



# Suppressive and facilitatory spatial interactions in amblyopic vision

Dennis M. Levi<sup>a,\*</sup>, Srividhya Hariharan<sup>b</sup>, Stanley A. Klein<sup>a</sup>

<sup>a</sup> School of Optometry, University of California, Berkeley, CA 94720, USA

<sup>b</sup> College of Optometry, University of Houston, Houston, TX 77204-6052, USA

Received 1 August 2001; received in revised form 1 March 2002

---

## Abstract

Amblyopic vision is characterized by reduced spatial resolution, and inhibitory spatial interactions (“crowding”) that extend over long distances. The present paper had three goals: (1) To ask whether the extensive crowding in amblyopic vision is a consequence of a shift in the spatial scale of analysis. To test this we measured the extent of crowding for targets that were limited in their spatial frequency content, over a large range of target sizes and spatial frequencies. (2) To ask whether crowding in amblyopic vision can be explained on the basis of contrast masking by remote flanks. To test this hypothesis we measured and compared crowding in a *direction-identification* experiment with masking by remote flanks in a *detection experiment*. In each of the experiments our targets and flanks were comprised of Gabor features, thus allowing us to control the feature contrast, spatial frequency and orientation. (3) To examine the relationship between the suppressive and facilitatory interactions in amblyopic contrast detection and “crowding”.

Our results show that unlike the normal fovea [Levi, Klein, & Hariharan, *Journal of Vision* 2 (2002a) 140] crowding in amblyopia is neither scale invariant, nor is it attributable to simple contrast masking. Rather, our results suggest that suppressive spatial interactions in amblyopic vision extend over larger distances than in normal foveal vision, similar to peripheral vision of non-amblyopic observers [Levi, Hariharan, & Klein, *Journal of Vision* 2 (2002b) 167], for targets of the same size. Observers can easily detect the features that comprise our targets (Gabor patches) under conditions where crowding is strong. Thus, our speculation is that crowding occurs because the target and flanks are combined or pooled at a second stage that is coarse in the amblyopic visual system, following the stage of feature extraction. In amblyopic vision, this pooling takes place over a large spatial distance. © 2002 Elsevier Science Ltd. All rights reserved.

---

## 1. Introduction

Spatial interactions are a critical and ubiquitous feature of spatial vision, which serve to sharpen perception of form, enable features to be grouped into forms, and which are thought to have their neural basis in lateral interconnections in the visual nervous system (see Gilbert (1998) for a review). Experimental strabismus damages these connections in cats (Lowel & Singer, 1992) and monkeys (Tychsen & Burkhalter, 1995). Spatial interactions may be either suppressive (reducing sensitivity) or facilitatory (enhancing sensitivity).

One form of suppressive spatial interaction is contour interaction or crowding. The term “crowding” was first coined by Stuart and Burian (1962) to describe the observation that amblyopes frequently showed worse visual acuity when presented with a line of letters, than

when the letters were isolated. However, more recently crowding (or contour interaction) has been used more generally to describe the deleterious influence of nearby features on visual discrimination (see Flom (1991) for a review of crowding and contour interaction). Crowding may cause a letter flanked by adjacent bars or letters to be more difficult to identify than the same letter presented in isolation (e.g. Flom, Weymouth, & Kahneman, 1963; Toet & Levi, 1992). In amblyopic vision, crowding extends over much greater distances than in the fovea (e.g., Flom et al., 1963; Hess & Jacobs, 1979; Levi & Klein, 1985). In their classical study, Flom et al., 1963 estimated the extent of crowding by having normal and amblyopic observers judge the orientation of a Landolt C, and varying the distance of surrounding flanks from the C. They found that the extent of crowding (i.e., the distance over which the flanks interfered with performance) was proportional to the minimum angle of resolution (MAR). Flom et al. (1963) suggested that crowding is related to the size of the receptive fields that are most sensitive to the target. Since

---

\* Corresponding author. Fax: +1-510-642-7806.

E-mail address: dlevi@spectacle.berkeley.edu (D.M. Levi).

amblyopic vision is characterized by reduced visual acuity (increased MAR), larger receptive fields will be engaged (since small receptive fields have low sensitivity), and this “scale shift” will result in proportionally larger crowding distances (see also Levi, Waugh, & Beard, 1994). This “scale shift” hypothesis makes three predictions. First, it predicts that in peripheral or amblyopic vision, the spatial extent of crowding (with broadband stimuli) will scale with (be proportional to) the uncrowded acuity. Indeed, for both letter acuity (Flom et al., 1963; Hess & Jacobs, 1979; Simmers, Gray, McGraw, & Winn, 1999) and Vernier acuity (Levi & Klein, 1985) the spatial extent of crowding appears to scale with the unflanked letter or Vernier acuity respectively in amblyopia. Secondly, the scale shift hypothesis also predicts that the spatial extent of crowding will depend on the size or spatial frequency of the target, i.e., crowding will be size (or spatial frequency) invariant (this point can be thought of as the definition of the scale shift hypothesis). Indeed we have shown that in the normal fovea, the extent of crowding depends on target size over a 50-fold range of target sizes (Levi, Klein, & Hariharan, 2002a). Third, it predicts that the extent of crowding would be similar in normal and amblyopic vision when the targets are large relative to the acuity limit.

As noted above, several studies have addressed the first prediction. However, a recent study (Hess, Dakin, Tewfik, & Brown, 2001) shows that in some strabismic amblyopes, the extent of contour interaction may be as much as five times larger in the amblyopic eye, even when scaled in terms of the acuity. This result is important because it casts doubt on the notion that the mechanism of crowding is qualitatively similar in normal foveal vision and in amblyopia, differing only by a scale factor (the acuity). One purpose of the present paper was to test the scale-shift hypothesis for crowding in amblyopic vision. To test this hypothesis, we measured the extent of crowding for targets that were limited in their spatial frequency content, over a large range of target sizes and spatial frequencies. Our bandlimited (0.825 octaves) stimuli ensure that the initial (linear) filters selected in amblyopic vision will be similar in scale to those selected for foveal viewing.

In normal foveal vision, crowding may be explained as a form of contrast masking by remote flanks. Thus, in normal vision, the threshold elevation for crowding is similar to threshold elevation for masking as predicted by a “Test-Pedestal” model (Levi et al., 2002a). Thus, a second purpose of the present paper was to ask whether crowding in amblyopic vision can be explained in the same way.

Spatial interactions may be facilitatory (enhancing sensitivity) as well as suppressive. For example, Polat and Sagi (1993, 1994) reported that remote Gabor patches could facilitate contrast detection in observers with

normal vision. They suggested that the facilitation that they observed (in normal foveal vision) was due to long-range cortical connections. A number of physiological studies have shown that responses of neurons in V1 can be modulated (either increased or decreased) by surrounding stimuli outside the classical receptive field (see for example, Gilbert (1998) and Fitzpatrick (2000) for reviews) due to long- and short-range interactions. Interestingly, Polat, Sagi, and Norcia (1997) reported that the facilitation evident in normal vision is weaker or absent in humans with naturally occurring amblyopia, and they suggested that the long-range interactions, so important for normal vision, are compromised by the amblyopic process. In their experiments with amblyopes, the effects were small, and variable. In their study, the observer’s task was to detect a Gabor patch in the presence of a pair of flanking Gabor maskers with a contrast of 40%. While normal observers showed strong facilitation of detection when the flankers were nearby (2–3 wavelengths), the amblyopic eyes showed less facilitation. However, they also showed less “suppression” (masking) at smaller separations. It is likely that the effect of the flanks will depend upon their visibility (i.e., the strength of the flank *relative* to the observers’ detection threshold). A ubiquitous finding is that amblyopic eyes have reduced contrast sensitivity, particularly at high spatial frequencies (Levi, 1991). Thus, it is quite possible that reduced contrast sensitivity decreased the visibility of the fixed contrast masks used by Polat et al. (1997), making them less effective in the amblyopic eyes.

Strabismic amblyopes show deficits in certain tasks involving perceptual grouping (which are sometimes presumed to be underpinned by lateral interactions). However, it is uncertain whether the deficits are a consequence of the reduced extent of global, integrative processes (Kovacs, Polat, Pennefather, Chandna, & Norcia, 2000), or whether they simply reflect deficits carried over from cortical units feeding into these global processes (e.g., Hess, McIlhagga, & Field, 1997; Levi & Sharma, 1998). In support of the latter, Hess et al. (1997) suggested that poor perceptual grouping in strabismics can be modeled by increased positional uncertainty (i.e., uncalibrated neural jitter) of cortical units, and Levi and Sharma (1998) showed that some context-dependent integration operates normally in strabismic amblyopes when their contrast sensitivity deficits are taken into account. Thus a third purpose of this study was to examine the relationship between the suppressive and facilitatory interactions in amblyopic contrast detection and “crowding”.

## 2. General methods

Our targets and flanks, and all the experimental details were identical to those described in detail elsewhere

(Levi et al., 2002a), so only a brief description of the methods will be given here. Targets and flanks comprised of Gabor or occasionally Gaussian patches, were displayed using a Cambridge Research Systems VSG 2/3 graphics card. Examples of our stimuli, with and without flanks, are shown in Fig. 1, and many more examples can be seen in Figs. 1, 2, 9 and 14 of Levi et al., 2002a. A total of six normal observers (including two of the authors) and seven amblyopic observers (two anisometropic, two with strabismus, and three with both strabismus and anisometropia) participated in parts of this study (see Table 1 for clinical details). Viewing was

monocular with the untested eye occluded with a black patch.

### 3. Experiment 1: is crowding in strabismic amblyopia size dependent?

#### 3.1. Methods

The “target” was an E-like figure comprised of 17 circular Gaussian (Fig. 1, top) or Gabor patches (Fig. 1, center). On each trial the target was briefly presented (for 195 ms) with one of four orientations (up, down, left, right) selected at random. The observer’s task was to identify the orientation. The target patches always contained a horizontal carrier, and each patch was separated from its neighbor by three standard deviations (center-to-center). The Gabor wavelength was half the separation, giving phase coherence across patches. This wavelength corresponded to a bandwidth of 0.825 octaves. The four surrounding flanking “bars” were each comprised of five Gaussian or Gabor patches (Fig. 1). Unless otherwise specified the orientation and spatial frequency of the flanks were identical to those of the target, and flank contrast was 90%.

