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Cortical End-stopped Perceptive Fields: Evidence from Dichoptic and Amblyopic Studies

CONG YU,* DENNIS M. LEVI*f

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Psychophysical length and width spatial interactions associated with a line target were measured in normal observers dichoptically and in observers with naturally acquired amblyopia to investigate the neural locus of end-stopped perceptive fields. Results show (1) interocular transfer of psychophysical end-stopping, flank-inhibition, and length and width summation; and (2) severe, but significantly different, loss of end-stopping and flank-inhibition in the central visual fields of amblyopic eyes. Together, these results suggest a cortical basis for end-stopped perceptive fields, and that psychophysical end-stopping and flank-inhibition are a consequence of distinct cortical inhibition. The damaging effects of amblyopia on end-stopping and flank-inhibition are weaker and less different from each other under transient conditions. Our results provide further evidence supporting the suggestion that end-stopped perceptive fields are the psychophysical analogs of cortical end-stopped receptive fields. © 1997 Published by Elsevier Science Ltd.

End-stopping Flank-inhibition Perceptive field Westheimer paradigm Amblyopia

INTRODUCTION

Receptive field end-stopping and flank-inhibition were first reported by Hubel & Wiesel (1962, 1965, 1968) in cat and monkey striate cortex. End-stopping is seen in receptive fields of many simple and complex cells (e.g., Dreher, 1972). An end-stopped cell responds best to an elongated stimulus of optimal length. Beyond that length the response of the cell is inhibited because the stimulus enters the inhibitory end-zones of the receptive field. Flank-inhibition is seen in simple cell receptive fields which have a distinctive summation center and antagonistic flank regions. Stimuli wider than the center of a simple cell's receptive field will reduce or inactivate the response of the cell when they encroach on the antagonistic flanks. Thus, an end-stopped simple cell receptive field is tuned to both the length and width of the stimulus.

Psychophysical end-stopped spatial interaction areas or "perceptive fields" (Jung & Spillmann, 1970) resembling end-stopped simple receptive fields have been demonstrated with a modified Westheimer paradigm (Yu & Essock, 1996a). 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 inhibitory influence (Westheimer, 1965, 1967). Thus, with a line target, the desensitization and sensitization branches of the length spatial interaction functions obtained under the variable-length background condition suggest central length summation and end-stopping, respectively, and those of the width spatial interaction functions obtained under the variable-width background condition suggest central width summation and flank-inhibition, respectively. These end-zone, flank, and central summation regions together form elongated end-stopped perceptive fields which resemble, and are assumed to be the psychophysical analogs of, typical end-stopped simple cell receptive fields (Yu & Essock, 1996a,b).

Because the Westheimer function has a long history of being interpreted as reflecting the behavior of retinal cell receptive fields (e.g., Enoch, 1978; Spillmann *et al.*, 1987; Westheimer, 1967, but see Lennie & Macleod, 1973; Yu & Levi, 1997a), a demonstration of a cortical locus of end-stopped perceptive fields is critical to linking the psychophysical evidence to cortical end-stopped receptive fields. As the first step to investigate the processing level of end-stopped perceptive fields, the spatial scaling properties of psychophysical end-stopping, flank-inhibition, and length and width central summation of the perceptive fields were measured at several retinal eccentricities (Yu & Essock, 1996b). The extent of end-stopping and flank-inhibition increases rapidly with the eccentricity. The E_2 values of the spatial

*College of Optometry, University of Houston, Houston, TX 77204-6052, U.S.A. fTo whom all correspondence should be addressed [*Fax* + 1-713-743-1888; *Email* dlevi@uh.edu].

scaling functions of end-stopping and flank-inhibition (0.45 and 0.77 deg, respectively) are similar to the E_2 value estimated for cortical magnification (Levi *et al.*, 1985), indicating that both psychophysical end-stopping and flank-inhibition are likely to be limited by cortical factors (Levi *et al.*, 1985). Moreover, the nearly two-fold difference in the E_2 values between psychophysical end-stopping and flank-inhibition (i.e., the size of end-zones increases nearly twice as fast as does the size of flanks across the visual field) also suggests that they may be based on different cortical mechanisms. Such a difference is supported by neurophysiological differences in receptive field end-stopping and flank-inhibition (Bolz & Gilbert, 1986).

On the other hand, the extent of length and width central summation, although similar to each other, increases much more slowly across the visual field, with an average E_2 value of 2.05 deg, comparable with E_2 values of cone and ganglion cell spacing, as well as the E_2 value of the center size of cortical receptive fields (Levi *et al.*, 1985; Wilson *et al.*, 1990). Thus, the neural locus of central summation cannot be determined from the spatial scaling measurements, although a cortical origin seems likely since other parts of the perceptive fields (i.e., end-zones and flanks) are cortical.

