

Naso-Temporal Asymmetry of Spatial Interactions in Strabismic Amblyopia

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ABSTRACT: *Purpose.* Naso-temporal asymmetries of visual acuity and contrast sensitivity have been reported in strabismic amblyopia and attributed to asymmetries of interocular suppression, in this study, we investigated the naso-temporal asymmetry of cortical spatial interactions in two strabismic amblyopes (one esotrope and one exotrope). *Methods.* Length and width Westheimer functions were measured on both amblyopes at the 10 deg retinal eccentricity of both nasal and temporal visual fields. *Results.* Spatial interactions in the two amblyopic eyes were more degraded in the temporal visual fields than in the nasal visual fields. A comparison with results from the preferred eyes suggested that this asymmetry was caused mainly by a loss of spatial interactions in the temporal visual fields of amblyopic eyes, with those in the nasal visual fields being normal. *Conclusion.* Our results suggest that intracortical connections underlying cortical spatial interactions might have been degraded by amblyopia. This degradation exists not only in the areas of the strabismic visual cortex responding to foveal stimuli but also in those responding to stimuli presented in the temporal visual fields. (*Optom Vis Sci* 1998;75:424-432)

Key Words: naso-temporal asymmetry, spatial interaction, strabismic amblyopia, Westheimer effect

Amblyopia is a developmental anomaly associated with unilateral loss of spatial visual functions attributable to constant strabismus, anisometropia, or form deprivation. Visual acuity, contrast sensitivity, and positional acuity are typically reduced in the fovea of amblyopic eyes. Abnormalities are also seen in various types of spatial interactions between different objects, such as the crowding effect in letter recognition, spatial facilitation between spatially separated objects, and the Westheimer effect²⁻⁵ in foveal vision.

Several reports have suggested naso-temporal asymmetries of visual acuity and contrast sensitivity in strabismic amblyopia. Sireteanu and Fronius⁶ reported that the visual acuity loss in eso-tropic amblyopic eyes, which is confined to the central part of the visual field, is more severe in the nasal retina than in the temporal retina, in contrast to anisometropic amblyopic eyes, in which symmetric visual acuity loss occurs across the retina. Similar naso-temporal asymmetries of incremental threshold and contrast sensitivity loss in esotropic amblyopia also have been reported by other investigators.⁷⁻⁹ In this paper, we report a novel and pronounced type of naso-temporal asymmetry in two amblyopes, one esotropic and the other exotropic: both show greater loss of spatial interactions in the temporal visual field (nasal retina) than in the nasal visual field (temporal retina).

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We applied a variation of the Westheimer paradigm^{10,11} to evaluate spatial interactions in the nasal and temporal visual fields of strabismic amblyopic eyes. In a conventional Westheimer paradigm,^{10,11} increment thresholds for a spot target centered on a circular background of various diameters are measured. Typically, thresholds first increase until reaching a peak (desensitization), then decrease until reaching a plateau (sensitization), as the background diameter increases. The sensitization, or Westheimer effect, is explained as the results of spatial interactions between the center and the antagonistic surround of a perceptive field responding to the spot target.^{10,11} This perceptive field has been commonly interpreted as an analog to the center-surround organization of retinal cell receptive fields,¹⁰⁻¹² a view that has been challenged recently by the demonstration of a cortical component of the Westheimer effect.⁵ In our variation of the Westheimer paradigm, increment thresholds for a single line centered on a rectangular background of variable length or width^{13,14} are measured. The resulting desensitization and sensitization along the length and width dimensions are referred to as length and width Westheimer functions, respectively.¹⁴ Evidence from spatial scaling studies,¹⁵ which measured the spatial scales of desensitization and sensitization in both length and width functions across the visual field, from dichoptic studies,⁴ which measured length and width functions while presenting the target and background to different eyes, and from amblyopic studies,⁴ which measured

length and width functions on amblyopic eyes (see below), suggests that these spatial interaction functions have a conical origin and likely reflect center-surround spatial interactions in conical spatial filters. Specifically, desensitization in length and width functions is taken as mirroring central length and width summation in spatial filters, and sensitization in length and width functions as mirroring spatial filter end stopping and flank inhibition, respectively. Moreover, foveal length and width functions measured in strabismic amblyopes show moderately increased central summation and severely depressed or even absent flank inhibition and end stopping,⁴ suggesting significant foveal loss of spatial interactions and the alteration of spatial filter organization by amblyopia.

In this study, length and width Westheimer functions for line stimuli of equal visibility were measured on two strabismic amblyopes and one normal observer at a retinal eccentricity of 10 deg in both the nasal and temporal visual fields. The results show impaired spatial interactions in the temporal visual fields but intact interactions in the nasal visual fields. Thus, in strabismic amblyopia, naso-temporal asymmetries exist not only in basic visual processes such as visual acuity and line detection but also in more complex processes such as spatial interaction. This naso-temporal asymmetry of spatial interactions might reflect an asymmetry in the organization of spatial filters in the temporal and nasal afferents to the visual cortex resulting from the different effects of abnormal binocular vision in early development.