In order to assess the influence of the flanks on pattern perception we measured the contrast threshold for identifying the orientation of the target using a four-alternative method of constant stimuli. Each threshold estimate, corresponding to the contrast resulting in 72.4% correct performance ( $d' \approx 1.6$  corresponding to the Weibull function threshold for 4-AFC), was based on 100 trials. The contrast thresholds presented in the Results section are the weighted means of at least four individual threshold estimates. The error bars represent plus or minus one sem and include both within and between run variation. From run to run, we varied the flank distance (including infinity which provided a measure of the unflanked performance) and the viewing distance in order to vary the target size.

Four amblyopes, all with constant strabismus participated in this experiment. The normal observers from Levi et al. (2002a) as well as the non-amblyopic eyes of present observers served as normal controls.

#### 3.2. Results

##### 3.2.1. Crowding in strabismic amblyopic vision extends over larger distances

In foveal vision, the extent of crowding depends on target size over a wide range of target sizes ( $\approx 50$ -fold range of target sizes—Levi et al., 2002a). In strabismic amblyopic vision (Fig. 2 solid symbols), for a given target size, crowding extends over larger distances, even with our bandlimited stimuli.

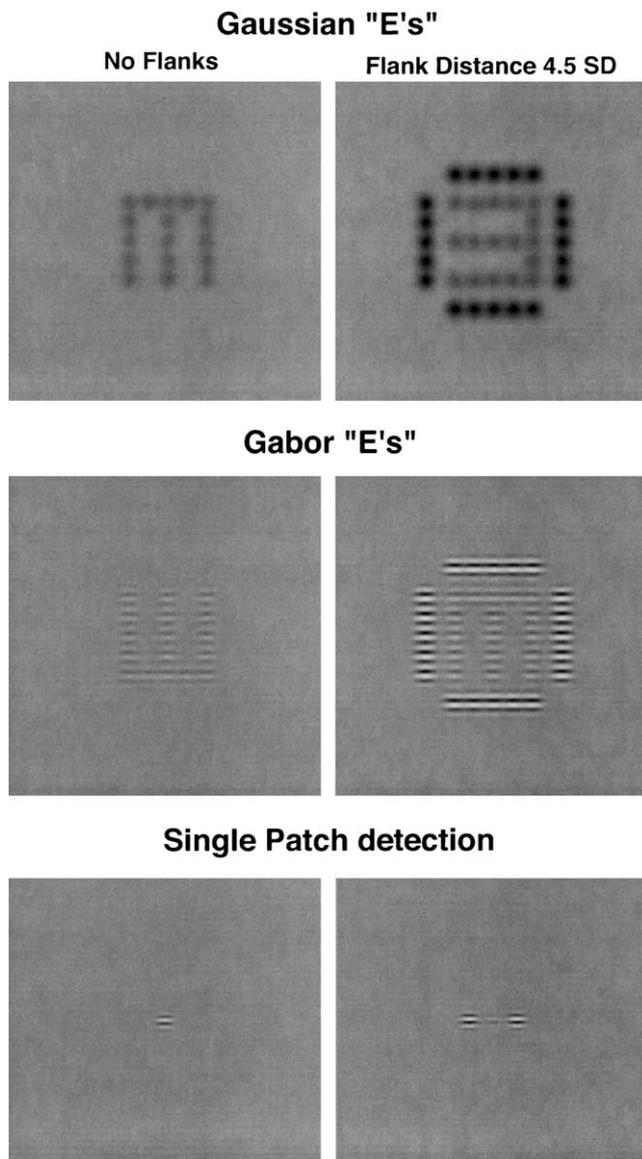


Fig. 1. Examples of our unflanked (left column) and flanked (right column) stimuli. The top row shows ‘E’s composed of 17 Gaussian patches, the middle row ‘E’s’ composed of 17 Gabor patches, and the bottom row a single Gabor patch. In each case the flank-to-target distance is 4.5 times the Gabor or Gaussian envelope standard deviation (see Section 3.1).

Table 1  
Visual characteristics of amblyopic observers

Observer	Age	Sex	Eye	Rx.	Acuity <sup>a</sup>	Fixation <sup>b</sup>	Strabismus
<i>Anisometric<sup>c</sup></i>							
AM	23	F	O.D.	+2.50/−1.0 × 005	20/45	Central	None
			O.S.	−0.25 DS	20/20	Central	
SL	26	M	O.D.	+6.25	20/38	Central	
			O.S.	+2.25	20/15	Central	None
<i>Strabismic</i>							
RH	32	M	O.D.	−1.00/−0.50 × 170	20/15	Central	
			O.S.	−1.50/−1.50 × 10	20/59	Unsteady	Microtropia l. et., 2 <sup>Δ</sup>
AH	22	F	O.D.	+0.25/−1.00 × 95	20/68	0.50° nasal	Constant r. et., 10 <sup>Δ</sup>
			O.S.	−0.25/−0.50 × 100	20/25	Central	
<i>Strab. &amp; Aniso.</i>							
DS	26	M	O.D.	+2.25 DS	20/40	2° nasal	Constant r. et., 8 <sup>Δ</sup>
			O.S.	+0.50 DS	20/20	Central	
DM	40	F	O.D.	−0.50/−0.25 × 92	20/20	Central	
			O.S.	+2.50/−1.0 × 160	20/80	0.50° nasal	Constant l. xt., 3 <sup>Δ</sup>
QM	20	M	O.D.	−0.50/−0.25 × 180	20/20	Central	
			O.S.	+1.75/−2.50 × 180	20/50	3° nasal	Constant l. et., 7 <sup>Δ</sup>

<sup>a</sup> 75% correct on davidson-eskridge charts.

<sup>b</sup> Fixation determined with haidinger's brushes and visuoscopy.

<sup>c</sup> No constant strabismus, and hyperopic anisometropia > +1.5d or myopic anisometropia > 4d.

There are several points of interest in Fig. 2: first in the non-amblyopic eyes of the amblyopic observers (open symbols) the distance over which flanks influence performance depends on the target size (Levi et al., 2002a). Second, the extent of crowding is increased in amblyopic eyes (solid symbols) when compared with the fellow non-amblyopic eyes. This is most evident for small targets (shown by small symbols). Interestingly, the increased extent of crowding can occur under conditions where the unflanked thresholds are essentially normal, as can be seen in the data of DS. For this observer, any alterations in the extent of crowding cannot be attributed to a loss of contrast sensitivity.

We quantified the extent of crowding, by fitting Gaussian functions to the data (lines in Fig. 2) and specifying the critical distance for crowding as the flank distance that causes the unflanked threshold to double (Levi et al., 2002a). The critical distance (specified in arcmin) is plotted as a function of target size for both Gaussian and Gabor E's (target size is the inside abscissa E's—Fig. 3).

In normal foveal vision the critical distance (in minutes) is more or less proportional to target size, falling close to the line of unity slope for both Gaussian E's and Gabor E's (Fig. 3). For a fixed size Gaussian E target (Fig. 3—gray symbols—the full crowding functions are shown in Fig. 4 as threshold elevation) the critical distance is bigger in amblyopic vision. Similar results are obtained when the flanks consist of just two patches, (the second and fourth patch of the five patch maskers) (data not shown). With very small Gaussian targets the extent of crowding in the amblyopic eyes is about four to seven times larger than normal. The result with

Gaussian targets are similar to those of previous workers (e.g., Flom et al., 1963; Hess et al., 2001). The stimuli are broadband, and therefore the increased extent of crowding may be a consequence of the amblyopic visual system engaging large (low) spatial frequency filters. Interestingly, qualitatively similar results are obtained with band-limited Gabor patches (colored symbols in Fig. 3). For very large target sizes (greater than about 150 min) the critical distance approaches (but is larger than) that of the normal fovea; however, for smaller targets the critical distance becomes considerably larger in the amblyopic eye. We shall argue below that a simple scale shift that depends on acuity cannot account for our results. An acuity dependent scale shift would lead to a hard "floor" (Fig. 3), where the extent of crowding is independent of target size. Rather, our results suggest a more complex scale shift, since the extent of crowding depends on target size.

In normal foveal vision, crowding is scale invariant, and is primarily determined by target size (SD). When replotted as threshold elevation (i.e., flanked threshold/unflanked threshold) versus target-to-flank distance expressed in standard deviation units (SDU—i.e., target-to-flank distance (in arcmin), divided by patch SD (in arcmin)), foveal performance over a wide range of pattern sizes collapses into a more or less unitary function (see Fig. 7 of Levi et al., 2002a). In the amblyopic eyes (Fig. 4), it is clear that crowding is not scale invariant. When plotted as threshold elevation versus target-to-flank distance (in SDU) it is clear that for small targets, the crowding does not scale to target size, but is disproportionately large—instead of the extent of crowding being  $\approx 2.5$  SDU as in the fovea, it may be as

