receptive neitas were first reported (Huber & wieser, 1965, 1968), little information is available concerning the perceptual correlates of this receptive field property. Relatively recently several authors have proposed that end-stopped units play a central role in important perceptual abilities, such as: the detection of curved segments, corners, and line terminators in the visual image; the determination of foreground from background in regions of object occlusions; the reporting of illusory contours; and the accomplishment of low-level image segmentation (von der Heydt et al., 1984; Dobbins et al., 1987; von der Heydt & Peterhans, 1989; Versavel et al., 1990; Heitger et al., 1992; Wilson & Richards, 1992). Although originally viewed (Hubel & Wiesel, 1965, 1968) as a defining characteristic of a third class of cells beyond simple and complex cells (i.e. hypercomplex cells), end-stopping has been found in a majority of simple and complex cells and thus is now typically viewed as an additional dimension along which both simple and complex cells vary (Dreher, 1972; Schiller et al., 1976; Gilbert, 1977; Henry, 1977; Murphy & Sillito,

with inmotory regions beyond the ends of the elongated receptive field center and is often termed "end-zone inhibition" (e.g. Bolz & Gilbert, 1986).

In the present research we investigate whether regions beyond the ends of a target line on a psychophysical task display antagonism similar to end-stopping in receptive fields. Specifically, we have adapted a paradigm popularized by Westheimer (1965, 1967) for measuring regions of spatial interactions around a test target. Westheimer and others noted that the effect of light near a small spot-shaped target suggested a local area of summation surrounded by an area of antagonism, much like center/surround receptive field antagonism (Westheimer, 1965, 1967; Fiorentini & Maffei, 1968; Enoch & Sunga, 1969; Oehler, 1985; Spillmann et al., 1987). These regions of perceptual spatial interactions have subsequently been called "perceptive fields" to emphasize their similarity to receptive field shape (Jung & Spillmann, 1970). Indeed, when tested directly, single cells have been shown to display responses comparable to the human response on an equivalent test paradigm (Essock et al., 1985). Responses of both humans and single cat cells are "desensitized" by near-by light and subsequently "sensitized" by light just outside of this central area (see also Shapley & Enroth-Cugell, 1984; Essock et al., 1985; Cleland & Freeman, 1988; Hayhoe, 1990).

In the standard psychophysical paradigm, the increment threshold for a small spot (e.g. 1') superimposed on

<sup>\*</sup>Department of Psychology, University of Louisville, Louisville, KY 40292, U.S.A.

<sup>†</sup>Department of Ophthalmology and Visual Science, University of Louisville, Louisville, KY 40292, U.S.A.

<sup>‡</sup>To whom all correspondence should be addressed at present address: College of Optometry, University of Houston, Houston, TX 77204, U.S.A. [Email yucong@bayou.uh.edu].

-		
_		
3		
<u> </u>		
	inhibition its magnitude or spatial properties. In the	of the 2.9 dee v 2.1 dee mention server (Eight III). The
	minoriton, its magnitude of spatial properties. In the	of the 2.8 deg × 2.1 deg monitor screen (Field III). The
	present research, psychophysical end-stopping is inves-	test field was a small line $(1' \times 5')$ in most experiments)
.e		
- 5		
,		
	}	

tions in a variation of the Westheimer paradigm. We demonstrate the existence of antagonistic end-zones in human target detection, map the size, strength, and orientation properties of the perceptual end-stopping, demonstrate that multiple antagonistic regions exist, and report that the spatial interactions closely match cortical

ĥ.

Fig. 1. In most experiments either the length or the width of the background field was fixed and the other dimension was varied. In other experiments, the rectangular background was fixed and combined with additional shapes whose configuration was varied. The sides of the rectangular backgrounds were parallel to the sides of



FIGURE 2. Width summation and flank antagonism at 0 deg (vertical) target orientation. Increment threshold is plotted as a function of background width with background length fixed at 6'. In this and all later figures, increment threshold is plotted as  $\log(I + \Delta I) - \log I$  and error bars represent  $\pm 1$  SEM, and error bars plotted for group means indicate the average of the subjects' standard errors.

the test line in all experiments. The luminance of the screen and background field were 6.8 and 47.7  $cd/m^2$ , respectively, and the luminance of the test line was varied by a staircase procedure.