In order to further examine the locus of psycho-physical end-stopping and flank-inhibition, as well as to decide at what level the central summation is limited, the present study measures length- and width-dimension spatial interactions in normal observers with dichoptic stimulus presentation, and in observers with naturally acquired amblyopia. The dichoptic measurements demonstrate the interocular transfer of both the sensitization and desensitization effects along both the length and width dimensions, suggesting that not only psychophysical end-stopping and flank-inhibition, but also central summation, are cortical. The amblyopic measurements reveal abnormal cortical modulation of both length and width spatial interactions, with more severe effects on the sensitization branches of both the length and width functions (end-stopping and flank-inhibition). Moreover, consistent with suggestions from spatial scaling experiments that psychophysical end-stopping and flank-inhibition are mediated by different cortical mechanisms, amblyopia affects end-stopping more severely than flank-inhibition. This difference diminishes under transient conditions when the background is flickered at 10 Hz. In general, the dichoptic and amblyopic results are consistent with the spatial scaling results, and with the notion that length and width spatial interactions reflect the behavior of cortical end-stopped receptive fields, and that psychophysical end-stopping and flank-inhibition are consequences of distinct intra-cortical inhibition.

*We define amblyopia as a unilateral loss of visual acuity in the absence of any clinically observable pathological anomaly, associated with constant strabismus, anisometropia, or both (Ciuffreda *et al.*, 1991).

GENERAL METHODS

Observers

Normal observers. Three females aged 19-24 yr served in the dichoptic experiments. All were slightly myopic and wore appropriate lenses to correct the vision of each eye to 20/20 or better. Their stereopsis, examined with the Randot Stereotest (Stereo Optical Co., Inc.), was normal (20 sec). They had no prior psychophysical experience and were naive as to the purpose of the study.

Amblyopic observers. Three amblyopes,* two highly experienced in psychophysical observations and having moderate amblyopia (AJ and RH), one less experienced and having mild amblyopia (JB), participated in the amblyopic measurements. Observers RH (male, 25 yr) and JB (male, 38 yr) were strabismic. RH had corrected vision of 20/15 in the preferred eye (O.D.) and 20/48 in the amblyopic eye (O.S.). JB had corrected vision of 20/15 in the preferred eye (O.S.) and 20/30 in the amblyopic eye (O.D.). Observer AJ (female, 26 yr) was strabismic and anisometropic, with corrected vision of 20/15 in the preferred eye (O.S.) and 20/60 in the amblyopic eye (O.D.).

Apparatus and stimuli

The stimuli were generated by a Vision Works computer graphics system (Vision Research Graphics, Inc.) and presented on a U.S. Pixel Pxl9 monochrome monitor with a resolution of 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 monitors was made linear by means of an 8-bit look-up table. A pair of twisted nematic liquid-crystal shutter glasses were used to control the dichoptic stimulus presentation. The transmission rate was about 10%.

A potential difficulty with using shutter glasses for dichoptic displays is leakage or crosstalk. Measurements of leakage for our system are presented elsewhere (Mussap & Levi, 1995). We tested the possible effects of crosstalk in the present experiments on two observers. A 19' circle was presented to one "occluded" eye and the detection rate for that circle was measured for the other eye with a two-alternative forced-choice (2AFC) staircase procedure, with all other conditions matching the experimental conditions (see details below). The minimal luminance required to detect the circle (i.e., to detect the crosstalk) was about four times as high as the background luminance used in the experiments. There was little difference between the results of the two observers. Thus, we believe that crosstalk had little effect on the results we report here.

The basic stimulus configuration consisted of a 1' x 5' line target centered on a rectangular background of variable length or width (Fig. 1). The luminance of the screen and background field were 6.8 and 23.8 cd/m^2, respectively, in the dichoptic experiments (including both dichoptic and monoptic stimulus conditions, see below). These values were then reduced by the shutter-glasses to about 0.68 and 2.38 cd/m^2. In the experiments with amblyopic observers, these luminance values were 2.5

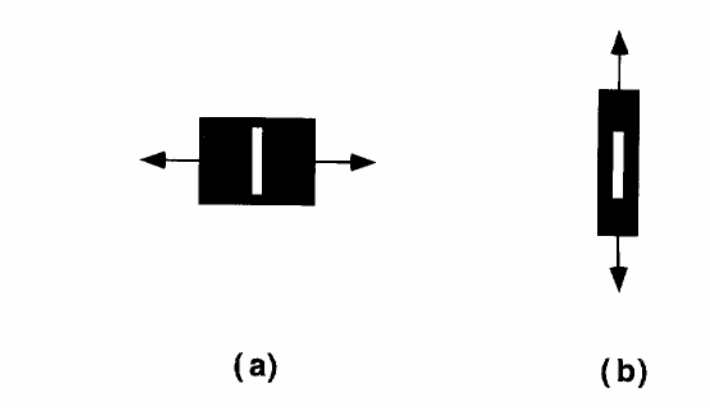

FIGURE 1. The general configuration of stimuli: a 1' x 5' test line superimposed on a rectangular background with: (a) length fixed at 6' and width varied; and (b) width fixed at 3' and length varied.

and 26.7 cd/m^2 , respectively (since comparisons are made within observers, the difference in luminance values for normal and amblyopic observers is not a serious difficulty). The luminance of the line target was varied according to a staircase procedure. The viewing distance was 5.64 m.

Procedure

A successive 2AFC staircase procedure with a convergence rate of 75% was used. The background field was presented in each of the two intervals (400 msec) and during the inter-stimulus interval (600 msec). In one of the two intervals the test line was also presented for 400 msec. The screen luminance always remained constant both throughout and between trials. Each trial was preceded by a 6.3' x 6.3' fixation cross (binocular in dichoptic measurements) in the center of the screen which disappeared 100 msec before the beginning of the trial.