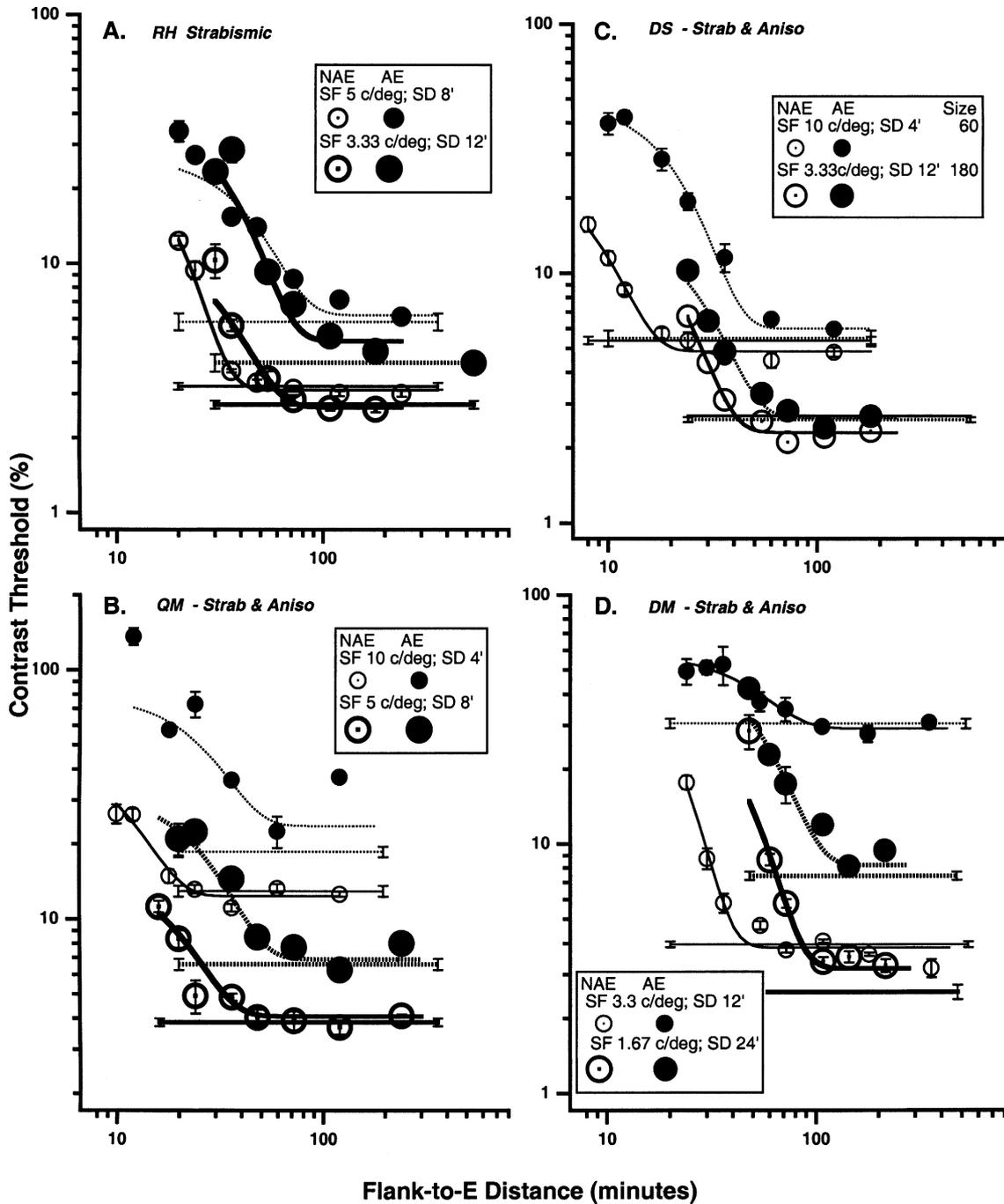


Fig. 2. Contrast thresholds versus flank distance for Gabor E's. Each panel shows data for both eyes of an amblyopic observer for two target sizes (coded by symbol size). In each panel, open symbols show the non-amblyopic eye; solid symbols are the amblyopic eye. Unflanked thresholds are shown by the lines (solid—NAE; dotted—AE).

large as 15 SDU in the central field of strabismic amblyopes (e.g. DS with Gaussian E's—Fig. 4—note that if the flanks were tiny Gaussians, the extent in SDU might have been even larger). This result is consistent with the recent study of Hess et al. (2001), showing that even after scaling for acuity, some amblyopes show crowding which is much more extensive than that of the normal fovea. It is also worth noting the small threshold ele-

vation (less than a factor of two) of observer DM. This is because her unflanked thresholds are so high (as can be seen in Fig. 2).

### 3.2.2. The effect of flank contrast

In strabismic amblyopia crowding can occur when the flanks are barely visible. In the experiments described so far the flank contrast was always high (90%).

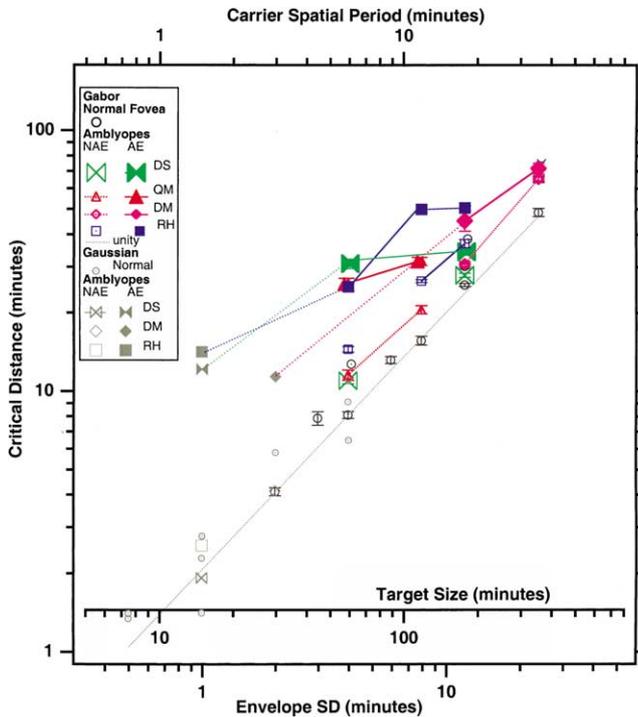


Fig. 3. The critical distance (i.e., the flank distance at which thresholds are elevated by a factor of 2, specified in arc min) versus target size for Gabor E's for the normal fovea (open black circles), and for each eye of the four amblyopic observers. Note that target size = 5 \* separation between patches; separation between patches = 3 \* SD and separation = 2 \*  $\lambda$ . The gray symbols are for Gaussian E's.

To test the effect of flank contrast, we placed the flanks at a distance (24' or 6 SDU) where they have little effect on performance of the normal (or non-amblyopic) eye, and varied the flank contrast. Fig. 5 shows the threshold elevation plotted as a function of flank contrast (specified in units of the flank contrast detection threshold). As expected, there is little or no threshold elevation for the non-amblyopic eyes (in fact, if anything QM shows some facilitation). In contrast, although the amblyopic eye of QM shows somewhat more threshold elevation than that of RH, for both observers, thresholds of the amblyopic eyes are elevated even with flank contrasts *below* the flank detection threshold. Note that we measured contrast thresholds for detecting the flanks using signal detection methodology (Levi et al., 2002a), and threshold is specified as the flank contrast yielding  $d' = 1$  (equivalent to 84% correct, when the false alarm rate is 50%). Thus, for flank contrasts of around 0.5 times threshold, the flanks would be visible on only a small fraction of the trials. This surprising result suggests the interesting possibility that crowding may occur before the amblyopic loss renders the flank invisible. A saturating effect of contrast, similar to that of observer RH, has been recently reported for peripheral crowding (Palomares, Pelli & Majaj, personal communication).

The main point of this figure is to show that the effect of contrast is qualitatively different in the amblyopic eye than it is in the preferred eye of these observers. For normal observers (and the preferred eyes of amblyopes) at this large separation (6 SDU), flanks produce no significant threshold elevation at any contrast level. For the amblyopic eyes, even below the flank detection threshold, flanks elevate thresholds.

### 3.2.3. The effect of flank orientation

In normal fovea, crowding is orientation specific. When the target and flanks have orthogonal carrier orientations, there is little or no threshold elevation (see Fig. 5 of Levi et al. (2002a)). In contrast, even orthogonally oriented flanks elevate thresholds in strabismic amblyopia. Fig. 6 shows that for the amblyopic eyes (ordinate) of two strabismic amblyopes both vertical (cross-oriented) and horizontal (iso-oriented) flanks (at a distance of 18' or 4.5 sdu) elevate thresholds for an E with a horizontal carrier to a much greater extent than the non-amblyopic eyes (abscissa). Threshold elevation is weaker, but still substantial (about a factor of 2–2.5) with orthogonally oriented flanks compared to identically oriented flanks and target (about a factor of 3.5–5.5). In contrast, the non-amblyopic eyes (abscissa) show no threshold elevation for orthogonal flanks and only slight threshold elevation (less than a factor of 1.5) with similar flank and target orientations. In normal foveal vision even overlapping flankers with orthogonal orientations do not elevate thresholds under conditions where iso-oriented flanks produce strong threshold elevation (Levi et al., 2002a).

### 3.2.4. Crowding causes 180° errors

Under conditions where crowding occurs, normal observers viewing foveally make a preponderance of 180° (mirror reversal, i.e., left versus right or up versus down) errors (Levi et al., 2002a). Fig. 7 shows the proportion of 90° and 180° errors under conditions where crowding occurs (small flank distances—top panel) and under conditions where there is little or no crowding (large flank distances—lower panel). In amblyopic viewing, as in the normal fovea, under conditions of crowding there is a preponderance of 180° errors, suggesting that crowding is not simply a loss of visibility, but rather a specific loss of positional information. Under conditions of crowding the observer is able to correctly judge whether the “legs” of the E are oriented vertically or horizontally, but is unable to correctly identify the location of the gaps. In Experiment 2, we measured crowding using a 2-AFC direction discrimination task, in which observers were required to make a 180° judgement, thus eliminating the need to extract the orientation of the cue.

