for the sizes of center and surround region of the perceptive field plotted as a function of the retinal eccentricity.

relation of psychophysical spatial interactions and retinal ganglion cell receptive field properties. Several experiments measured the spatial interactions at different retinal eccentricities (Westheimer, 1967; Enoch, 1978; Spillmann *et al.*, 1987). Westheimer (1967) measured the spatial scaling of only the center of the perceptive field and found it to be about the same as the spatial scaling of resolution acuity. However, in his measurement the spot target was not magnified to equate its effective size at each retinal eccentricity, which may have resulted in retinal under-sampling and made the data less accurate. Spillmann *et al.* (1987) reported the spatial scaling of perceptive fields in both human and monkey. They found that sizes of the center and surround both increase with retinal eccentricity, and that the slope of the surround function is steeper.

In this experiment, we first measured central summation and surround antagonism at the 0 deg retinal eccentricity for a 1'-diameter spot centered on a circular background. Results are shown in Fig. 4(a). The diameter of the summation center (background diameter at which peak threshold occurs) and inhibitory surround on each side (half of the peak-to-plateau distance in terms of background diameter) are about 6 and 3', respectively, for HY, and 6 and 4', respectively, for YC* The same functions were then measured at the 5 and 10 deg retinal eccentricities. For each subject, the diameter of the spot target was magnified by his/her local scaling factor of the spot target (Experiment 1). This factor was 2.02' for HY and 2.32' for YC at the 5 deg retinal eccentricity and 3.06' for HY and 2.82' for YC at the 10 deg retinal eccentricity. Data collected at the 5 deg retinal eccentricity are plotted in Fig. 4(b). The size of the central summation region is 17' in diameter (F = 2.90, E_2 = 2.63 deg) for HY and 23' (F = 3.87, E_2 = 1.74 deg) for YC. The size of the surround-inhibition region is 26' (F = 8.70, E_2 = 0.65 deg) for YC. Data collected at the 10 deg retinal eccentricity are plotted in Fig. 4(c). The size of the central summation region is 28' in diameter (F = 4.67, E_2 = 2.73 deg) for HY and 32' (F = 5.33, E_2 = 2.31 deg) for YC. The size of the surround-inhibition region is 43' (F=14.17, E_2 = 0.76 deg) for HY and 42' (F = 10.50, E_2 = 1.05 deg) for YC.

Figure 4(d) plots the scaling factors as a function of retinal eccentricity. It shows that the spatial scaling factors for the surround and the center both increase linearly with retinal eccentricity, and that the surround function is steeper than the center function. The average E_2 value is 2.35 deg for center functions (slope = 0.43) and 0.88 deg for surround functions (slope = 1.14). The general trend of spatial scaling is comparable to Spillmann and colleagues' human and monkey data, which also showed steeper scaling in the surround function.

*To be consistent with the values reported for rectilinear stimuli in Experiments 2 and 3, these values are reported as the full width (diameter) of the center and the extent of the surround on one side (i.e. the "thickness" of an annulus).

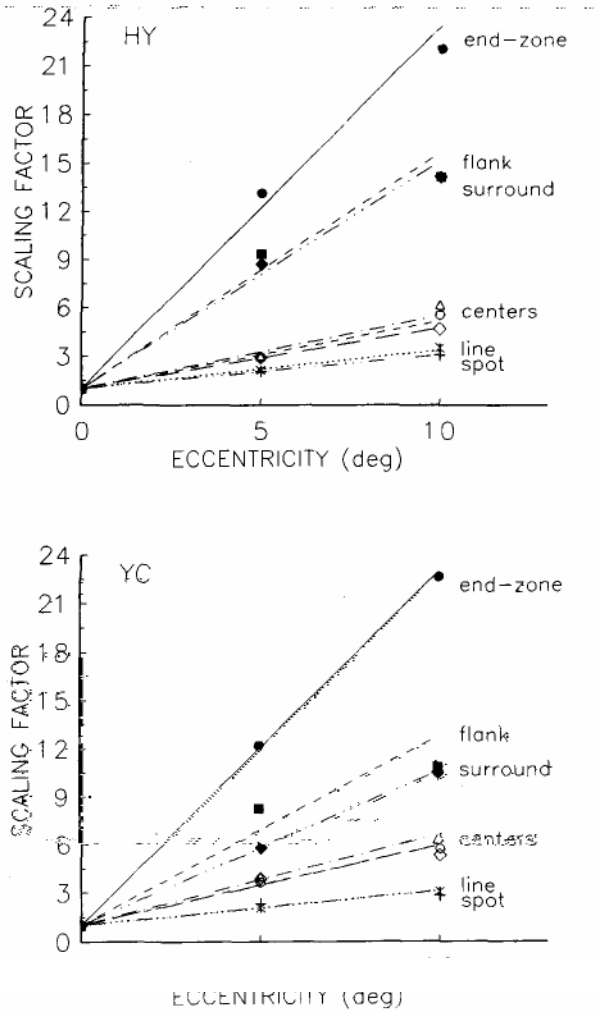

FIGURE 5. Summary of spatial scaling functions in each experiment replotted from earlier figures [Figs l(b), 2(d), 3(d) and 4(d)]. The scaling functions fall into four groups: (1) end-zone scaling (filled circles); (2) antagonistic flank regions for a line target (filled squares) and antagonistic surround for a spot target (filled diamonds); (3) width (triangles) and length (circles) of center region for a line target and diameter (diamonds) of center region for a spot target; and (4) local scaling factors for line (x) and spot (+) targets.