Each staircase consisted of four practice reversals and six experimental reversals. The mean of the six experimental reversals was used to estimate the increment threshold, defined as the difference between log target luminance at threshold and log background luminance (log(AL + L)—log L). A dichoptic experimental session usually consisted of 10-12 randomly presented conditions of various background sizes, half monoptic and half dichoptic, and lasted for about 50 min. An amblyopic experimental session usually consisted of 14-15 randomly presented conditions, between six and seven for the preferred eye and eight for the amblyopic eye, and lasted for 90 min or less. Each datum represents the mean of five replications for each condition, and the error bars represent +1 SEM.

EXPERIMENT 1: DICHOPTIC MEASUREMENTS OF PSYCHOPHYSICAL END-STOPPING AND FLANK-INHIBITION

This experiment measured the dichoptic length and width functions with the line target presented to one eye and the rectangular background to the other eye (dichoptic condition). It provides a strong test of whether the spatial interactions along both the length and width dimensions are formed after binocular convergence of the visual input. As a control, the target and background were also presented to the same eye (monoptic condition). When measuring length functions, the background width was fixed at 3', and the background length was varied from 6' to 27' or 35' in five or six steps. The fixed background width of 3' guaranteed that the background was well within the perceptive field center (5-6' wide) in the width dimension, so that it would not interact with the antagonistic flanks and clean length functions could be measured (Yu & Essock, 1996a). Some of the background length steps used here had been previously found to be critical in evaluating the extent of length desensitization (summation) and sensitization (end-stopping) (Yu & Essock, 1996a). When measuring width functions, the background length was fixed at 6' and the width was varied from 3' to 19' in five steps. The fixed background length of 6' also guaranteed that the background was well within the perceptive field center (10-11' long) in the length dimension so that it would not interact with the antagonistic end-zones and clean width functions could be measured. The background width steps used here had also been found to be critical in evaluating the extent of width desensitization (summation) and sensitization (flank-inhibition). During this experiment, length and width functions were measured in separate sessions in a counterbalanced order.

Our results show the inverted-V shapes typical of the Westheimer function in length functions [Fig. 2(a)] and width functions [Fig. 2(b)] under both monoptic and dichoptic conditions. These results suggest that both the desensitization and sensitization processes of length and width functions can be achieved by dichoptically induced background effects. In other words, all components of the perceptive fields, the summation centers, end-zones, and flanks, appear to be formed after binocular convergence as early as in area VI of the visual cortex. This conclusion is consistent with the cortical limitations of psychophysical end-stopping and flank-inhibition suggested by the spatial scaling measurements (Yu & Essock, 1996b). It also indicates a cortical origin for central summation which spatial scaling experiments could not determine. Each pair of the dichoptic and monoptic length or width functions peak at the same background length or width. Many of them also reach the plateau at similar background sizes. The close agreement in the shapes of the functions suggests that dichoptic and monoptic functions are probably based on the same length or width mechanisms. The overall dichoptic threshold is higher than the monoptic threshold in both length and width functions, suggesting that the dichoptically presented background has a stronger masking effect on target detection than does the monoptically presented background. This effect probably indicates some general interocular inhibition which appears to be nonspecific to central summation and surround inhibition, consistent with Fox & Check's (Fox & Check, 1966) finding that stimuli presented to one eye tend to raise thresholds in the