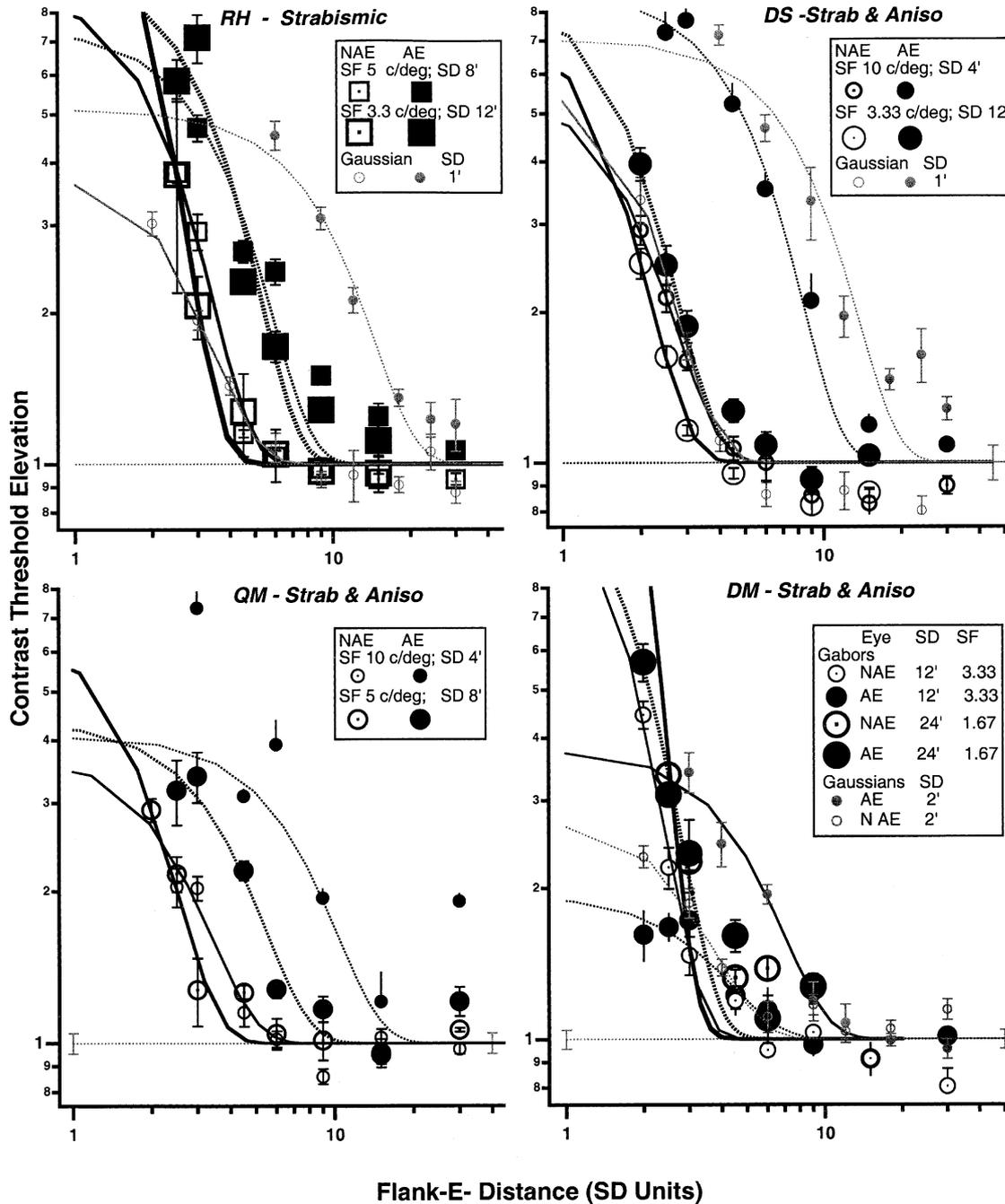


Fig. 4. Foveal crowding is scale invariant; crowding in the amblyopic eye is not. The data of Fig. 2 are replotted as threshold elevation (i.e., flanked threshold/unflanked threshold) versus target-to flank distance expressed in standard deviation units (SDU—i.e., target-to-flank distance (in arc min), divided by patch SD (in arc min)). Also shown (small symbols) are the Gaussian data. When plotted in this way, non-amblyopic eye performance (open symbols) over a wide range of pattern sizes collapses into a more or less unitary function, however, amblyopic performance does not.

#### 4. Experiment 2: crowding in a direction discrimination experiment

##### 4.1. Methods

The “target” was the same E-like figure comprised of 17 circular Gabor patches as in Experiment 1, but in this experiment we measured contrast thresholds for identi-

fying the direction of the E-like pattern using a two-alternative method of constant stimuli. In separate experiments we measured contrast thresholds for left versus right discrimination and for up versus down discrimination. In this experiment there were only two flanking “bars” (see Levi et al., 2002a—Fig. 9), each comprised of five Gabor patches. In the left versus right experiments, the flanks were placed on either side of

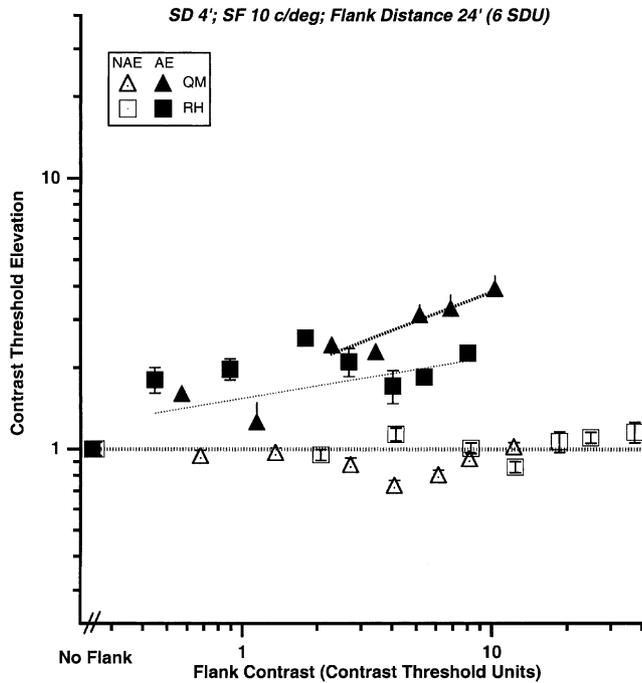


Fig. 5. Threshold elevation plotted as a function of flank contrast (specified in units of the flank contrast detection threshold) for each eye of two amblyopes. The flank distance was fixed at 24' or 6 SDU.

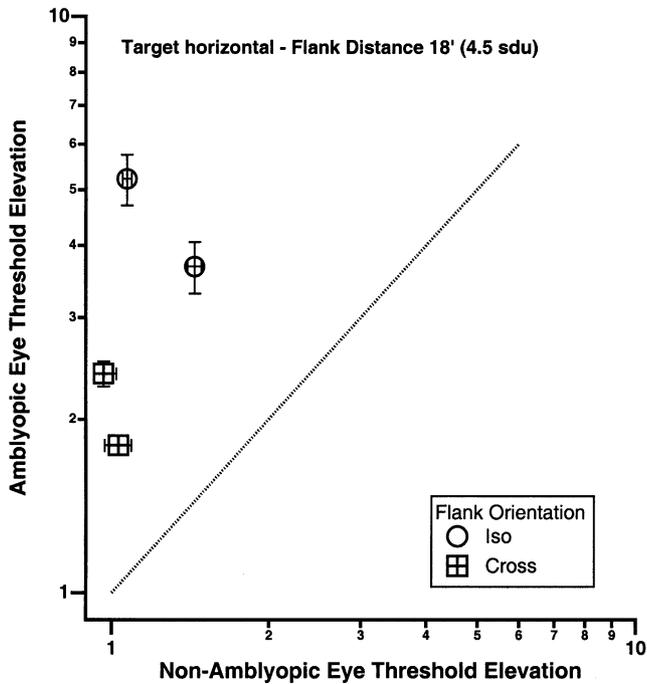


Fig. 6. The effect of flank orientation. This figure plots the threshold elevation for the amblyopic eyes (ordinate) of two strabismic amblyopes (RH and DS) against that of their non-amblyopic eyes (abscissa) for flanks which have the same orientation as the target (Iso—horizontal carrier—circles) or the orthogonal orientation (Cross—vertical carrier—squares). The flank distance was 4.5 SDU.

the E. In the up versus down experiments, they were placed above and below it. Six amblyopic observers and

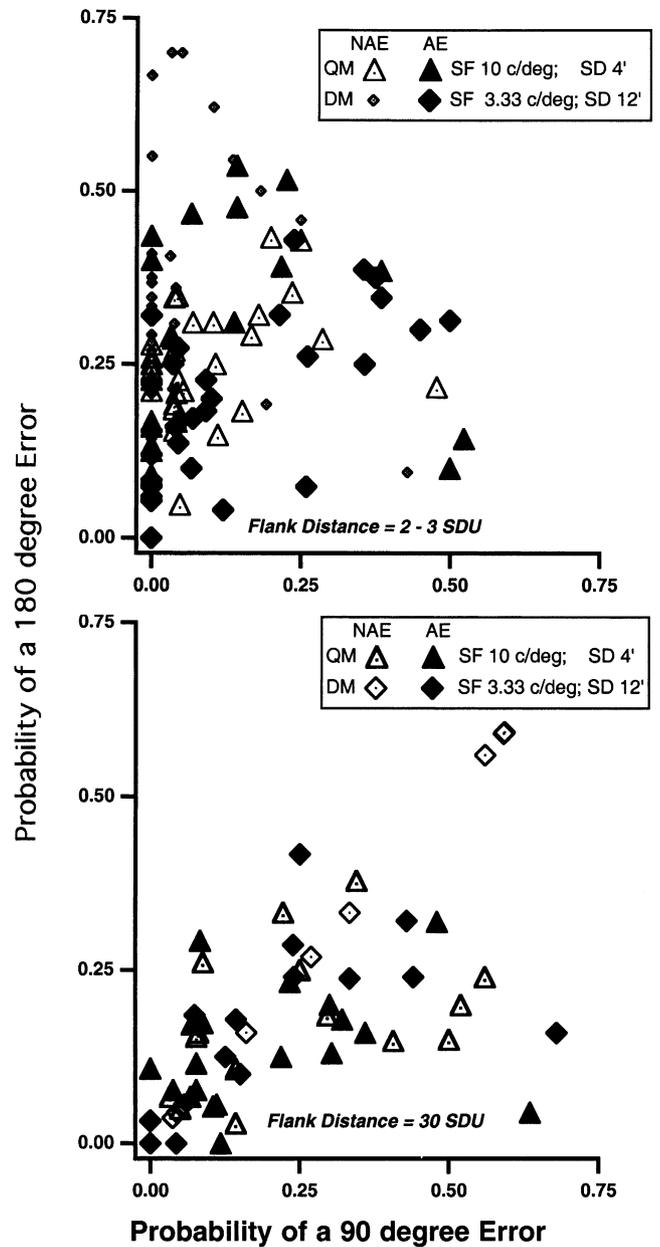


Fig. 7. Confusion analysis. We classified the errors as either 180° errors (mirror image errors) or 90° errors (non-mirror image errors). This figure plots the proportion of 180° versus 90° errors under conditions where crowding occurs (small flank distances [2–3 SDU]—top panel) and under conditions where there is little or no crowding (large flank distances [30 SDU]—lower panel) for each eye of two amblyopic observers.

three normal controls participated in this experiment. We have several motivations for this experiment: first, it does not require the observer to extract the global orientation; second, the separate measures (up–down versus right–left) allow us to examine possible anisotropies in crowding; and third, we will use this data to compare with the results of Experiment 3 to determine whether crowding in amblyopia reflects simple contrast masking.

4.2. Results

Amblyopes, like normals, show crowding for 180° direction discriminations with our E patterns. Toet and Levi (1992) reported large anisotropies in crowding in peripheral vision. Interestingly, several of the amblyopes show large asymmetries between the extent and strength

of crowding for up versus down compared to left versus right discriminations. The data of observer DS (Fig. 8, middle panel) show an example of this; however, there is not a distinct pattern of anisotropy in the amblyopic eye. For DS, left versus right discrimination shows stronger crowding; for other observers (e.g. SL and DM, not shown) up versus down shows stronger crowding.

