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Identify mechanisms of amblyopia in Gabor orientation identification with external noise

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Abstract

In this study, we applied the external noise method and the PTM model to identify mechanisms underlying performance deficits in amblyopia. Amblyopic and normal observers performed a Gabor orientation identification task in fovea. White external noise was added to the Gabor stimuli. Threshold versus external noise contrast (TvC) functions were measured at two performance criterion levels. For a subset of observers, we also manipulated the center spatial frequency of the Gabor. We found that two independent factors contributed to amblyopic deficits: (1) increased additive internal noise, and (2) deficient perceptual templates. Whereas increased additive noise underlay performance deficits in all spatial frequencies, the degree of perceptual template deterioration increased with the center spatial frequency of the Gabor.
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1. Introduction

Amblyopia is a developmental visual disorder characterized by reduced vision in the absence of any detectable structural or pathological abnormalities that does not improve with refractive correction (Ciuffreda, Levi, & Selenow, 1991; McKee, Levi, & Movshon, 2003). As a result of the presence of certain sensory impediments during early visual development, such as strabismus (ocular misalignment) or anisometropia (unequal refractive error), amblyopia has been identified as a cortical rather than a peripheral, pre-cortical impairment. Research based on animal models of amblyopia found that V1

neurons responding to high spatial frequency patterns in the amplyopic eye exhibited abnormal contrast sensitivity and spatial properties (Crewther & Crewther, 1990; Eggers & Blakemore, 1978; Kiorpes, Kiper, O'Keefe, Cavanaugh, & Movshon, 1998; Movshon et al., 1987). However, the neuronal deficits in the case of strabismic and anisometropic amblyopia do not sufficiently account for the behavioral deficits measured with the same stimuli, suggesting that neural deficits in amblyopia are not limited to a subset of neurons in V1 (Kiorpes et al., 1998). Consistent with this view, disruption in the binocular organization of extra-striate cortical areas has been documented in primate (Movshon et al., 1987) and cat amblyopes (Schroder, Fries, Roelfsema, Singer, & Engel, 2002). Abnormal activities in extra-striate cortical areas have also been reported in PET (Imamura et al., 1997) and fMRI studies on human amblyopes (Barnes, Hess, Dumoulin, Achtman, & Pike, 2001; Sireteanu et al., 1998). However, a complete neural account of

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amblyopia is still unavailable (Barnes et al., 2001; Daw, 1998; Kiorpes & McKee, 1999).

In this study, we attempted to characterize mechanisms of amblyopia at the overall observer level using the external noise approach (Lu & Dosher, 1998). Traditionally, spatial vision is characterized through measures of contrast sensitivity functions and various visual acuities, such as Snellen acuity, grating acuity, and Vernier acuity (McKee et al., 2003). More recently, a more elaborated method, the external noise approach (Barlow, 1956; Rose, 1948; Tanner & Birdsall, 1958), has become increasingly prevalent in vision research (Ahumada, 1987; Ahumada & Watson, 1985; Burgess, Wagner, Jennings, & Barlow, 1981; D'Zmura & Knoblauch, 1998; Gegenfurtner & Kiper, 1992; Geisler, 1989; Hay & Chesters, 1972; Legge, Kersten, & Burgess, 1987; Lu & Dosher, 1999, 2001; Nagaraja, 1964; Pelli, 1981, 1990; Pelli & Farell, 1999; Tjan, Braje, Legge, & Kersten, 1995; Van Meeteren & Barlow, 1981). The method adds systematically increasing amounts of external noise to the signal stimuli and measures how much signal contrast is required to maintain one or several constant threshold performance levels in detecting or identifying the signal (the "Threshold versus Contrast" or "TvC" function). Contrast sensitivity is then described in terms of intrinsic limitations of the perceptual system: internal additive noise, contrast-gain control or multiplicative noise, nonlinear transducer, and statistical uncertainty (Burgess & Colborne, 1988; Eckstein, Ahumada, & Watson, 1997; Lu & Dosher, 1999; Pelli, 1985; Pelli & Farell, 1999). Initially used to characterize and compare human observers in different perceptual tasks (Burgess, Shaw, & Lubin, 1999), the external noise approach has recently been extended to assay alterations of the intrinsic characteristics of the observer when the state of the observer changes, including attention (Dosher & Lu, 2000a, 2000b; Lu & Dosher, 1998), perceptual learning (Chung, Levi, & Tjan, 2005; Dosher & Lu, 1998; Gold, Bennett, & Sekuler, 1999), and adaptation (Dao, Lu, & Dosher, 2006).