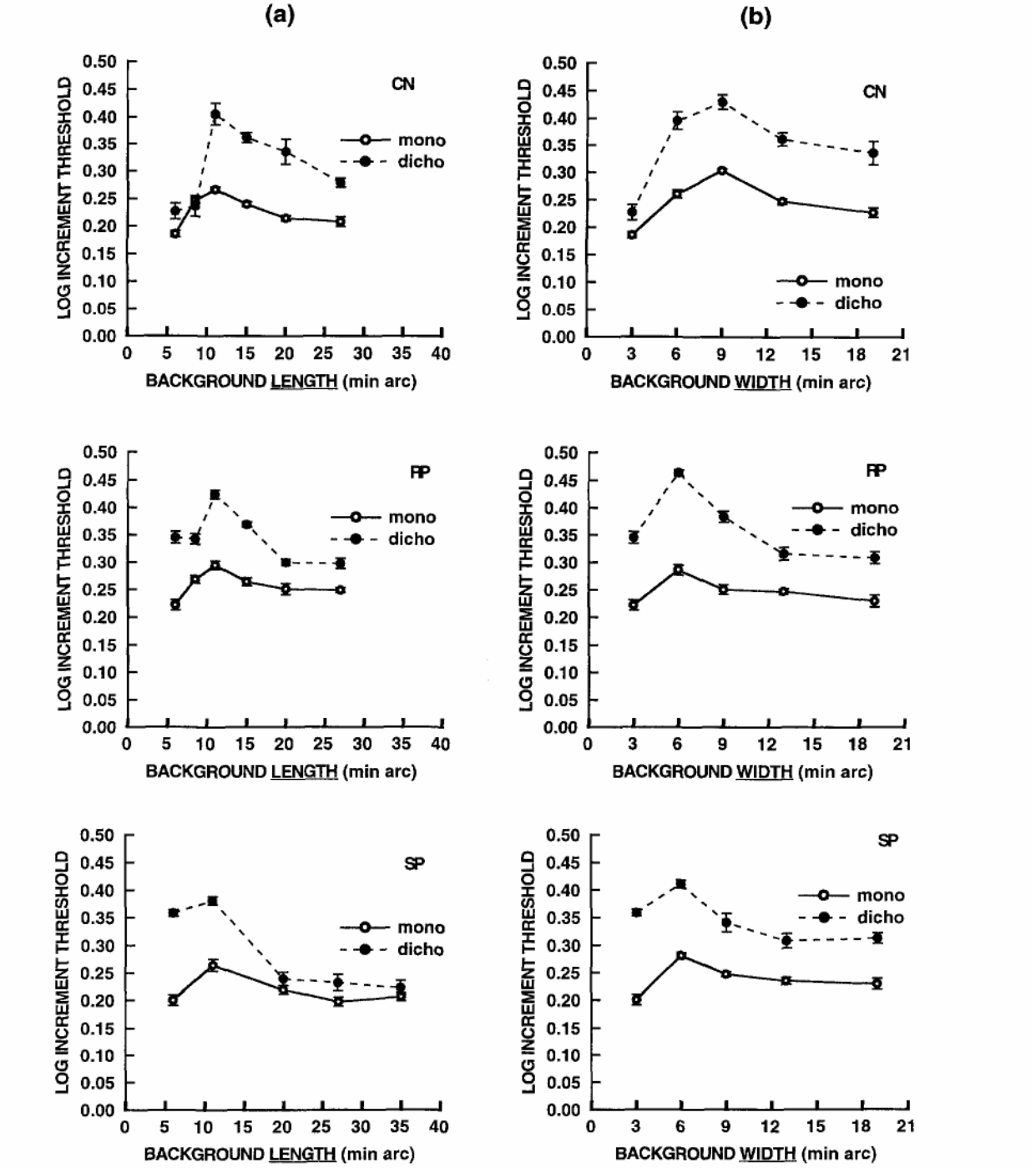

FIGURE 2. Dichoptic and monoptic thresholds as a function of the background length or width, (a) length functions; (b) width functions. In this and all later figures, increment threshold is plotted as log(/ + A/)—log 7 and error bars represent + 1 SEM.

other eye. Similar effects were also reported in masking experiments in which dichoptic masking was found to be more effective in elevating test grating threshold than monoptic masking (Legge, 1979; Levi & Harwerth, 1982).

EXPERIMENT 2: PSYCHOPHYSICAL END-STOPPING AND FLANK-INHIBITION IN HUMANS WITH NATURALLY ACQUIRED AMBLYOPIA

In this experiment length and width functions were measured in three amblyopes. Several lines of evidence suggest that the retinal structures of amblyopic eyes of humans and primates are basically intact and that the defects are mainly cortical. Hendrickson *et al.* (1987) and Movshon *et al.* (1987) studied the anatomy and physiology of the retina, LGN, and cortex in the same monocularly blurred animals and found that the retina and all other eye tissues are normal, but the spatial properties of neurons in striate cortex are remarkably affected. Essentially normal pattern ERGs in deep amblyopes (Hess & Baker, 1984) and spatial and

temporal properties of LGN neurons in long-term deprived monkeys (Blakemore & Vital-Durand, 1986; Levitt *et al.*, 1989) were also reported. Meanwhile, in the striate cortex, surgical strabismus and prism rearing lead to a massive loss (around 80% or more) of binocular neurons (Baker *et al.*, 1974; Crawford & von Noorden, 1979, 1980). Neurons driven through the amblyopic eye show reduced contrast sensitivity, particularly at high spatial frequencies in monkeys reared with chronic atropinization (Kiorpes *et al.*, 1987; Hendrickson *et al.*, 1987; Movshon *et al.*, 1987) and experimental strabismus (Movshon & Kiorpes, 1993). These studies provide strong support for the notion that the primary effects of amblyopia are cortical. Thus, we believe that amblyopia could serve as an ideal means to evaluate the potential modulation by the visual cortex on the length and width spatial interaction functions.

Length functions [Fig. 3(a)] and width functions [Fig. 3(b)] were measured in separate sessions in a counter-balanced order. In each session both the amblyopic and