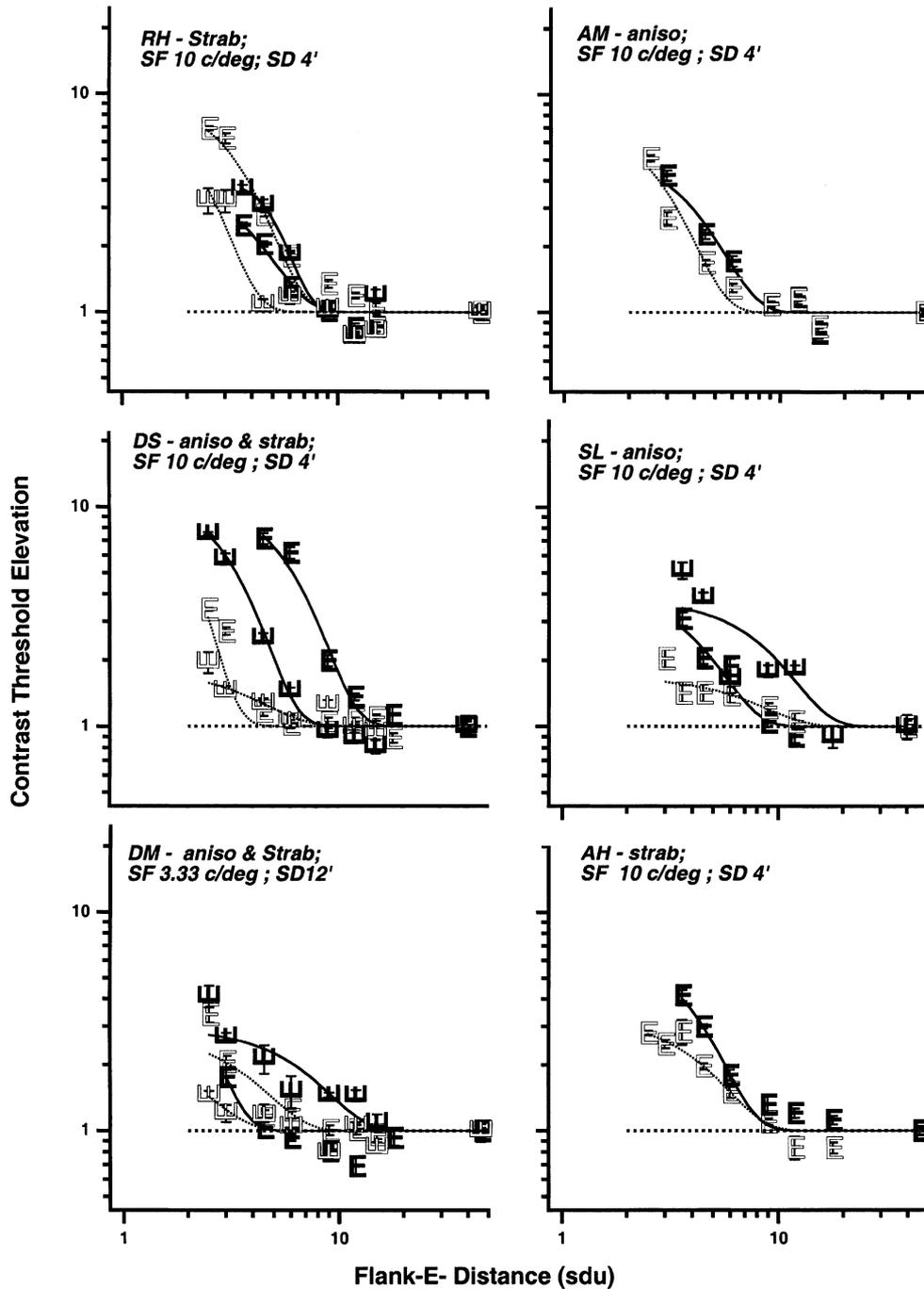


Fig. 8. Crowding occurs for 180° direction discrimination for E's for each eye of 6 amblyopes. White E's are data of the non-amblyopic eyes; black E's the amblyopic eyes. Four of the observers were tested for both left versus right discriminations and up versus down discriminations (as coded by the orientation of the 'E's').

### 5. Experiment 3: masking and facilitation of detection by remote flanks

#### 5.1. Methods

We measured contrast thresholds for detecting a single Gabor patch in the presence of surrounding flanks consisting of Gabor patches, similar to Polat and Sagi (1993, 1994). The target in this experiment was a single Gabor patch with a horizontal carrier, identical to the patches used to form the E targets in Experiments 1 and 2 (Fig. 1, bottom). In order to ensure high flank visibility, the flanks were a pair of high (90%) contrast Gabor patches, typically with the same size, spatial frequency and orientation as the targets. The flanks were either collinear with the target (one on either side) or non-collinear (above and below). In control experiments we also varied the flank contrast. To make the detection experiment comparable to the crowding experiments (i.e., a single temporal presentation), we measured contrast thresholds for the briefly presented (195 ms) target using a rating scale method of constant stimuli. The thresholds reported here represent the average of at least four blocks of 100 trials/block, weighted by the inverse error. The error bars shown in the figures represent  $\pm 1$  sem, and include both within and between run variation. Specific experimental details are as in Levi et al. (2002a). Five amblyopes participated in this experiment.

#### 5.2. Results

Fig. 9 shows the results plotted as threshold elevation, for collinear (left panels) and non-collinear (right panels) of four amblyopes, three with constant strabismus (top 3 panels) and one with anisometropia (AM—bottom panel). The curves fit to the data are difference-of-Gaussian fits, and the gray curves in the top panel represent the fits to the data of three normal control observers. The pattern of results for the non-collinear case is similar in the three observers with strabismus, and shows strong suppression for small separations (less than about three SDU), with little or no facilitation at larger separations. Interestingly there is little difference in the pattern of results between the two eyes. For the collinear flanks, there are considerable individual differences. RH shows a similar pattern in the two eyes, with modest suppression at small separations and little or no facilitation at larger separations. DS shows marked facilitation with his non-amblyopic eye, but much broader suppression and less facilitation in his amblyopic eye. We note that some of the non-amblyopic eyes also show less facilitation than normal observers (compare Fig. 9 with Fig. 15 of Levi et al., 2002a). DM (who was tested at a lower spatial frequency) shows marked facilitation in both eyes. Interestingly, two anisometropic amblyopes also exhibit differences in facili-

tation in the amblyopic eye. For collinear patches, AM's amblyopic eye shows facilitation similar to normal observers, but weaker than with her preferred eye (bottom panel) and SL (not shown) showing none. We note that facilitation seems to be rather delicate, and may also depend on flank contrast. Fig. 10 shows the effect of flank contrast at a fixed distance (4.5 SDU where we find strong facilitation in normal observers) of two of the amblyopes. Note that at this separation DS shows no significant facilitation at any contrast level with his amblyopic eye, while RH shows some facilitation in both eyes, but only at low (2–4 CTU) not high contrast levels.

We are interested in two specific issues: first, whether the suppression (threshold elevation) in the detection task can explain the crowding seen in amblyopes, i.e., whether crowding in amblyopia is simply contrast masking, and second whether facilitation is diminished in the amblyopic visual system.

In the normal fovea, the magnitude of threshold elevation in the detection task is closely related to the amount of threshold elevation in the 2-AFC crowding task, as predicted by our test-pedestal model (Levi et al., 2002a). To address the first issue in Fig. 11A, we have plotted the threshold elevation for crowding (2-AFC E direction discrimination) against threshold elevation for masking (solo detection) for paired conditions (e.g. L/R E versus collinear solo at the same flank distance; or U/D E versus non-collinear solo at the same flank distance). Each symbol in Fig. 11A represents a paired measure. As a concrete example, a paired measure would correspond to plotting a pair of points at the same abscissa value from Figs. 8 and 9. Thus, for a fixed flank distance, threshold elevation for the up/down discrimination (shown by an upward E symbol in Fig. 8) would be plotted on the ordinate of Fig. 11A against the corresponding threshold elevation for non-collinear single patch detection (shown by an hourglass symbol in Fig. 9) on the abscissa of Fig. 11A. The open gray circles in Fig. 11A are data for the 3 normal control observers, and open squares are the preferred eyes of the amblyopes. The colored symbols are data of the amblyopic eyes. Data inside the red box show facilitation for solo detection (i.e., abscissa values below 1) and data inside the green box show facilitation for E direction discrimination (i.e., ordinate values below 1). Clearly there are many more points inside the red box than inside the green, showing that there is considerably more facilitation of detection. This may not be surprising since the presence of multiple patches in the E already act like flanks for reducing uncertainty. The additional flanks would thus have less effect. However, with the exception of DM (yellow diamonds) and anisometropic amblyope AM (blue circles), the amblyopic eyes show less facilitation than the normal or non-amblyopic eyes. This point can be seen more clearly by comparing the am-