GENERAL DISCUSSION

In this study, the spatial scaling of spatial interactions was measured for elongated and circular perceptive fields across retinal eccentricity. Scaling for components of elongated perceptive fields (center width, center length, flank width and end-zone length) and components of centeraend

category, with equivalent scaling for length and width of elongated centers, and for diameter of circular centers. Center scaling is close to, but consistently steeper than, local scaling functions for increment threshold of line or spot stimuli (i.e. targets with no background present). These line and spot local scaling functions are identical to each other, the least steep, and form the fourth category.

Both the psychophysical end-stopping and flank-inhibition are most likely limited by cortical factors. The E_2 values of 0.45 deg for end-stopping and 0.77 deg for flank-inhibition fall squarely into the 0.3-0.9 deg range (Levi *et al.*, 1985; Wilson *et al.*, 1990), corresponding to human cortical magnification, and cannot be explained by the much slower increase of cone and ganglion cell spacing across eccentricity. That these inhibitory processes reflect cortical organization is also supported by the earlier demonstrations of orientation anisotropies in end-stopping (Yu & Essock, 1996) and flank-inhibition (Essock & Krebs, 1992; Essock *et al.*, 1997). In addition, the large scaling difference between psychophysical end-stopping (E_2 = 0.45 deg, slope = 2.23) and flank-inhibition (E_2 = 0.77 deg, slope = 1.31) indicates that these two types of antagonism may themselves be based on different cortical mechanisms, a conclusion consistent with the neurophysiological differences between receptive field end-zones and flanks (see Introduction section), and further supported by more recent evidence that psychophysical end-stopping is more severely impaired than flank-inhibition in amblyopic eyes (Yu & Levi, 1996). Thus, we conclude that psychophysical end-stopping and flank-inhibition reflect two different types of cortical inhibitory processes which appear to be receptive field end-stopping and flank-inhibition. The scaling difference between psychophysical end-stopping and flank-inhibition demonstrates that measurement of psychophysical spatial scaling may be able not only to differentiate retinal and cortical visual processing, but also to distinguish visual functions constrained by different cortical mechanisms. Why psychophysical end-stopping has a steeper spatial scaling than flank-inhibition is not yet known. It might be due to the fact that the population of end-stopped cells is relatively small and thus a larger sampling or higher magnification factor (lower E_2) would be required to equate the foveal and peripheral performances on tasks related to end-stopping.

The scaling of central summation shows functions that are much less steep in comparison to psychophysical end-stopping and flank-inhibition. This difference clearly indicates that the factors limiting central summation are different from those limiting end-stopping and flank-inhibition. However, whether central summation is limited by retinal or cortical factors cannot be decided by the spatial scaling function alone, since the width and length E_2 values (2.21 and 2.00 deg) fall into the range (1.5-4 deg) corresponding to the spatial scaling of either cones, ganglion cells, or cortical receptive field center sizes (Levi *et al.*, 1985; Wilson *et al*, 1990). This issue might be clarified by further dichoptic testing.

These findings indicate that even center/surround spatial interactions observed with circular stimuli are partly based on post-retinal processing. First, the center and surround spatial scaling functions obtained with a spot target are essentially identical to center (either width or length) and flank functions, respectively, measured with line targets, suggesting a correspondence between the center mechanisms and between the flank and surround mechanisms whether measured with spot or rectilinear stimuli. Since the E_2 value of surround antagonism, like that of flank-inhiSmigh9, matches the E_2 value of cortical magnificatgh9, a role of cortical processing is indicated. Second, both Spillmann and colleagues' and our data indicate that the size of the surround increases with retinal eccentricity at a higher rate than does the size of the center, whereas recent single-unit recordings of P and M macaque ganglion cells (Croner & Kaplan, 1995) indicate that center and surround sizes of neurons increase at the same rate. Thus, a post-retinal factor appears to affect the scaling factor of the surrounds observed on the conventional Westheimer paradigm. Based on these findings, we conclude that the weighting functions of the center/surround mechanisms inferred with the Westheimer paradigm include modificatgh9 by some cortical, probably inhiSmiory process. That is, the exact shape of the Westheimer paradigm functions reflects some cortical influence in addmigh9 to retinal center/surround organizatgh9.

An alternatgve account of differences in spatgal scaling has been presented by Whitaker *et al.* (1992a, b) who measured spatgal scaling in a number of posmigh9 and movement acuity tasks, including vernier acuity, bisectgh9 acuity, spatgal interval discriminatgh9, and referenced and unreferenced displacement detection. The enormous differences of E_2 values across these tasks (over 100-fold) led them to propose that E_2 values may be primarily decided by a task-dependent scale selection mechanism in the visual system, rather tha9 by the locus of the visual system (e.g. retinal or cortical) or the particular neurological pathways (e.g. a particular cell type or subset of cells). In the current study, the role of task-dependence was obviated since functions (center, flank and end-zone) were measured in the same increment threshold task with an identical target. The dramatgc scaling differences that we report for these different spatgal interactions provide strong evidence that differences in scaling between different neural levels or pathways is an important factor in determining the psychophysical spatgal scaling performance and E_2 values.

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