## Procedure

A successive two-alternative forced-choice (2AFC) procedure was used. The background field was present in each of the two intervals (680 msec) and during the interstimulus interval (340 msec). In one of the two intervals the test line was also presented. The screen luminance always remained constant both throughout and between trials. Each trial was preceded by a  $6.3' \times 6.3'$  fixation cross in the center of the screen which disappeared 100 msec before the beginning of the trial. Intervals were marked by tones, and another tone provided 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 correct response raised test luminance by three steps. Step size was  $0.6 \text{ cd/m}^2$  in the experimental phase and  $3.6 \text{ cd/m}^2$  at the beginning of the practice phase with step size decreasing to  $1.8 \text{ cd/m}^2$  by the end of the practice phase.





FIGURE 3. Length summation and end-zone antagonism at 0 deg target orientation. Increment threshold is plotted as a function of background length with background width fixed at 3'.





\*Electrophysiological reports indicate that end-stopping is typically present at both end-zones, but often asymmetrical in strength (Orban et al., 1979a, b; Yamane et al., 1985) or length (Peterhans & von der Heydt, 1993). Since perceptive fields are likely to reflect the composite properties of a number of similar units detecting the target, we will assume symmetry when inferring perceptive field size from desensitization-sensitization curves.



visual responses for H–V targets and also with greater intra-channel orientation inhibition at H–V orientations (Essock & Krebs, 1992). Both of these findings suggest a cortical locus for these line-target perceptive fields.

In this experiment we wanted to determine whether there was an oblique bias of perceptual end-zone inhibition comparable to the orientation bias of flanking small but consistent orientations, the tablet shows a small but consistent orientations, the tablet shows a small but consistent orientations background is a sociated with oblique orientations was slightly weaker (i.e. slower sensitization as background size is increased). This effect is similar to but smaller than the weaker flank inhibition demonstrated previously with this



FIGURE 5. Length summation and end-zone antagonism at 90 deg, horizontal, (solid line) and 0 deg, vertical, (dotted line) orientations from two observers.

_			
	r		
<u> </u>			

This experiment investigated whether a different extent of the end-zone regions and length of the summation area was associated with target lines of different lengths. Three observers (HH, XY, and YC) were tested with 1' wide target lines that were either 2.5, 7.5, or 10' in length. Threshold was measured as a function of the length of a 3' wide background. Average thresholds are shown in Fig. 6(A) for 2.5, 7.5, and 10' lines along with the average data for a 5' line replotted

them.

The increase in length of the summation area with increased test line length corresponds quite closely to the amount by which the length of the test line was increased in each case. That is, the length of the summation area is directly attributable to the length of the test line. The extent of the central summation zone is 6' greater than the length of the test line test line regardless of line length

end-zone length =  $0.06 \times$  test-line length + 6.25). Thus, the length of the center region scales with test line length, but the length of the end-zone regions do not. Over this range of line lengths, the perceptive fields can be thought of as consisting of a central summation region extending about 3' beyond each end of the test line, regardless of length of line, and an antagonistic end-zone region extending c. 6.5' beyond each end of the central region. For these test conditions, the extent of the spatial interactions is clearly greater in the length dimension than in the width dimension. The antagonistic regions background lengths (3' wide). The increment stimulus consisted of two 1' × 1' squares separated by a 3' vertical gap (that is, a 1' × 5' test line with the central 1' × 3' area removed). Results (Fig. 7) clearly show spatial interactions comparable to those for a full 1' × 5' line target; peak desensitization occurs at the 11' background size and sensitization levels off in the neighborhood of the 20' background. These results are consistent with the common suggestion in the literature that line stimulus can be defined functionally either psychophysically or neurophysiologically by the endpoints of the line



FIGURE 8. Width summation and flank antagonism measured with background whose length (11') covered the summation area. (A) Mean data and data obtained with a 6'-long background (dashed line) replotted from Fig. 2(A). (B) Individual data.

ů.				
а <sub>с</sub> а				
			, t	
_ %				
		-		
1				
<u>a</u>				
à				
	Y			
	<b>V</b>			
	V			

summation regions. The greater level of threshold 9(B)], suggesting that the desensitization seen with a 3'-

A-		

-	
	-

covered the central summation area and the bars of the 'X' were extended across the corner regions where the prior experiments suggested inhibitory spatial interactions. The bars of the 'X' were varied in length from 10.5', a value not extending outside of the central background rectangle, to 24', the full extent of the possible inhibitory region (a  $14' \times 20'$  rectangle).

The results (Fig. 13) show a general trend of decreased

increment threshold tasks exist (Waugh *et al.*, 1993), such an effect does not fit well with the observed effects (specifically a localized increase in increment threshold over a highly localized region corresponding only to medium-size bar lengths between 16-18' length).