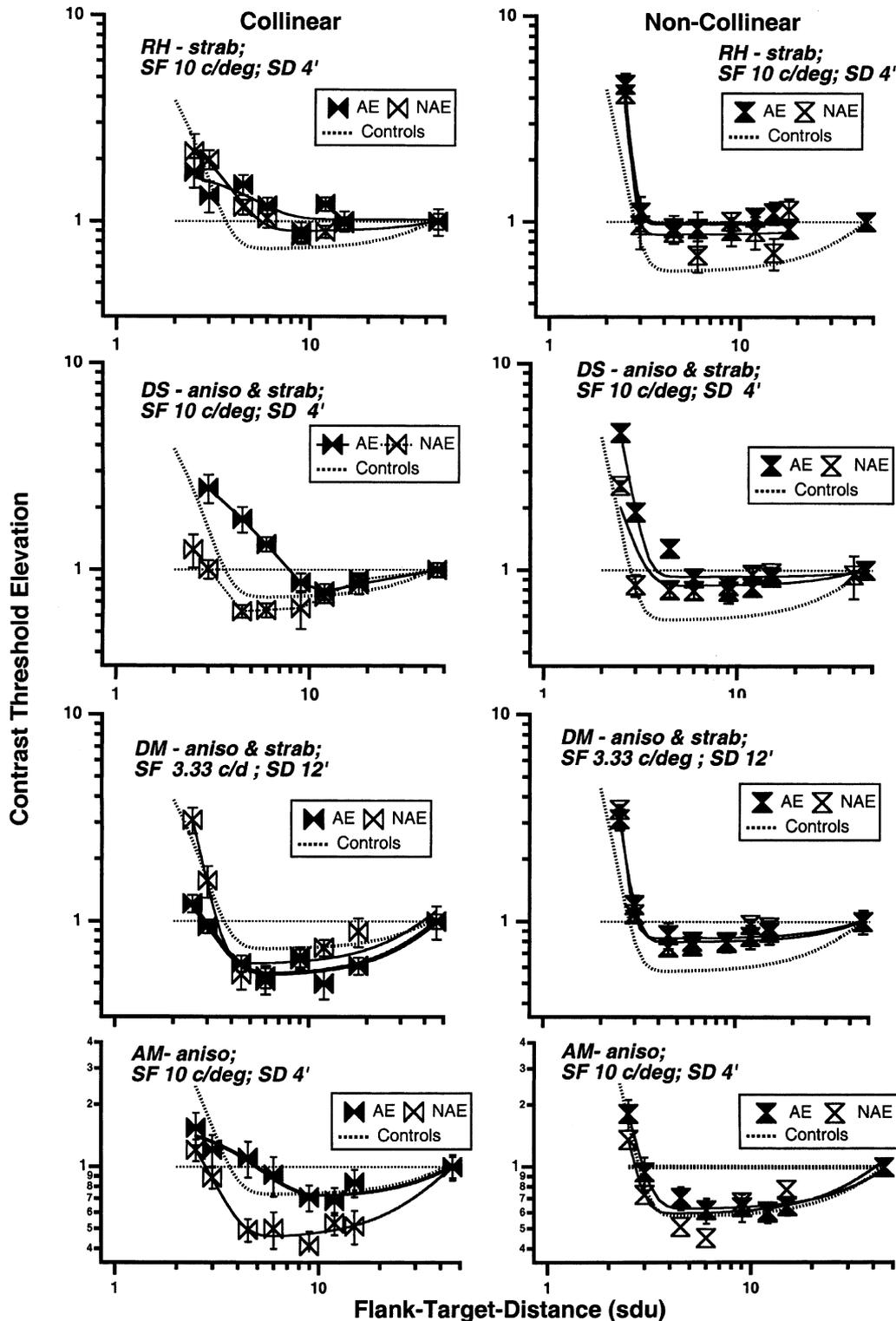


Fig. 9. Threshold elevation for detecting a single patch with a pair of flanks. The data are plotted as a function of flank distance (in SDU), for collinear (left panel) and non-collinear (right panel) flanks of four amblyopes. The top three all had constant strabismus, the bottom amblyope is a pure anisometrope. The dotted gray lines in the top panels show the fits to the data of three normal control observers.

blipic to the non-amblyopic or normal controls (heavy dotted curve) in Fig. 9, and by inspecting the maximum facilitation in Fig. 11B (discussed below). For values above about 1 on the abscissa, threshold elevation for

the two tasks is quite similar for the control observers, and their data cluster around the 1:1 line. However, for the amblyopic eyes, like the normal periphery, threshold elevation for identification of the E direction is often

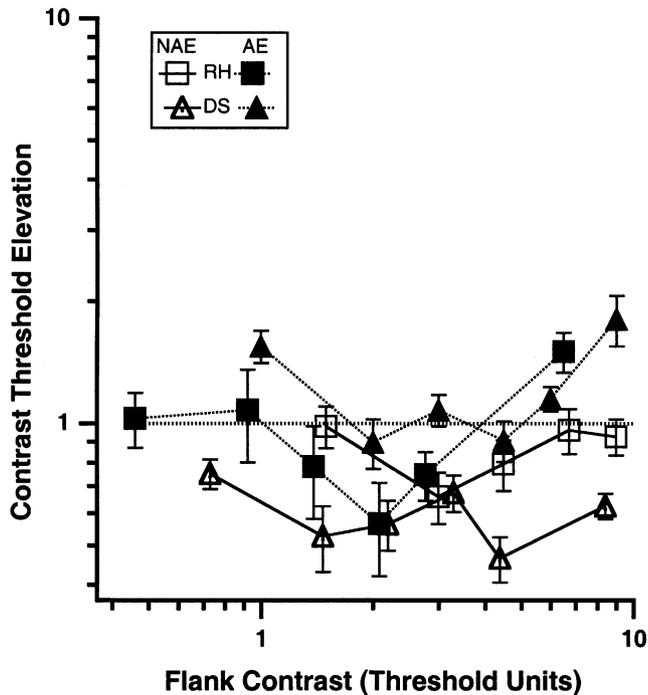


Fig. 10. The effect of flank contrast at a fixed distance (4.5 SDU) of two of the amblyopes.

much stronger than threshold elevation for detecting a single patch. For example, DS (green triangles) shows threshold elevation for the single patch of less than a factor of 2, coupled with threshold elevation for the E which may be as much as a factor of 8! This may be more readily seen in Fig. 12, which compares the data of Experiments 1–3 in the amblyopic eyes of two observers. The comparison is particularly revealing in DS (lower panel), where the 4-AFC data of Experiment 1 lie between the left versus right and up versus down data of Experiment 2. Most revealing is the fact that at a flank distance of 3 SDU, this observer shows a 6-fold threshold elevation for up versus down ‘E’ discrimination, but slight facilitation for the paired (non-collinear) solo detection task. Thus, crowding, in amblyopic eyes seems to be more than simple contrast masking. It is also interesting to note that some of the non-amblyopic eyes of the amblyopic observers also show considerably more threshold elevation for the E-identification task than for simple detection. Thus, as suggested by others, the non-amblyopic eyes may not be altogether normal (e.g. Kandel, Grattan, & Bedell, 1980).

Figs. 11A and 12 shows considerably more crowding in the identification experiments (Experiments 1 and 2) than in the single patch detection experiment. Could the pattern of results be related to task complexity rather than crowding? We do not believe so, because Levi and Sharma (1998) showed that the pattern of results for identifying the global orientation of Gabor textures was similar in normal and amblyopic eyes, when all of the

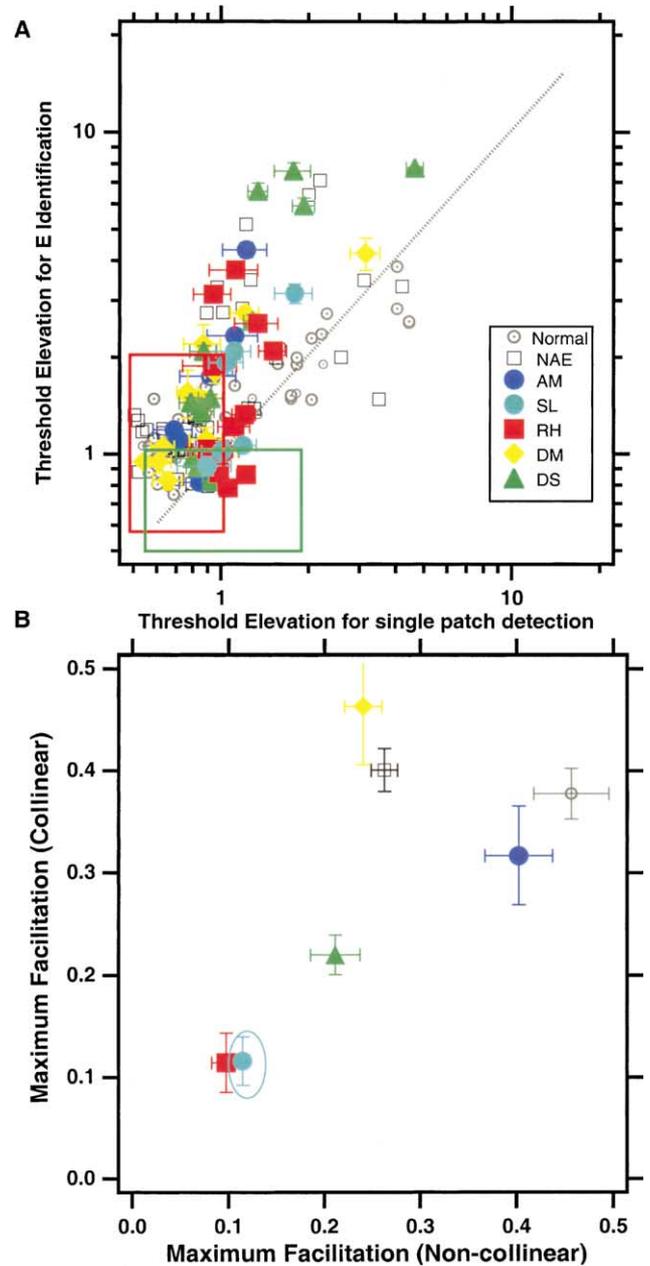


Fig. 11. (A) Threshold elevation for crowding (E direction discrimination) versus threshold elevation for masking (solo detection) for paired conditions (e.g. L/R E versus collinear solo at the same flank distance; or U/D E versus non-collinear at the same flank distance). Each symbol represents a paired measure in the normal fovea (open circles), non-amblyopic eyes (open squares) or amblyopic eyes (solid symbols). Data within the red box show facilitation for solo detection. Data within the green box show facilitation for E—direction discrimination. (B) Maximum facilitation (i.e. one – threshold elevation) for detection with collinear flanks versus that for non-collinear flanks (note that SL did not perform the non-collinear task, and his collinear data, are plotted on the diagonal and marked by a blue circle) for normal observers (mean shown by the open circle) non-amblyopic eyes (open square) and amblyopic eyes (solid symbols).

local elements were at the same (near threshold) contrast level.

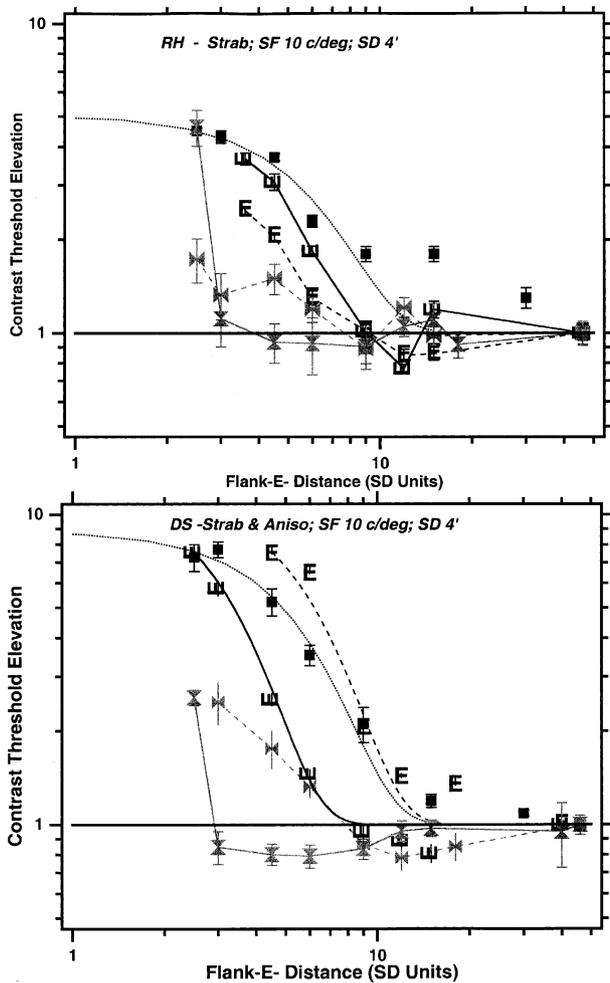


Fig. 12. Compares the data of Experiments 1–3 in the amblyopic eyes of two amblyopic observers, RH and DS. The 4-AFC data of experiment 1 are shown by solid squares; the 2AFC data of Experiment 2 are shown by 'E' (left versus right—by horizontal E's; up versus down by vertical E's). The solo detection data of Experiment 3 are shown by bow-ties (collinear) and hourglasses (non-collinear).