METHODS

Observers

Two amblyopes (AJ and RH) and one normal observer (LN) participated in the experiments. The two amblyopes (RH, male, 25 years old; AJ, female, 26 years old) were well documented and highly experienced in psychophysical observations. Both RH and AJ were small-angle strabismic, but RH was esotropic and AJ was exotropic. AJ was also anisometropic. The detailed visual characteristics of both amblyopes are listed in Table 1. Neither subject had undergone surgery, and inspection of early-childhood photographs of observer AJ revealed exotropia as early as about 4 to 5 years of age. The normal observer (LN, male, 20 years old) was emmetropic and had no previous psychophysical experience. None of the observers was aware of the purpose of the study. The protocols were reviewed by The University of Houston Institutional Review Board, and informed consent was received from all observers.

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 (3.8 X 3.0 deg at a distance of 5.64 m). 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 a 15 bit look-up table. Observers were positioned by means of a chin rest at 5.64 m from the screen for foveal viewing and one-fourth of the foveal viewing distance (1.41 m) for peripheral viewing at the 10 deg retinal eccentricity. Viewing was monocular by the dominant eye (right eye) of the normal observer and both the amblyopic and preferred eyes of the amblyopes. Experiments

were run in a dimly lit room, with a low-watt light on the back of the monitor.

The typical stimulus (Fig. 1) was an increment target line centered on a rectangular background and presented at the 10 deg retinal eccentricity* on either the temporal or the nasal side of the horizontal meridian of the visual field. In a given experiment, only one dimension (e.g., length or width) of the rectangular background 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 during the measurements of length Westheimer spatial interaction functions. When the width Westheimer spatial interaction functions were measured, both the target line and the background were set to horizontal. In this way, the width of the background was varied vertically so that the retinal eccentricity would remain fairly constant, particularly when the background was very wide. Previous data¹⁴ demonstrated that results from horizontal and vertical conditions do not differ. The luminance of the monitor screen was constant (6.8 cd/m²) during all the experiments, as was the luminance of the rectangular background (26.7 cd/m²). The luminance of the target line was varied by a staircase procedure as the dependent measure. In experiment 1, increment thresholds for a foveal line (with no background) and its magnified forms at the 10 deg nasal and temporal retinal eccentricities were also measured.

Procedure

A successive two-alternative forced-choice procedure was used. The background was presented in each of the two intervals (400 ms each) separated by an interstimulus interval (400 ms). In one of the two intervals, the target line was also presented for the same duration (400 ms). In foveal viewing, each trial was preceded by a fixation cross that disappeared 100 ms before the beginning of the trial. For peripheral viewing, the fixation cross was present during 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 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 mean of six experimental reversals was defined as the increment threshold. One experimental session usually consisted of 9 to 10 background conditions presented in a random order and lasted for about 40 min. Each datum represents the mean of five replications for each condition, and the error bars represent ± 1 SEM.

EXPERIMENT ONE: MEASUREMENTS OF SCALING FACTORS

To compare spatial interactions between the nasal and temporal visual fields within and across the preferred and amblyopic eyes

* Because of the 1.5 deg temporal eccentric fixation, the stimuli were actually presented in the temporal visual field of about 8.5 deg retinal eccentricity or in the nasal visual field of about 11.5 deg retinal eccentricity in AJ's amblyopic eye. Therefore, the measured spatial interaction defects in (his eye, which are shown mainly in the temporal visual field, could be smaller than their actual values, and the naso-temporal asymmetry of spatial interactions could be even larger than demonstrated.

TABLE 1.

Visual characteristics of the two amblyopic observers.

Observer	Type	Eye	Prescription	Acuity ^a	Fixation ^b	Strabismus
RH	Strabismic	OD	-1.00/-0.50 × 170	20/15	Central	Microtropia left esotropia, 2 ^A
		OS	-1.50/-1.50 × 10	20/48	Unsteady	
AJ	Strabismic/ anisometropic	OD	+5.50/-2.50 × 20	20/60	1.5 deg temporal	Constant right exotropia, 4 ^A
		OS	-0.25	20/15	Central	

^a Seventy-five percent correct on Davidson-Eskridge charts.^b Fixation determined with Haidinger's brushes and visuoscopy.

and between the fovea and the periphery, the visibility of stimuli at all testing retinal locations should be equated, because visual spatial sensitivity might be different as a result of the visual defect, the hemisphere difference, and the decline of neural sampling with increasing retinal eccentricity.¹⁶ Such a measure would ensure that any variation in length and width Westheimer functions reflects the change of spatial interaction, not the sensitivity difference. To do so, we measured scaling factors for the line targets in both the nasal and temporal visual fields of the preferred and amblyopic eyes' required to match the visibility of a foveal line target. These scaling factors were used in later experiments to magnify peripheral stimuli to equate their visibility. Specifically, increment thresholds for a foveal 1 × 5 arc min line (without the background present) were measured, as were those for a series of its magnified forms at the 10 deg retinal eccentricity in the nasal and temporal visual fields of each eye. The magnification factors were 2.00, 2.66, 3.33, 4.00, and 4.66 for both the length and the width of the line. The luminance of the screen was 26.7 cd/m², the same as the background field luminance in later experiments.