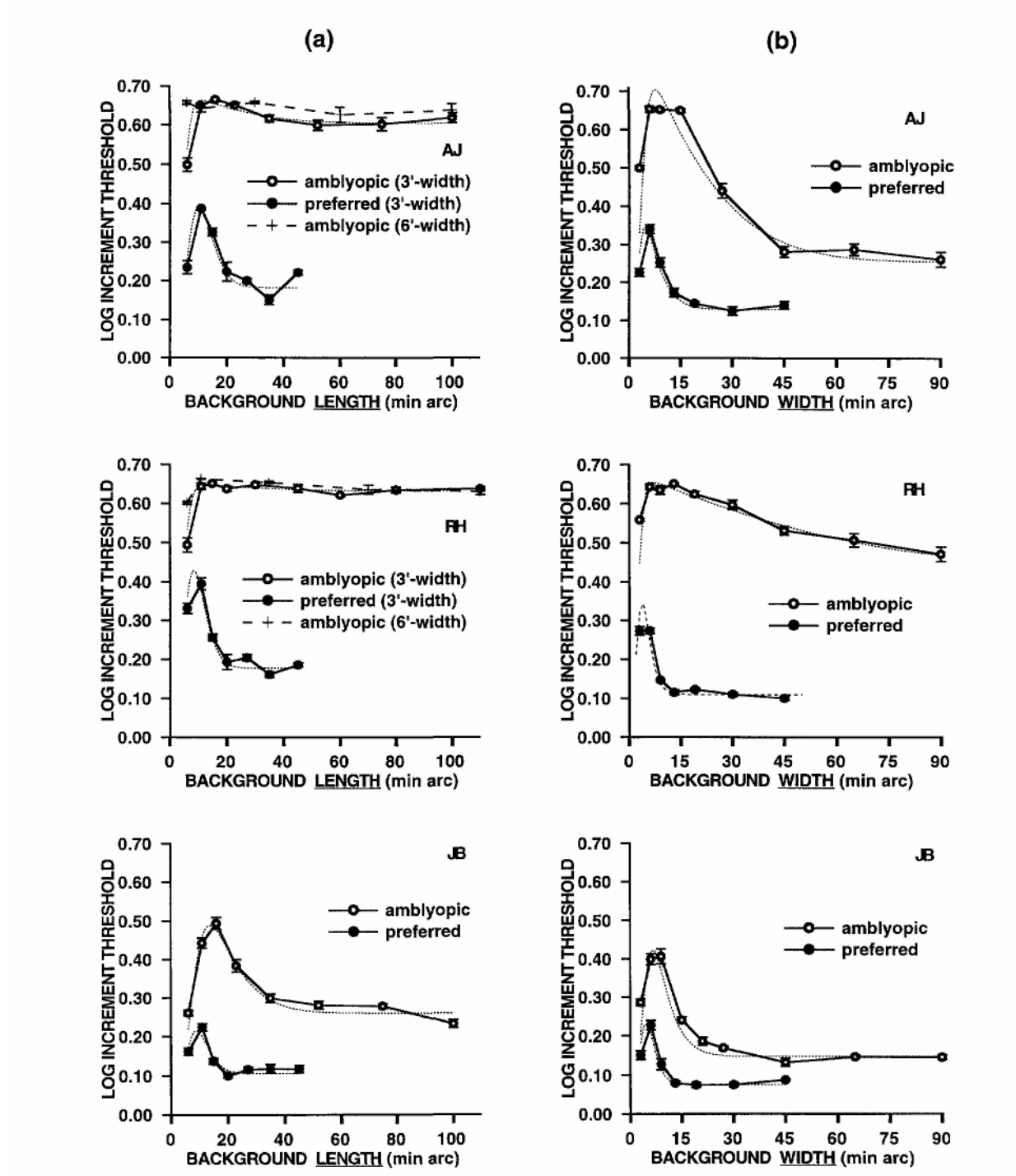

FIGURE 3. Length functions (a) and width functions (b) measured on amblyopic eyes and preferred eyes (solid lines) and their DoG fits (dotted lines). Length functions measured with a 6'-wide background (3'-wide in all other length function measurements) as a control condition are also presented in observers AJ and RH's length function figures (dashed line).

non-amblyopic functions were measured. The most striking feature of these functions is that end-stopping in two observers (AJ and RH) with moderate amblyopia is nearly abolished. In their length functions, threshold does not decrease, or decreases only very slightly, after reaching the peak (<0.03 log units for RH and <0.06 log units for AJ). Interestingly, the damaging effect of amblyopia is less severe on flank-inhibition of the same two observers, as suggested by the clear after-peak threshold reduction in their width functions (0.18 log units for RH and 0.39 long units for AJ). The different effects of amblyopia on end-stopping and flank-inhibition, although much less strong, are also evident in functions of observer JB, who had only very mild amblyopia and whose length function shows clear end-stopping. For this observer, sensitization in the length function (end-stopping) is wider (reaching half of the peak threshold at a background length of about 80') and slightly weaker (0.26 log units), while sensitization in the width function (flank-inhibition) is narrower (reaching half of the peak threshold at a background width of about 20') and slightly stronger (0.27 log units).

To confirm that this difference is not caused by the areal summation difference of the background in length and width experiments, a control length condition was also examined in observers AJ and RH, in which the background width was set at 6', the same as the background length in the width experiments, and the threshold as a function of background length was measured. The results are shown in AJ and RH's length function figures [Fig. 2(a), top two figures, dashed lines]. Like the original length functions, these control functions show no threshold reduction. The threshold before the peak is even higher in these control functions. This is because more central summation has actually been elicited by the 6'-wide background, since the width of the central summation area is more than 6', as suggested by the corresponding width functions.