The general configuration of these spatial interactions is shown in Fig. 14. It represents a perceptive field with a tapered excitatory center, a tapered inhibitory surround

•			
•			
	region, oey	/0110	
	region, oey	/9/10	
		/9110	
9. 50	<u>regron, oey</u>	/0110	
	<u></u>	/0110	
		/ong	
		/0110	
		/0110	
	- <del></del>		

~	
,	
1	
н	

size of M-cell receptive fields (Oehler, 1985), the retinal central region is linked with additional excitatory regions

poration of significant end-zone antagonism and possibly secondary spatial interaction regions as well will be required. The interactions sketched in Fig. 14 indicate that a y-axis weighting function that is itself multilobed, such as a DOG with a greater spatial scale than in the xdirection, might be more appropriate than a simple single-lobed weighting function.

## REFERENCES

- Bacon, J. & King-Smith, P. E. (1977). The detection of line segments. *Perception*, 6, 125–131.
- Bolz, J. & Gilbert, C. D. (1986). Generation of end-inhibition in the visual cortex via interlaminar connections. *Nature*, 320, 362–365.
- Carlson, C. R. & Klopfenstein, R. W. (1985). Spatial-frequency model for hyperacuity. *Journal of the Optical Society of America A*, 2, 1747–1751.
- Cleland, B. G. & Freeman, A. W. (1988). Visual adaptation is highly localized in the cat's retina. *Journal of Physiology*, 404, 591–611.
- Crook, J. M., Lange-Malecki, B., Lee, B. B. & Valberg, A. (1988). Visual resolution of macaque retinal ganglion cells. *Journal of Physiology*, 396, 205–224.
- D'Amico, J., Yager, D. & Bichao, C. (1992). Oscillations in Westheimer functions: Psychophysical evidence for multiple

VISION Research, 30, 937-903.

- Heitger, F., Rosenthaler, L., von der Heydt, R., Peterhans, E. & Kubler, O. (1992). Simulation of neural contour mechanisms: From simple to end-stopped cells. *Vision Research*, 32, 963–981.
- Henry, G. H. (1977). Receptive field classes of cells in the striate cortex of the cat. *Brain Research*, 133, 1–28.
- von der Heydt, R. & Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity. *Journal of Neuroscience*, 9, 1731–1748.
- von der Heydt, R., Peterhans, E. & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science*, 224, 1260–1262.
- Hubel, D. H. & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology*, 160, 106–154.
- Hubel, D. H. & Wiesel, T. N. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *Journal of Neurophysiology, 28, 229–289.*
- Hubel, D. H. & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, 195, 215-243.
- Jung, R. & Spillmann, L. (1970). Receptive-field estimation and perceptive integration in human vision. In Young, F. A. & Lindslay D. B. (Eds), *Early experience and visual information processing in perceptual and reading disorders* (pp. 181–197). Washington DC: National Academy of Sciences.
- Klein, S. A. & Levi, D. M. (1985). Hyperacuity thresholds of 1 sec: Theoretical predictions and empirical validation. *Journal of the Optical Society of America A*, 2, 1170–1190.

5	
17	
16-	
1.	
-	
<b>,</b>	
1	
4	
2	
i/	
1	
_	

e mer		
<b>6</b>		
-		
_		
_		
' <u> </u>		
	<u>M</u>	
1	「「「「「「「「「」」」、「「「「「」」」、「「「」」、「「」」、「「」」、	

Sillito, A. M. (1977). The spatial extent of excitatory and inhibitory zones in the receptive field of superficial layer hypercomplex cells. *Journal of Physiology, 273*, 791–803.

- Spillmann, L., Ransom-Hogg, A. & Oehler, R. (1987). A comparison of perceptive and receptive fields in man and monkey. *Human Neurobiology*, 6, 51–62.
- Sullivan, G. D., Oatley, K. & Sutherland, N. S. (1972). Vernier acuity as affected by target length and separation. *Perception and Psychophysics*, 12, 438–444.

Sun, M. & Bonds, A. B. (1994). Two-dimensional receptive-field

(Suppl.), 35, 3472.

Yu, C., McCarley, J. S. & Essock, E. A. (1995). Psychophysical endstopping, flank inhibition, and central summation of perceptive fields are based on different neural substrates. *Investigative Ophthalmol*ogy and Visual Science (Suppl.), 36, 2146.

Acknowledgements—This research was supported by Fight-For-Sight Grant GA90095 and a Grant-in-Aid of Research from Sigma Xi.