The peripheral data were fitted with an exponential equation, $T = aM^b$, where T refers to increment threshold, M to magnification factor, and a and b are free parameters. The magnification factor was taken as the scaling factor for each hemifield condition when the peripheral threshold matched the foveal threshold. Examples of the results obtained with this procedure are shown in Fig. 2. The scaling factors under different experimental conditions are listed in Table 2 for each observer.

Table 2 shows that the scaling factors between the nasal and temporal visual fields of the preferred and normal eyes were basically the same (3.90 vs. 3.88 in terms of mean magnification factors). The scaling factors in the nasal and temporal visual fields of the amblyopic eye were the same for RH and slightly different for AJ (a difference of 0.25 in terms of the magnification factor), which does not suggest a naso-temporal asymmetry of increment

thresholds as shown in previous studies. However, there were larger differences between the preferred and amblyopic eyes in each visual hemifield. The scaling factor difference in the nasal visual field was 0.41 for RH and 0.42 for AJ, and in the temporal visual field it was 0.17 for RH and 0.36 for AJ, with amblyopic eyes always having higher scaling factors; this suggests reduced sensitivity in both hemifields of amblyopic eyes, although not all cases show significant differences.

EXPERIMENT TWO: LENGTH AND WIDTH SPATIAL INTERACTIONS IN THE NASAL AND TEMPORAL VISUAL FIELDS OF AMBLYOPIC EYES

After matching the visibility of stimuli under different experimental conditions (experiment 1), the net effects of amblyopia on length and width spatial interactions could be examined in the nasal and temporal visual fields. Length and width functions were measured at the 10 deg retinal eccentricity of nasal and temporal visual fields in AJ's and RH's preferred and amblyopic eyes as well as in LN's normal (right) eye.

The target lines were the magnified version of a 1 × 5 arc min line in both width and length dimensions (magnified by each observer's corresponding scaling factors determined in experiment 1). For the measurement of each length function, the width of the background was set at 3 arc min times the corresponding scaling factor, and the length was varied from 6 to 105 times the scaling factor. For the measurements of each width function, the length of the background was set at 6 arc min times the corresponding scaling factor, and the width was varied from 3 to 70 times the scaling factor. In this way, not only was the visibility of stimuli in the nasal and temporal visual fields of both eyes equated, but the results also could be compared with foveal data for the same two amblyopes⁴ whose length and width functions were measured with a 1 × 5 arc min target line centered on either a 3 arc min-wide background of variable length (foveal length functions) or a 6 arc min-long background of variable width (foveal width functions).

+

fixation point



FIGURE 1.

An example of stimuli. The increment target line is centered on a rectangular background on the 10 deg temporal visual field. In this case, the background length is varied to measure the length Westheimer function.

Comparison of spatial interactions between nasal and temporal visual fields

Amblyopic and nonamblyopic length spatial interaction functions are shown in Fig. 3, (a) and (b), respectively. The background lengths or widths in each function have been normalized by their corresponding scaling factors to make the background scales on the x axes comparable across conditions. In this way, backgrounds of a

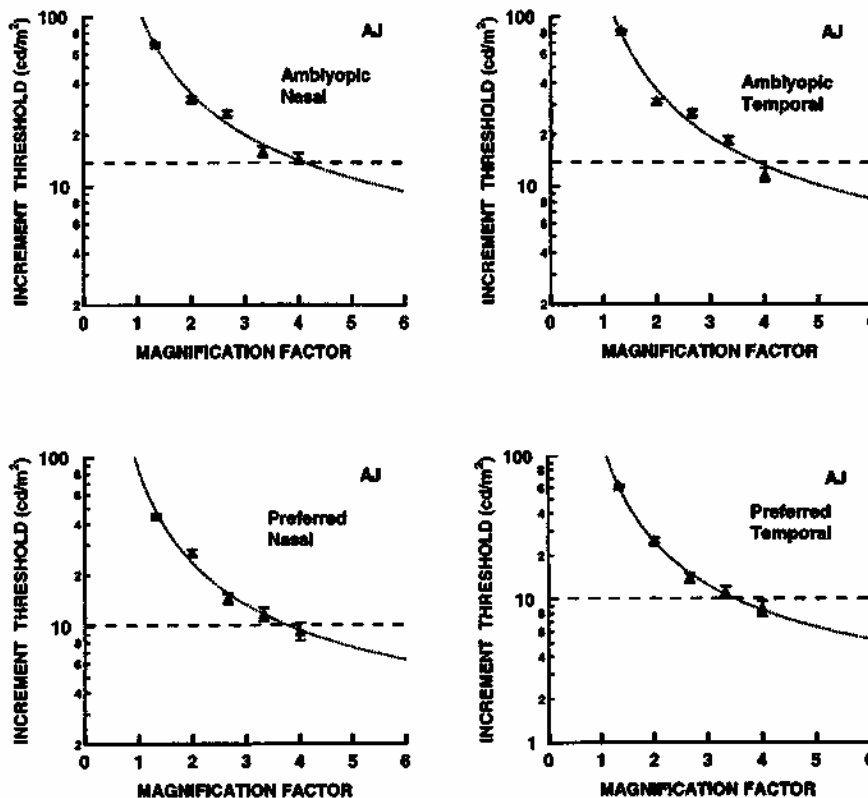


FIGURE 2.