In general, the threshold level of the amblyopic functions is much higher than that of non-amblyopic ones owing to the well known and significant loss of contrast sensitivity of amblyopic eyes (Hess & Howell, 1977; Levi & Harwerth, 1977). However, amblyopia affects the desensitization and sensitization branches of the amblyopic functions in a different manner. As suggested above, the most notable abnormality is the absence of end-stopping in AJ and RH's length functions. Moreover, other sensitization branches of the amblyopic length and width functions, especially those in AJ and RH's amblyopic width functions, are considerably enlarged as compared with those of the non-amblyopic ones. On the other hand, the desensitization process in both length and width functions of amblyopic eyes is less affected. The peak shift of the amblyopic functions suggests only moderately enlarged (at most two-fold) desensitization branches or perceptive field center length and width. In contrast, the sensitization branches of amblyopic functions expand at a rate ranging from four times (JB, flank-inhibition) to infinity (RH, end-stopping). Therefore, amblyopia has much more severe effects on the extent of end-stopping and flank-inhibition than on the extent of central summation. Interestingly, these amblyopic functions measured in the central visual field are comparable with functions measured in the periphery of normal adult observers (Yu & Essock, 1996b). All show considerably extended sensitization branches and only moderately enlarged desensitization branches. This similarity suggests that foveal mechanisms with finer receptive fields are selectively abolished in amblyopic eyes.

To provide a deeper understanding of the effects of amblyopia on these functions, all the functions in Fig. 3 were fitted by DOG (Difference of Gaussian) functions (dotted lines). The parameters for each fit are listed in Table 1. As Table 1 shows, the negative gaussian components (end-stopping and flank-inhibition) of the

TABLE 1. Parameters of DOG fitting for each function in Fig. 3 and the mean percentage changes of parameters in amblyopic functions relative to those in non-amblyopic functions

	A_1	σ_1	A_2	σ_2
AJ length preferred	1.190	5.39	0.914	5.73
AJ length amblyopic	0.027	2.66	0.009	18.34
AJ width preferred	0.050	1.82	0.012	5.92
AJ width amblyopic	0.037	2.29	0.010	20.17
RH length preferred	0.408	4.40	0.218	5.00
RH length amblyopic	0.027	2.58	0.009	21.05
RH width preferred	0.143	1.89	0.031	3.24
RH width amblyopic	0.050	1.68	0.009	44.04
JB length preferred	0.201	4.60	0.117	5.17
JB length amblyopic	0.019	4.78	0.010	13.79
JB width preferred	0.508	2.64	0.224	3.19
JB width amblyopic	0.038	2.69	0.013	6.82
Mean % change				
Length amblyopic	−95.9	−30.4	−97.7	234.3
Width amblyopic	−82.2	5.1	−88.1	475.4
Overall	−89.0	−12.7	−92.9	354.8

A, and/4_2 refer to the amplitudes of the positive and negative gaussians of DOG functions, respectively, and a-1 and a'_2 are space constants.

amblyopic functions are consistently weaker and much broader than those of the non-amblyopic functions. On average, the amplitude (A_2) is about 93% weaker, and the space constant s_2 is increased more than three and a half times in the amblyopic functions. The positive gaussian components (summation) of the amblyopic functions are also weaker, the amplitudes (A_1) being about 89% less. Table 1 also shows that the average space constant s_1 has a 12.7% decrease, which, however, is mainly contributed by AJ and RH's amblyopic length functions (51% and 41% decrease, respectively) showing basically no end-stopping. s_1 is actually only slightly altered in all three amblyopic width functions and JB's amblyopic length function (4.8% increase on the average), indicating that the extent of summation might only be affected under certain extreme circumstances. Thus, the apparent expanded summation area shown in the amblyopic functions is mainly a consequence of significantly reduced inhibition, plus reduced summation in some cases, not the expansion of the summation area itself. In general, these analyses are consistent with the conclusion that amblyopia mainly affects the extent of surround inhibition, rather than that of central summation.

EXPERIMENT 3: EFFECTS OF TEMPORAL MODULATION ON PSYCHOPHYSICAL END-STOPPING AND FLANK-INHIBITION IN AMBLYOPES

In this experiment we measured length and width functions under transient background conditions with background flicker. We were interested in whether the different effects of amblyopia on end-stopping and flank-inhibition shown under sustained background conditions (Experiment 2) would also apply to transient conditions, and, especially, whether the abolished end-stopping shown in two amblyopes under sustained background conditions could be restored. The background was temporally modulated by a 10 Hz counterphase sine-wave, with the mean luminance equal to the background luminance in Experiment 2 (26.7 cd/m^2), and the modulation depth from 2.5 to 47.9 cd/m^2. Other conditions were the same as in Experiment 2.

Length and width functions measured under current conditions are presented in Fig. 4(a, b), respectively. Amblyopic functions measured with a sustained background are also replotted from Fig. 3 for comparison (dotted line). The most distinct result under transient stimulation is the partial restoration of end-stopping in AJ and RH's amblyopic length functions. The after-peak threshold decreases were 0.38 and 0.22 log units for AJ and RH, respectively, compared with less than 0.06 and 0.03 log units in their sustained amblyopic length functions, suggesting that the transient components of end-stopping have not been entirely eliminated by amblyopia.* As a result, the effects of amblyopia on end-stopping and flank-inhibition differ less than they would have under sustained background conditions. However, end-stopping is still not as strong as flank-inhibition for two of the three observers (RH and JB), as indicated by the slower after-peak threshold reduction in their length functions. Thus, even under transient conditions, it appears that amblyopia could have a stronger effect on end-stopping. In general, end-stopping and flank-inhibition in each observer's transient amblyopic function, as suggested by steeper sensitization, are stronger than their counterparts under sustained conditions. The overall average after-peak threshold decrease is about 0.31 log units, in contrast to about 0.20 log units under sustained conditions. However, the overall threshold level in each amblyopic function is still well above the threshold level of its corresponding non-amblyopic function, and more importantly, the extent of end-stopping and flank-inhibition of amblyopic functions is still enlarged to a considerable degree. The amblyopic length and width functions respectively reach their plateaus at about 55' and 50', in contrast to 20' and 15' in non-amblyopic functions. Therefore, even if the transient length and width spatial interactions are less affected by amblyopia, they are by no means normal.