Additional evidence that crowding in amblyopia is not simply masking is that unlike crowding which occurs with cross-oriented flank orientations (see Fig. 6), masking is eliminated when the target and flanks have orthogonal orientations. Interestingly, at least in the near periphery ( $5^\circ$ ), normal observers show orientation specific crowding (Levi, Hariharan, & Klein, 2002b). Thus, although crowding in amblyopic and peripheral vision are similar in their extent, they differ in their orientation specificity. This difference in orientation specificity appears to be the main qualitative difference between amblyopic and peripheral crowding.

To further address the question of facilitation, we have plotted each observer's maximum facilitation (i.e. 1 minus threshold elevation) for detection with collinear flanks versus that for non-collinear flanks (Fig. 11B) note that SL did not perform the non-collinear task, and his collinear data are plotted at a non-collinear value

equal to the collinear value. Note that the normal observers (mean shown by the gray dot) shows strong facilitation for both tasks. The amblyopic (and non-amblyopic eyes shown by gray square) show weaker facilitation for the non-collinear task, and three of the amblyopes also show considerably weaker facilitation for the collinear task. However, note that all amblyopic eyes show some facilitation with two of the five amblyopes showing substantial facilitation.

## 6. Discussion

Crowding in amblyopic vision is neither scale invariant, nor is it attributable to simple contrast masking. Rather, our results suggest that inhibitory spatial interactions in amblyopic crowding are larger than in the normal fovea for a comparable target size, and that crowding may occur over a large relatively fixed spatial distance. Moreover, consistent with the data of Polat et al. (1997) we find that at least some amblyopes have less facilitation than is seen in the normal fovea. Based on their results, Polat et al. concluded that amblyopes have abnormal long-range neural connections. Below we consider several alternative explanations both for the reduced facilitation, and for the extended inhibitory spatial interactions in amblyopic vision.

### 6.1. Spatial scale selection by first stage filters

Does the extended crowding in amblyopia reflect a spatial scale shift to larger receptive fields (lower spatial frequencies)? This is the 'scale-shift' hypothesis of Flom et al. (1963). Most previous studies of peripheral crowding used broadband stimuli (e.g. letters) that are close to the acuity limit. Thus, crowding in amblyopia is typically measured with larger (broadband) stimuli than in the fovea, and this may indeed produce a shift in spatial scale. Clearly, with broadband stimuli, a shift in spatial scale of the first stage filters (which are sensitive to the carrier properties) may contribute to the increased crowding (Hess et al., 2001). However, our Gabor E stimuli are composed of narrow-band features, identical to the features used in the masking experiments, reducing the likelihood that the stimuli were analyzed by large (low spatial frequency) filters in the early stages of processing (i.e., linear filters in V1).<sup>1</sup> Our results show that amblyopic crowding extends over a greater distance even when tested with the same size (and spatial frequency) stimuli as the fovea. As shown in Fig. 3, the extent of crowding in normal foveal vision depends on the target size. For the normal fovea, the Gaussian and

<sup>1</sup> We examine the Fourier predictions for crowding with our 'E' patterns in the Appendix of Levi, Klein, and Carney (2000).

Gabor data overlap, and have a slope of approximately 1. However, in amblyopic vision the extent of interaction is larger for small targets, resulting in a shallower slope, and there appears to be a soft “floor”. Thus we argue that it is unlikely that the extended crowding in amblyopia is entirely due to a simple shift in spatial scale, toward larger (low spatial frequency) filters at an early stage of processing in V1.

There is additional evidence against a simple scale shift. Two recent studies, using quite different methods have addressed the question of scale selection for unflanked letters in amblyopia. Hess et al. (2001), used spatially filtered letters to measure scale selection for small Landolt C’s near the acuity limit, and Chung, Levi, Legge, and Tjan (2002) used spatially filtered letters to measure scale selection for a range of letter sizes. Both studies concluded that there is little or no shift in the spatial scale of analysis for unflanked letters in the amblyopic visual system. Interestingly, Hess et al. (2001) found that spatial scale selection for flanked C’s was abnormal, with several amblyopes using an anomalously higher spatial frequency than normal (Hess, Dakin, Kapoor, & Tewfik, 2000). The selection of a higher spatial frequency is counterintuitive, and is opposite to the scale shift prediction, however, a similar shift is seen in peripheral vision (Hess et al., 2000). Our band-limited stimuli were intended to minimize such a scale shift at the initial stage of linear filtering.

### 6.2. Spatial uncertainty

Amblyopic and peripheral vision are characterized by high degrees of spatial uncertainty (e.g. Hess & Field, 1994; Wang, Levi, & Klein, 1998). The facilitation which is clearly evident in foveal single patch detection with remote flanks, might be a consequence of the high contrast flanks acting to reduce spatial uncertainty (and possibly uncertainty about the spatial frequency, orientation, etc.) of the near threshold target (Levi et al., 2002a). The present results, in agreement with Polat et al. (1997), suggest that facilitation may be weaker in some amblyopes. This reduced facilitation could be a consequence of exaggerated spatial uncertainty, so that even the location (and other details) of the high contrast flanks is uncertain. The lack of facilitation produces an interesting paradox. Increased uncertainty typically raises (unflanked) thresholds, which one might think would result in flankers producing more rather than less facilitation. However, in order to obtain facilitation one needs to attend to just the very narrow region between the test and mask (Solomon, Watson, & Morgan, 1999). If the amblyope’s attention overlapped with the mask then one might get threshold elevation rather than facilitation. Thus, marked spatial uncertainty would contribute to reduced facilitation in amblyopia.

### 6.3. Long-range inhibitory connections

Polat and co-workers have argued that the facilitation by remote flankers observed in foveal detection is a consequence of excitatory long-range horizontal connections between neurons with matched orientations in cortical area V1. These horizontal connections may be both excitatory and inhibitory (e.g., Fitzpatrick, 2000; Gilbert, 1998), and extend up to about 1–2 mm in primate area V1 (Rockland & Lund, 1983; Blasdel, Lund, & Fitzpatrick, 1985; Fitzpatrick, Lund, & Blasdel, 1985; Lund, Yoshioka, & Levitt, 1993; Amir, Harel, & Malach, 1993). In their study, Polat et al. (1997) used a fixed (40%) contrast flanker, and the effects were small, and varied considerably among the amblyopic observers. Levi and Sharma (1998) argued that the reduced facilitation might have been due to the flankers being less effective in the amblyopic eyes, because of the well known loss of contrast sensitivity in amblyopia. However, the present results (see Fig. 10) show that some amblyopes show reduced facilitation even when the contrast sensitivity deficit is accounted for. Thus, our data largely replicate and expand on the findings of reduced facilitation first reported by Polat et al. (1997). However, we do not share Polat et al.’s conclusion regarding abnormal long-range neural connections for several reasons. First, it is clear from our data that the finding is not general. Observer AM (anisometric amblyope) shows facilitation that is comparable to the normal controls for both collinear and non-collinear flanks (see Fig. 9), and DM shows strong facilitation for collinear flanks. Second, the study by Levi and Sharma (1998) suggests that at least some context dependent effects are normal in the amblyopic visual system. More importantly, we have argued that long-range cortical connections in area V1 are too short to account for foveal crowding (Levi et al., 2002a). Specifically, we argued that in primate area V1, these long-range connections are about 1–2 mm, which, based on recent estimates of cortical magnification, translates to a distance of only about 3–6 min of arc in the fovea; far too short to account for the effects seen psychophysically. Moreover, the fixed 1–2 mm distance of these long-range connections predicts interactions over a fixed retinal distance (3–6 min) in the normal fovea, rather than interactions that are proportional to target size, as shown by the open symbols in Fig. 3.

We do not have a firm explanation for facilitation by remote flanks; however, we suspect that uncertainty reduction plays an important role in the strong facilitation evident in normal foveal vision (Levi et al., 2002a) and in the weak facilitation evident in peripheral (Williams & Hess, 1998; Xing & Heeger, 2000, 2001; Levi et al., 2002b) and amblyopic vision. As we discussed in the preceding section in amblyopic vision, uncertainty could be so great so that the location (and other details) of the

high contrast flanks is uncertain and the flanks get confused with the stimulus. However, even if the flanks reduce uncertainty, the window of attention may either be too large (so it includes the flanks) or mis-aimed (i.e., not directed to the appropriate location) resulting in masking rather than facilitation. Thus, we argue that a failure to find facilitation need not be due to abnormal long-range neural connections.

6.4. Second-stage pooling

When several features are presented together, perception of the spatial details of an individual feature depends on: (a) the ability of the visual system to resolve each feature (visual resolution), and (b) the ability of mechanisms at a subsequent stage to isolate each feature. Intriligator and Cavanagh (2001) refer to this as “attentional resolution”, and they showed that in peripheral vision, the limits imposed by visual resolution and attentional resolution are quite different. He, Cavanagh, and Intriligator (1996) have argued that peripheral crowding results from limitations set by attentional resolution. We prefer the more neutral notion that crowding reflects limited resolution at a stage beyond the initial filtering stage (see also Chung, Levi, & Legge, 2001). Our crowding task requires that the observer not only detect the features, but also isolate and localize the missing features (the gaps defining orientation of the E in a 180° discrimination). Based on our masking experiments, we know that amblyopic observers can easily detect the features under conditions where crowding is strong. Thus, our speculation is that the increased extent of crowding in amblyopic vision occurs because the target and flanks are combined or pooled at a second stage, following the stage of feature extraction. In amblyopic vision, like the periphery, this pooling takes place over a long distance. Another way of saying this is that the second stage filter or template for identifying a target in amblyopic vision is not well matched to the target, since the mismatched template fails to isolate the target from the masks.