Examples of data fitting and scaling factor derivation for observer A). Data were measured at the 10 deg nasal and temporal visual fields for both eyes. The raw data (A) are first fitted by an exponential equation (see text). The magnification factors for which fitted data (dotted curves) match foveal thresholds (dashed horizontal lines) are taken as scaling factors.

TABLE 2. Scaling factors for each visual hemifield at the 10 deg retinal eccentricity.

Observer	Nasal Preferred	Nasal Amblyopic	Temporal Preferred	Temporal Amblyopic
RH	4.11	4.52	4.42	4.59
AJ	3.69	4.11	3.50	3.86
LN	3.90		3.72	

certain size on the x axis are equivalent in terms of visibility, and their effects can be compared directly. The overall threshold level of the temporal-field length functions is significantly higher than that of the nasal-field length functions in the amblyopic eyes. The average threshold elevation in the temporal-field length functions of the amblyopic eyes relative to the nasal-field length functions of the same eyes was 0.24 log units for AJ, 0.33 log units for RH, and 0.29 log units on average. However, this difference was not seen in length functions of preferred and normal eyes. The average threshold elevation in the temporal-field length functions of the preferred eyes was -0.02 log units for AJ, 0.01 log units for RH, 0.03 log units for LN, and 0.01 on average, compared with that in the nasal-field length functions.

In spite of the overall threshold elevation in amblyopic temporal-field functions, the differences between AJ's and RH's amblyopic temporal- and nasal-field length functions were not uniform. In AJ's functions, the peak positions and prepeak threshold eleva-

tion (central summation; see introduction) differed only slightly, whereas the most notable difference occurred in after-peak threshold reduction (inhibition), which in the temporal-field function was very weak but was strong in the nasal-field function. The strongest after-peak threshold reduction (the strength of inhibition) in the temporal-field length function was only 0.09 log units, in contrast to 0.34 log units in the nasal-field length function. On the other hand, RH's temporal-field length function showed a larger peak position (23 in terms of the normalized background length) than did the nasal-field function (11 in normalized background length), indicating broader length summation. In contrast to the striking difference in the amblyopic eyes, nasal- and temporal-field functions in preferred and normal eyes were very similar. Nasal- and temporal-field functions were virtually identical in RH and the normal observer (LN), with an average difference of thresholds equal to 0.03 log units for RH and <0.01 log units for LN. AJ's functions also showed similar peak positions and overall