*This threshold reduction or sensitization is not a practice effect, because the control condition in Experiment 2, which still shows no sensitization, was measured during the current experiment, and because these two observers were highly experienced in psycho-physical observations.

GENERAL DISCUSSION

The neural locus of psychophysical end-stopped perceptive fields was investigated in normal observers with dichoptic stimulus presentation, and in observers with naturally acquired amblyopia. Our main results show interocular transfer of length and width spatial interactions, and severe suppression of end-stopping and flank-inhibition, especially end-stopping, in amblyopic eyes. These results, combined with those from spatial scaling measurements (Yu & Essock, 1996b), support the conclusion that end-stopped perceptive fields are formed at a cortical level, and that psychophysical end-stopping and flank-inhibition analogous to physiological end-stopping and flank-inhibition are consequences of distinct intracortical inhibition.

In a parallel study, we also found strong evidence from spatial scaling measurements (Yu & Essock, 1996b) and dichoptic and amblyopic experiments (Yu & Levi, 1997a) showing that the original Westheimer function measured with circular stimuli (Westheimer, 1967) is also cortical, at least to a large degree. These functions are basically the same as the present width functions measured with line target, showing very similar spatial scaling properties (almost identical E_2 values), interocular transfer of both desensitization and sensitization, and amblyopic cortical modulations. Probably most importantly, desensitization and sensitization in the original Westheimer function and the present width function are not only both cortical (Yu & Levi, 1997a; present paper), their E_2 values also match the E_2 values of cortical receptive field centers and the E_2 values of general cortical magnification, respectively (Yu &