6.5. Is crowding in amblyopia qualitatively different from that in the normal fovea?

Crowding in foveal and amblyopic vision appear to differ in two important ways. First, whereas foveal crowding depends on size, in amblyopic vision, crowding does not. Amblyopic crowding occurs over a large spatial extent. Second, foveal crowding is reasonably well predicted from masking of detection of a feature, whereas amblyopic crowding is stronger than would be predicted by simple contrast masking, and it is not orientation specific. Fig. 13 compares crowding in foveal vision of non-amblyopic eyes (open symbols) and amblyopic eyes (solid symbols) after discounting the effects

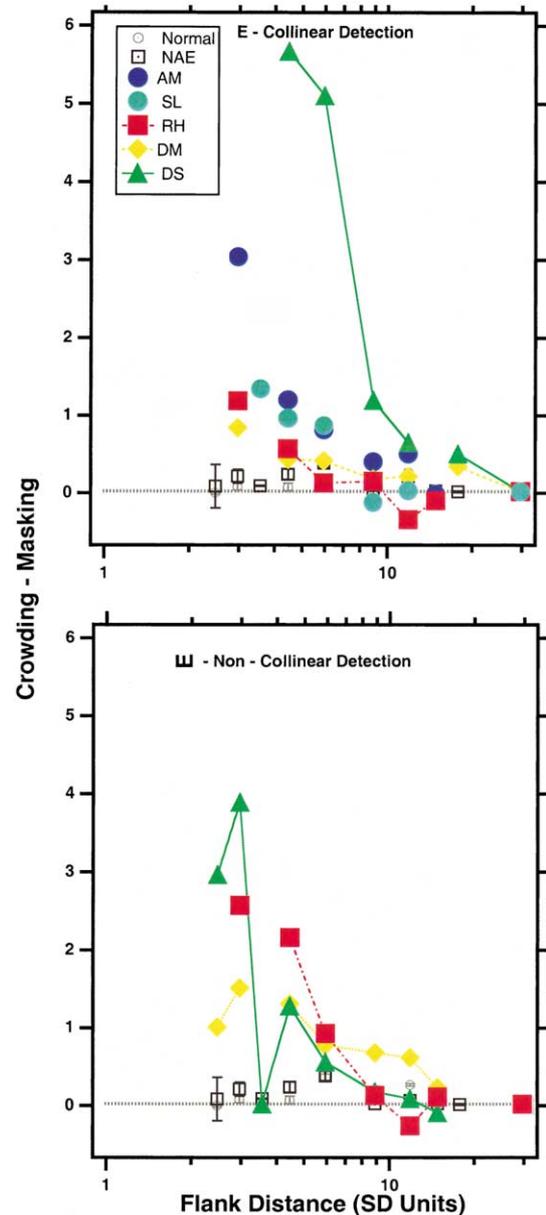


Fig. 13. Crowding with masking discounted in normal fovea (open gray circles), preferred eyes (open black squares) and amblyopic eyes (solid symbols). The data represent threshold elevation for crowding (from the 2-AFC “E” direction–identification experiment) after linearly subtracting out threshold elevation for masking (from the corresponding single patch detection experiment). The top panel is for left/right E identification—collinear detection; the bottom panel for up/down E identification—non-collinear detection. An ordinate value of zero indicates that crowding is masking.

of contrast masking. Clearly, after subtracting out the effects of masking, there is essentially no residual threshold elevation in the fovea or in the non-amblyopic eyes. In contrast, there is substantial and extensive threshold elevation in the amblyopic eyes. We suggest that this represents genuine “crowding”, unconfounded by contrast masking. Our speculation is that target identification involves two stages of processing: initial

filtering and a second-stage template. The initial filtering stage (which limits detection), appears to have reduced contrast sensitivity in the amblyopic visual system, and this can lead to a shift in spatial scale of analysis with broadband stimuli. In normal foveal vision the second stage filter (template), is exquisitely matched to the target (see also Levi et al., 2000). However, in amblyopic vision, limited resources result in abnormal pooling of information at the second stage, so that the template is not well matched to the stimulus. This view is consistent with the finding that crowding in the normal fovea and in amblyopic vision are qualitatively different (Hess et al., 2001). Our study also shows that this difference is not simply a consequence of a simple shift in the spatial scale of analysis.

### Acknowledgements

We are grateful to Hope Queener for programming these experiments. This research was supported by Research grants R01EY01728 and R01EY04776 and a core center Grant P30EY07551 from the National Eye Institute. Commercial Relationships: None.

### References

- Amir, Y., Harel, M., & Malach, R. (1993). Cortical hierarchy reflected in the organization of intrinsic connections in macaque monkey visual cortex. *Journal of Comparative Neurology*, *334*, 19–46.
- Blasdel, G. G., Lund, J. S., & Fitzpatrick, D. (1985). Intrinsic connections of macaque striate cortex: axonal projections of cells outside lamina 4C. *Journal of Neuroscience*, *5*, 3350–3369.
- Chung, S. T. L., Levi, D. M., & Legge, G. E. (2001). Spatial-frequency and contrast properties of crowding. *Vision Research*, *41*, 1833–1850.
- Chung, S. T. L., Levi, D. M., Legge, G. E., & Tjan, B. S., (2002). Spatial-frequency properties of letter identification in amblyopia. *Vision Research*, in press.
- Fitzpatrick, D., Lund, J. S., & Blasdel, G. G. (1985). Intrinsic connections of macaque striate cortex: afferent and efferent connections of lamina 4C. *Journal of Neuroscience*, *5*, 3329–3349.
- Fitzpatrick, D. (2000). Seeing beyond the receptive field in primary visual cortex. *Current Opinion in Neurobiology*, *10*, 438–443.
- Flom, M. C., Weymouth, F. W., & Kahneman, D. (1963). Visual resolution and spatial interaction. *Journal of the Optical Society of America*, *53*, 1026–1032.
- Flom, M. C. (1991). Contour interaction and the crowding effect. *Problems in Optometry*, *3*, 237–257.
- Gilbert, C. D. (1998). Adult cortical dynamics. *Physiological Review*, *78*, 467–485.
- He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature*, *383*, 334–337.
- Hess, R. F., & Field, D. (1994). Is the spatial deficit in strabismic amblyopia due to loss of cells or an uncalibrated disarray of cells? *Vision Research*, *34*, 3397–3406.
- Hess, R. F., McIlhagga, W., & Field, D. J. (1997). Contour integration in strabismic amblyopia: the sufficiency of an explanation based on positional uncertainty. *Vision Research*, *37*, 3145–3161.
- Hess, R. F., Dakin, S. C., Kapoor, N., & Tewfik, M. (2000). Contour interaction in fovea and periphery. *Journal of the Optical Society of America A*, *17*, 1516–1524.
- Hess, R. F., Dakin, S. C., Tewfik, M., & Brown, B. (2001). Contour interaction in amblyopia: scale selection. *Vision Research*, *41*, 2285–2296.
- Hess, R. F., & Jacobs, R. J. (1979). A preliminary report of acuity and contour interactions across the amblyope's visual field. *Vision Research*, *19*, 1403–1408.
- Intriligator, J., & Cavanagh, P. (2001). The spatial resolution of visual attention. *Cognitive Psychology*, *43*, 171–216.
- Kandel, G. L., Grattan, P. E., & Bedell, H. E. (1980). Are the dominant eyes of amblyopes normal? *American Journal of Optometry Physiological Optics*, *57*, 1–6.
- Kovacs, I., Polat, U., Pennefather, P. M., Chandna, A., & Norcia, A. M. (2000). A new test of contour integration deficits in patients with a history of disrupted binocular experience during visual development. *Vision Research*, *40*, 1775–1783.
- Levi, D. M., & Klein, S. A. (1985). Vernier acuity, crowding and amblyopia. *Vision Research*, *25*, 979–991.
- Levi, D. M., Klein, S. A., & Carney, T. (2000). Unmasking the mechanisms for Vernier Acuity: evidence for a template model of Vernier acuity. *Vision Research*, *40*, 951–972.
- Levi, D.M., Klein, S.A., & Hariharan, S., (2002a). Suppressive and facilitatory interactions in foveal vision. Foveal crowding is simple contrast masking. *Journal of Vision*, *2*, 140–166.
- Levi, D.M., Hariharan, S., & Klein, S.A., (2002b). Suppressive and facilitatory interactions in Peripheral Vision. Peripheral crowding neither size invariant nor simple contrast masking. *Journal of Vision*, *2*, 167–177.
- Levi, D. M., & Sharma, V. (1998). Integration of local orientation in strabismic amblyopia. *Vision Research*, *38*, 775–781.
- Levi, D. M., Waugh, S. J., & Beard, B. L. (1994). Spatial scale shifts in amblyopia. *Vision Research*, *34*, 3315–3333.
- Lund, J. S., Yoshioka, T., & Levitt, J. B. (1993). Comparison of intrinsic connectivity in different areas of macaque monkey cerebral cortex. *Cereb Cortex*, *3*, 148–162.
- Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: Suppression and facilitation revealed by lateral masking experiments. *Vision Research*, *33*, 993–999.
- Polat, U., & Sagi, D. (1994). The architecture of perceptual spatial interactions. *Vision Research*, *34*, 73–78.
- Polat, U., Sagi, D., & Norcia, A. M. (1997). Abnormal long-range spatial interactions in amblyopia. *Vision Research*, *37*, 737–774.
- Rockland, K. S., & Lund, J. S. (1983). Intrinsic laminar lattice connections in primate visual cortex. *Journal of Comparative Neurology*, *216*, 303–318.
- Solomon, J. A., Watson, A. B., & Morgan, M. J. (1999). Transducer model produces facilitation from opposite-sign flanks. *Vision Research*, *39*, 987–992.
- Stuart, J. A., & Burian, H. M. (1962). A study of separation difficulty: Its relationship to visual acuity in normal and amblyopic eyes. *American Journal of Ophthalmology*, *53*, 471–477.
- Toet, A., & Levi, D. M. (1992). The two-dimensional shape of spatial interaction zones in the parafovea. *Vision Research*, *32*, 1349–1357.
- Tychsen, L., & Burkhalter, A. (1995). Neuroanatomic abnormalities of primary visual cortex in macaque monkeys with infantile esotropia: preliminary results. *Journal of Pediatric Ophthalmology and Strabismus*, *32*, 323–328.
- Wang, H., Levi, D. M., & Klein, S. A. (1998). Spatial uncertainty and sampling efficiency in amblyopic position acuity. *Vision Research*, *38*, 1239–1251.
- Williams, C. B., & Hess, R. F. (1998). Relationship between facilitation at threshold and suprathreshold contour integration. *Journal of the Optical Society of America A*, *15*, 2046–2051.
- Xing, J., & Heeger, D. J. (2000). Center-surround interactions in foveal and peripheral vision. *Vision Research*, *40*, 3065–3072.
- Xing, J., & Heeger, D. J. (2001). Measurement and modeling of center-surround suppression and enhancement. *Vision Research*, *41*, 571–583.