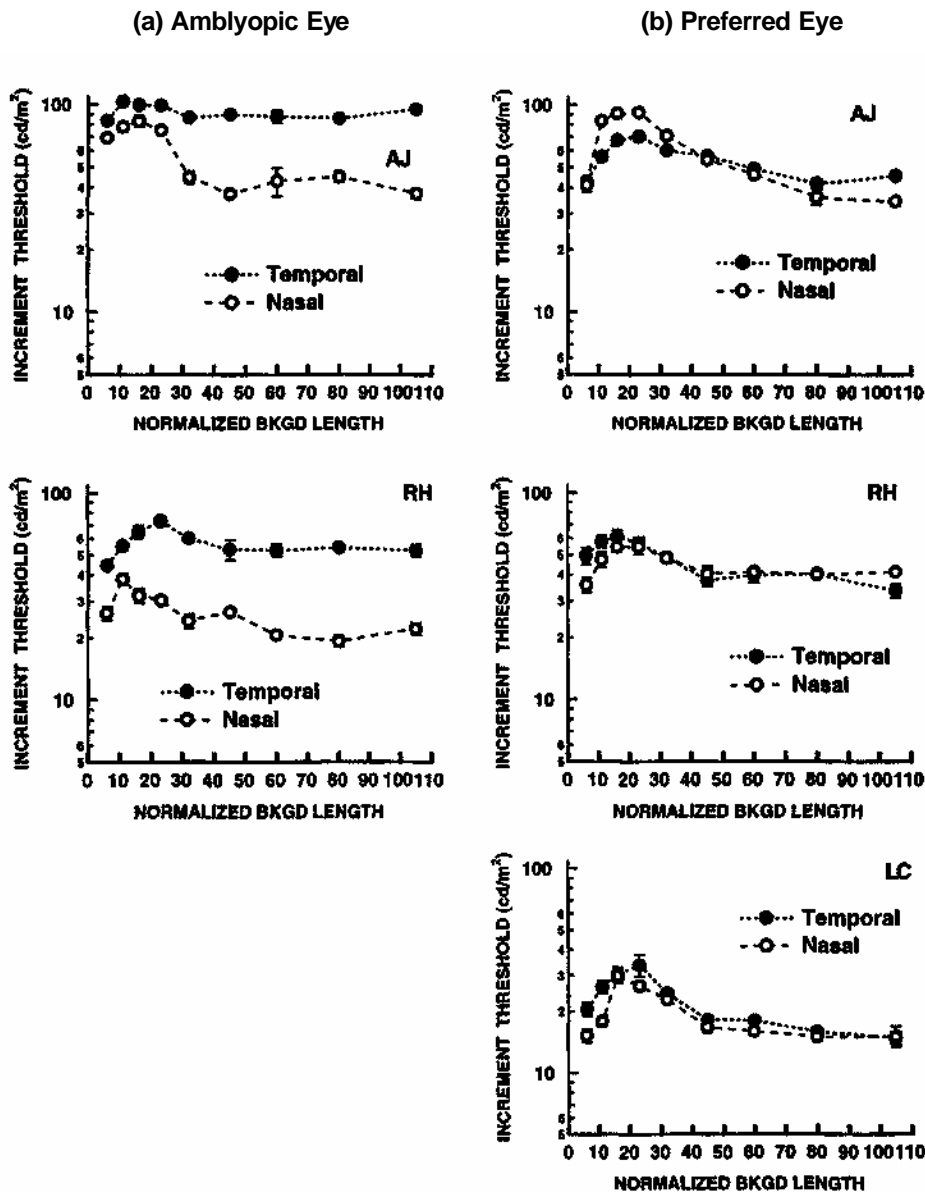


FIGURE 3.

Panels (a) and (b) show nasal- and temporal-field length Westheimer functions in amblyopic and preferred (normal) eyes, respectively. The background lengths in each function have been normalized by their corresponding magnification factors.

threshold levels (<0.02 log unit difference), but the nasal-field function showed higher thresholds around the peak, suggesting that temporal-field thresholds could be lower than the nasal-field thresholds, which was not seen in the amblyopic length functions. In general, these results indicate generally impaired length spatial interactions in the temporal visual fields of two strabismic amblyopic eyes, and inhibition appears to be more vulnerable to amblyopia than does central summation.

Amblyopic and nonamblyopic width spatial interaction functions are shown in Fig. 4, (a) and (b), respectively. Again, the overall threshold level of the temporal-field width function was significantly higher than that of the nasal-field width function in the amblyopic eyes. The average threshold elevation in the temporal-field width functions of the amblyopic eyes relative to the nasal-field width functions of the same eyes was 0.27 log units for AJ and

0.22 log units for RH. Specific alternations in the temporal-field width functions relative to the nasal-field width functions of AJ's and RH's amblyopic eyes were similar to the changes in their length functions. AJ's amblyopic width functions again showed similar central summation and peak positions, the main difference being weaker inhibition in the temporal-field function. The difference between nasal- and temporal-field inhibition was even stronger for width than for length (the mean and maximal differences were 0.32 and 0.68 log units, respectively, in contrast to 0.28 and 0.36 log units in AJ's length functions). The strongest after-peak threshold reductions in the temporal-field width function were 0.17 log units for AJ and 0.34 log units for RH, which were stronger than the corresponding values in the two observers' length functions (0.09 log units for AJ and 0.16 log units for RH), indicating less affected inhibition in the width functions. The reduc-