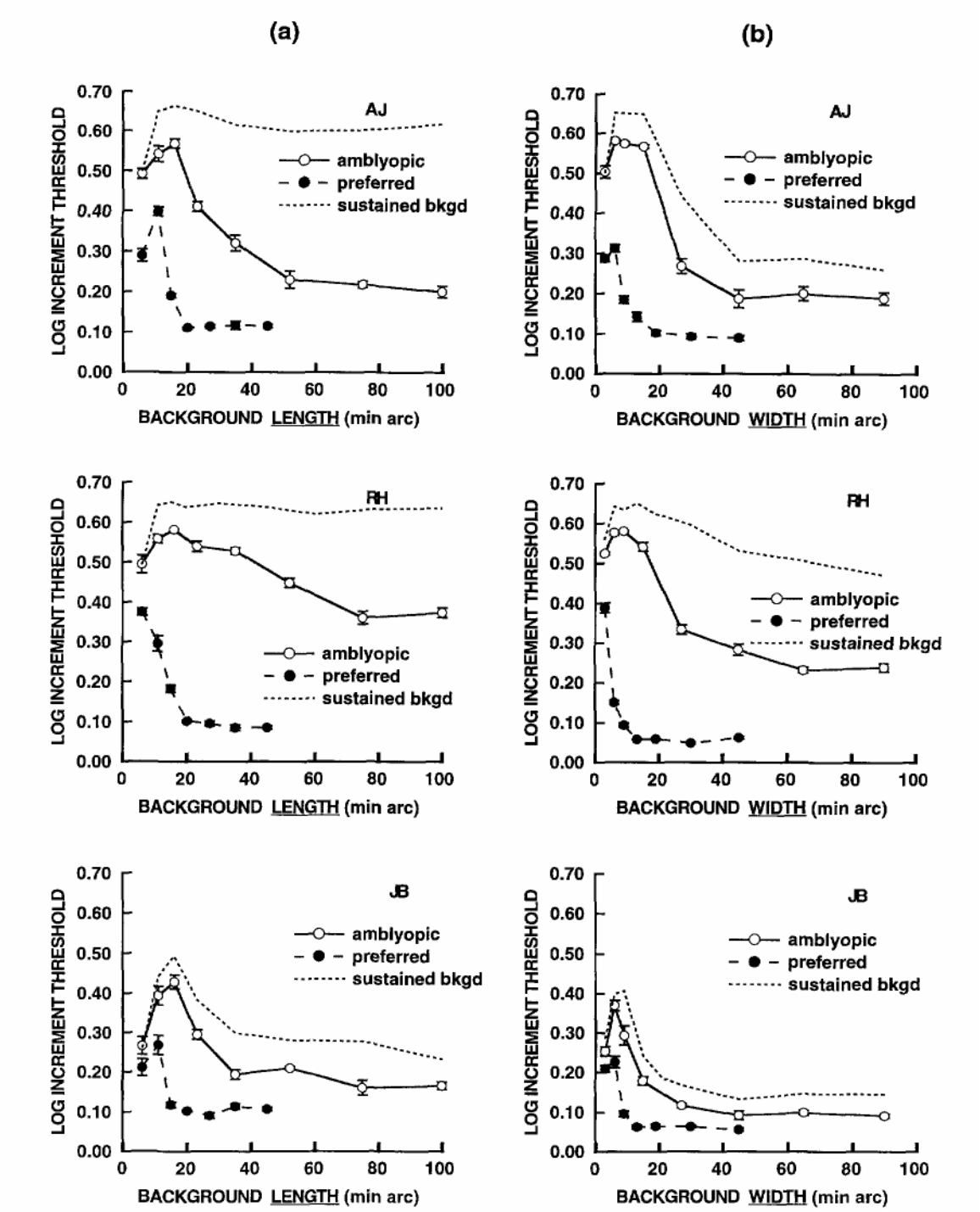

FIGURE 4. Length functions (a) and width functions (b) measured on amblyopic eyes and preferred eyes with transient stimulus presentation. Functions measured with sustained stimulus presentation (Fig. 3) were also replotted here for comparison (dotted line).

Essock, 1996b). Thus, we think that the Westheimer function might be better understood on the basis of size-tuned cortical spatial filters (e.g., Wilson & Gelb, 1984). A similar explanation was also suggested by Lennie & Macleod (1973) and Latch & Lennie (1977) who argued that the sensitization effect is caused by size-tuned spatial channels in the visual cortex.

On the basis of this understanding of the Westheimer function and the perceptive field, end-stopped perceptive fields can be ideally viewed as end-stopped psychophysical spatial filters or channels. This view is not only supported by the distinct spatial scaling properties of end-stopping relative to flank-inhibition, interocular transfer of both desensitization and sensitization, and distinct amblyopic cortical modulations, but is also favored by additional recent evidence. Firstly, psychophysical end-stopping was demonstrated in masking experiments (Yu & Levi, 1997b). Desensitization and sensitization similar to those in the length spatial interaction functions were revealed when a short D6 target of different spatial

frequencies was masked by another D6 of the same spatial frequency at various window lengths, suggesting that psychophysical spatial filters or channels are really end-stopped. Secondly, the length and width spatial interaction functions obtained from normal observers (Yu & Essock, 1996a) and amblyopes (present paper) have been used (Yu & Levi, 1997c) to successfully predict the facilitatory spatial interactions reported by Polat & Sagi (1993,1994) and Dresp (1993). These researchers reported that contrast sensitivity to a target can be facilitated to below baseline level by spatially separated inducing objects. We found that spatial facilitation to a target line occurred only when two high contrast inducers were placed at locations corresponding to the end-zones or flanks of end-stopped perceptive fields, suggesting that spatial facilitation probably results from end-stopping and flank-inhibition elicited by inducers, in that they may reduce the suppressive effects of divisive signals from a pool of neighboring filters and increase the gain of spatial filters (Yu & Levi, 1997c). This finding excludes some possible alternative explanations of psychophysical length and width Westheimer functions, such as simple luminance gain control, and confines the explanation to intracortical interactions involving cortical end-stopped spatial filters.

In end-stopped spatial filters, flank-inhibition could provide information about border and size, and end-stopping could provide information about line and edge termination. Together they could provide a two-dimensional description of a visual object, similar to Heitger *et* a/.'s (1992) computational model of contour processing. Like their model, end-stopped spatial filters have an important advantage over conventional spatial filters simulating simple cell receptive fields in that the processing of termination and corner information is among their basic features and therefore does not require additional orthogonal second-order filters to calculate the termination (Wilson & Richards, 1992). Recognizing the role of end-stopping in spatial filters could substantially improve the modeling of these basic functional units in visual pattern perception.

Probably the most striking finding of this study is the dramatic loss of end-stopping in the amblyopic eyes of two observers with moderate amblyopia. Although no neurophysiological data concerning the relationship between end-stopping and amblyopia are available, this finding suggests that end-stopping may be highly susceptible to the influence of amblyopia during its developmental course, since amblyopia is known to be a developmental anomaly of cortical mechanisms (e.g., Levi, 1990). In strobe-reared cats, Kennedy & Orban (1983) found that the proportion of end-stopped cells in areas 17 and 18 decreases from the normal level of 27-30% to 6-7%. Although visual defects caused by stroboscopic illumination are different from amblyopia, in that they present selective loss of motion perception and nearly normal contrast sensitivity and other types of form perception (Pasternak *et al*, 1985; Pasternak & Leinen, 1986), the loss of end-stopping in amblyopes and in strobe-reared cats may suggest that the suppression of end-stopping is a general consequence of abnormal visual experience. Kennedy & Orban (1983) also reported that the receptive field (center) width of cells in area 18 of strobe-reared cats subserving the central 5 deg of the visual field is more than doubled and does not increase with eccentricity. This is similar to our results in that the amblyopic perceptive field center is about two-fold (or more) wider than the non-amblyopic perceptive field center, and comparable with perceptive field center measured in the periphery of normal observers (Yu & Essock, 1996b). These findings suggest that the alterations of perceptive fields in amblyopic eyes may not be specific to amblyopia, but may reflect the more general modification of cortical receptive fields owing to the abnormal development of the visual system.

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