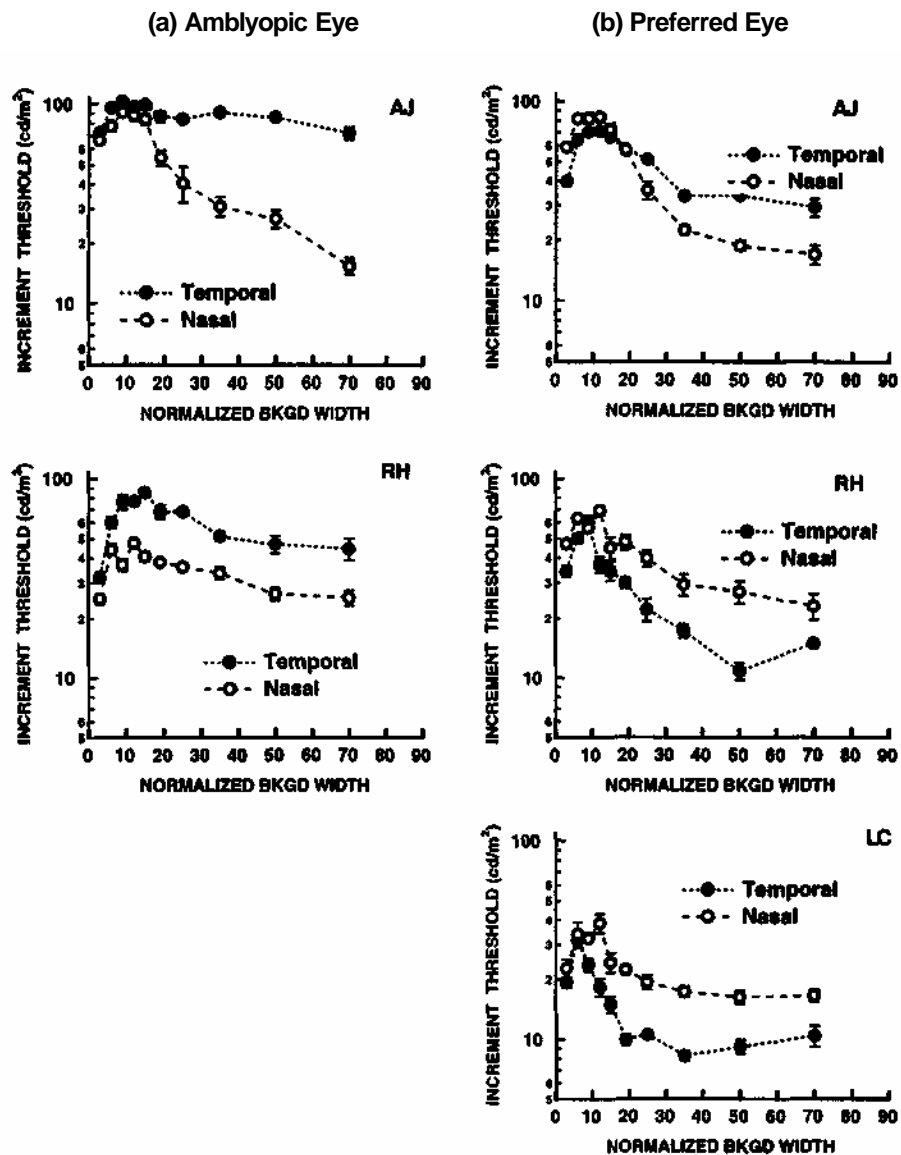


FIGURE 4. Panels (a) and (b) show nasal- and temporal-field width Westheimer functions in amblyopic and preferred (normal) eyes, respectively. The background widths in each function have been normalized by their corresponding magnification factors.

tion in the nasal-field width function was as strong as 0.80 log units for AJ, indicating substantially impaired inhibition in the temporal visual field of her amblyopic eye. However, the strength of inhibition in RH's nasal-field width function was 0.29 log units, similar to that of the temporal-field width function.

The results in preferred or normal eyes were less consistent. Two observers showed higher nasal-field thresholds and one showed higher temporal-field thresholds, mainly contributed by weaker inhibition in either temporal-field (AJ) or nasal-field functions (RH and LN). The average threshold increases in the temporal visual fields of the preferred eye were 0.04 log units for AJ, -0.17 log units for RH, -0.10 log units for LN, and -0.08 log units on average. These results suggest that temporal-field spatial interactions in preferred and normal eyes could be stronger than nasal spatial interactions in some cases, providing further evidence that temporal-field spatial interactions are more impaired by strabismic amblyopia.

Comparison of spatial interactions between amblyopic and preferred eyes

One interesting question is whether the spatial interaction loss in strabismic amblyopia occurs only in one visual hemifield or whether both hemifields are affected, albeit differently. Thus, we compared length and width spatial interactions in the temporal visual fields (Fig. 5) and nasal visual fields (Fig. 6) between the amblyopic and preferred eyes. In the temporal visual fields, the overall threshold levels in the amblyopic eyes were always higher than those in the preferred eyes (0.23 log units on average), with more severe sensitivity loss occurring in the width functions (0.29 log units on average). However, in the nasal visual fields, the threshold levels were similar between amblyopic and preferred eyes (-0.07 log units average loss, mostly contributed by RH's length functions, which showed 0.23 log unit higher thresholds in the preferred eye, and 0.03 to 0.06 log unit difference in other func-

Temporal Visual Fields

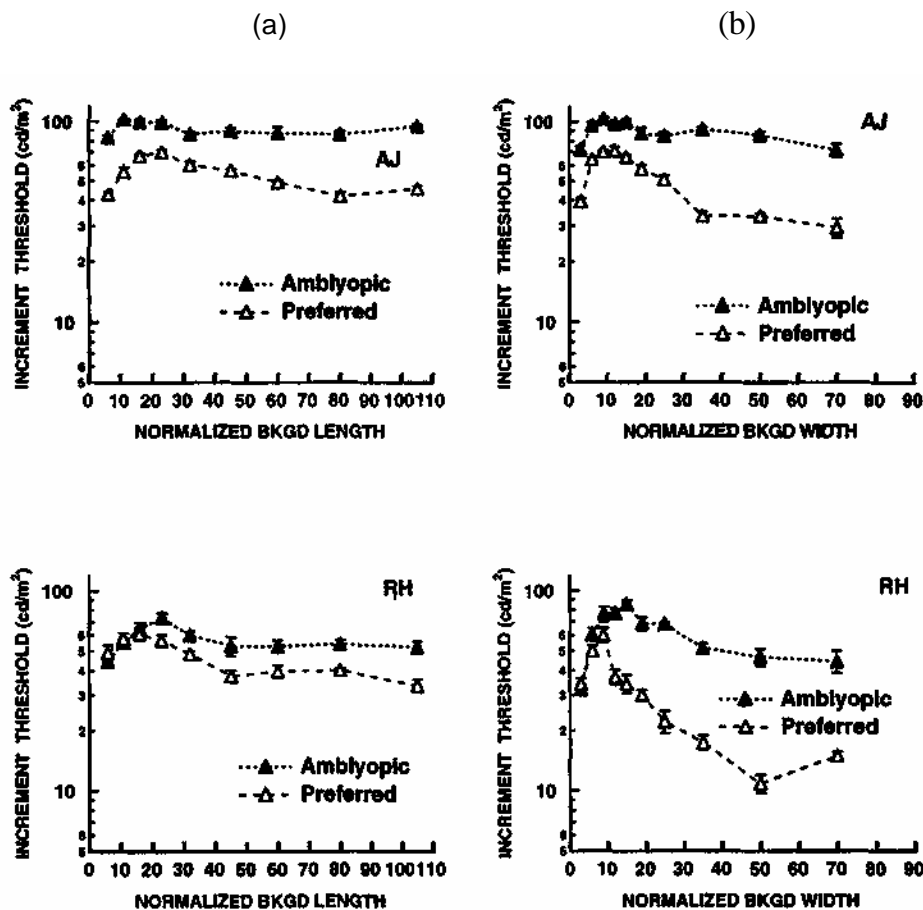


FIGURE 5. Temporal-field functions compared between amblyopic and preferred eyes, (a): Length functions, (b): Width functions.

tions). This difference suggests that only spatial interactions in the temporal visual fields of these two amblyopic eyes were affected by the visual defect, whereas those in the nasal visual fields were basically intact.

The average spatial interaction loss between the amblyopic and preferred eyes in two amblyopic observers' temporal- and nasal-field length and width functions are summarized in Fig. 7. The spatial interaction loss in the foveal length and width functions of the same two observers is also presented for comparison. The most severe visual spatial interaction loss occurred in the fovea, with an average loss of 0.69 log units over the four individual functions. The temporal visual fields were less, but still significantly, affected, with an average loss of 0.23 log units. The nasal visual fields essentially showed no effects of amblyopia on spatial interactions. The average loss was -0.07 log units, or in other words, no loss.

DISCUSSION

Our results indicate a novel type of naso-temporal asymmetry of cortical spatial interactions in strabismic amblyopia. At the 10 deg temporal and nasal retinal eccentricities, the asymmetries in our two amblyopes were contributed mainly by the loss of spatial in-

teractions in the temporal visual fields, compared with normal spatial interactions in the nasal visual fields. This loss of spatial interactions in the temporal visual fields is in general consistent with more severe loss of visual acuity and contrast sensitivity in the nasal retina, as reported previously. Moreover, this loss is not limited to esotropia but also occurs in exotropia.

The severe loss of visual function in the temporal visual field of strabismic amblyopic eyes is apparently unrelated to the asymmetry of visual development between nasal and temporal vision in humans.¹⁷ The sensitivity of the nasal visual field, which is slow to mature, is more vulnerable to abnormal visual input during its development. Thus, anything related to this developmental asymmetry should predict a more severe loss of visual functions in the nasal visual fields, rather than the temporal visual fields, as our results suggest.

Sireteanu and Fronius⁶ attributed naso-temporal asymmetries of visual acuity and contrast sensitivity in strabismic amblyopic eyes to asymmetric prolonged interocular suppression, on the basis that for several esotropes the more severe acuity loss in the nasal retina was also accompanied by deep interocular suppression. The simple suppression model of Sireteanu and Fronius⁶ and of Jam-

Nasal Visual Fields

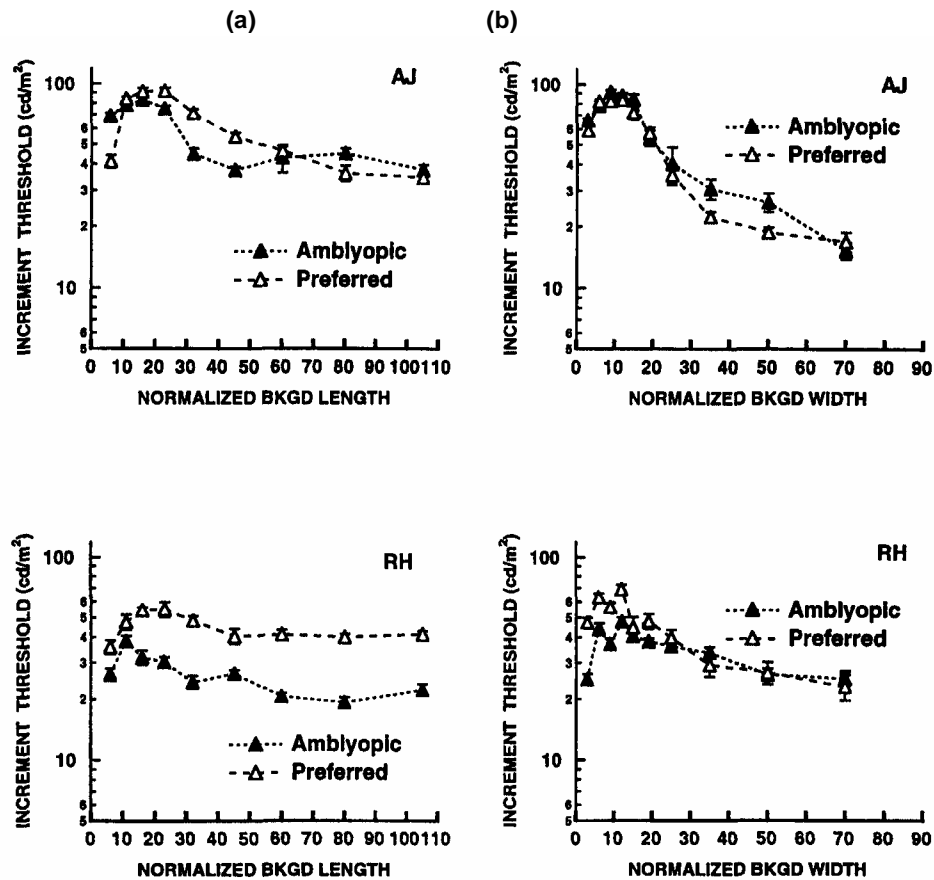


FIGURE 6. Nasal-field functions compared between amblyopic and preferred eyes. (a): Length functions. (b): Width functions.

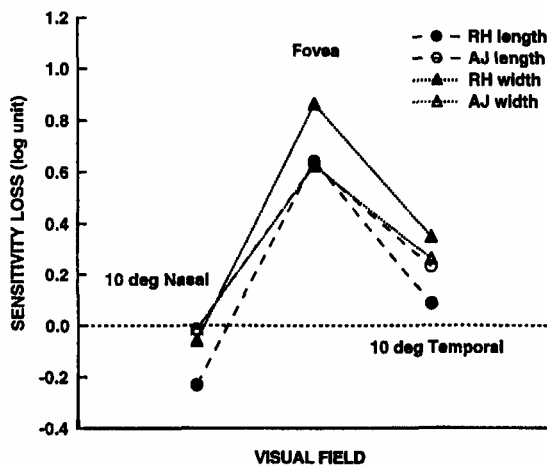


FIGURE 7. The average spatial interaction loss between the amblyopic and preferred eyes in two amblyopic observers' foveal, temporal-field, and nasal-field length and width functions. Foveal data are from a previous paper.

polsky¹⁸ suggests that, in esotropes, the nasal retina (temporal field) is suppressed, whereas in exotropes, the temporal retina (nasal field) is suppressed. However, this assumption fails to account

for the same naso-temporal asymmetry of spatial interactions in at least some exotropes, such as AJ in the current study and one exotrope in one of Sireteanu and Fronius's later studies.¹⁹ It also fails to account for the reduced resolution and increased contour interaction in the temporal field (nasal retina) of exotropic amblyope JL in the study of Hess and Jacobs.²⁰ Although it is clear from a large number of studies that strabismic suppression is always strong in the fovea of the deviated eye, the regional distribution of strabismic suppression is controversial and not well understood. Some works have reported suppression of the whole eye,²¹ whereas others have reported hemiretinal¹⁸ or discrete⁶ regions of suppression. Although workers are beginning to investigate the neurophysiological basis of suppression,²² we do not yet have a firm understanding of the cause of the naso-temporal asymmetry evident in our strabismic amblyopes.

The length and width Westheimer functions have been attributed to the center-surround spatial interactions in the cortical spatial filters. Thus, the reduction and the naso-temporal asymmetry of spatial interactions may reflect the abnormalities of spatial filter organization in the strabismic amblyopic visual system. Our previous results suggest that, in the fovea, the abnormalities are related mainly to dramatically reduced surround antagonism, including

flank inhibition and end stopping. Current data show that these abnormalities, to a lesser degree, still exist in spatial filters in cortical areas responding to the temporal peripheral visual field of the amblyopic eyes but are absent in cortical areas responding to the nasal peripheral visual field of the same amblyopic eyes. The abnormalities in foveal and temporal peripheral spatial filters might result from the alterations of intrinsic connections that affect the receptive field properties in the visual cortex.²³

In experiment 1, no naso-temporal asymmetry of increment thresholds for line detection was present in either amblyopic observer. However, these results may not be used to argue against the visual acuity and contrast sensitivity asymmetries observed in previous studies. One reason could be that the moderate amblyopia in both amblyopes (20/60 for AJ and 20/48 for RH) might not lead to an appreciable asymmetry of increment thresholds, which is consistent with some previous results.⁷ Moreover, both amblyopes had been observers in psychophysical experiments for a prolonged period, and the foveal visual acuity for RH had been dramatically improved from the initial value of 20/175 to the current 20/48. The learning effect might have further reduced potential acuity asymmetry to a negligible level. However, significant asymmetries of spatial interactions in the same two amblyopes suggest that these specific functions are not affected to the same degree, implying that at least some types of learning-led recovery of visual functions in amblyopia are function specific and may not be easily transferred to other functions. This specificity in perceptual learning is consistent with recent findings by Levi et al.²⁴

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