The external noise method was first applied to identify mechanisms of visual dysfunctions in clinical populations by Kersten, Hess, and Plant (1988). The authors measured TvC functions in a grating detection task for patients with cataract, macular degeneration, and amblyopia, and compared the pattern of results with those of the normal subjects. A linear amplifier model (LAM) of the human observer (Pelli, 1981) was used to fit the TvC functions. In the LAM, contrast threshold is described as a function of external noise by the following equation:

$$c_\tau = \sqrt{\frac{N_{ext}^2 + N_{eq}^2}{E_\tau}}, \tag{1}$$

where c_τ is the contrast threshold at performance criterion τ (e.g., 75% correct), E_τ is the sampling efficiency associated with the performance criterion, N_{ext}^2 is the variance of the (experimenter-controlled) external noise, and N_{eq}^2 is the variance of the equivalent intrinsic noise. Three amplyopic

patients (one anisometropia, two strabismus) were studied by Kersten et al. (1988). They found that two of them had normal or near normal sampling efficiency but increased equivalent internal noise, and one had lower sampling efficiency but near normal equivalent internal noise.

The external noise method has since been used by others to study amblyopia (Levi & Klein, 2003; Nordmann, Freeman, & Casanova, 1992; Pelli, Levi, & Chung, 2004; Wang, Levi, & Klein, 1998):

- Nordmann et al. (1992) measured grating contrast sensitivity functions on normal and amblyopic subjects with and without a superimposed random noise pattern. They found that the impact of external noise was virtually identical for amblyopes and subjects with normal binocular vision. Their results are consistent with reduced sampling efficiency in amblyopia, based on the LAM model.
- Wang et al. (1998) used a spatial perturbation paradigm to study spatial uncertainty and sampling efficiency in spatial position judgments. They found that spatial uncertainty in both anisometropic and strabismic amblyopes was about tenfold higher than normal subjects. But only strabismus amblyopes showed deficits in spatial integration.
- Levi and Klein (2003) evaluated the perceptual templates and internal noise of amblyopic and normal subjects in detecting and discriminating the positions of fuzzy bars by combining the external noise approach with the classification image technique (Eckstein & Ahumada, 2002) and the double-pass method (Burgess & Colborne, 1988). They concluded that performance decrements in amblyopes are attributable in part to a poorly matched template, but to a greater degree, to higher internal stimulus-dependent noise. In relation to the LAM, a poorly matched template corresponds to lower sampling efficiency. Because the internal noise in LAM is additive and independent of the stimulus, the LAM model cannot accommodate the stimulus-dependent noise in the Levi and Klein result.
- Pelli et al. (2004) used the external noise approach to characterize amblyopic letter identification. Based on the LAM, they concluded that loss of sampling efficiency was the predominant cause of amblyopic visual deficit. In low spatial frequencies (e.g., 2.3 c/d), the equivalent internal noise of the amblyopes was roughly the same as the normal subjects. But paradoxically, the equivalent internal noise of the mild amblyopes was *lower* than the normal subjects in higher spatial frequencies (e.g., 7.8 c/d).

To summarize, these external noise studies based on the LAM have greatly advanced our understanding of the underlying mechanisms of amblyopia. However, the results in the literature are not completely consistent. Some studies attributed amblyopic deficits to reduced sampling efficiency; others attributed them to increased additive

internal noise; and still others attributed them to increased stimulus-dependent noise. Although it is possible that some of the inconsistencies might have resulted from different characteristics of the subjects in these studies, it is also possible that the same amblyope may exhibit different deficits in different tasks or in the same task with different stimulus parameters. Studies that systematically test the same group of amblyopic observers over a wide range of tasks and/or stimulus conditions might resolve some of these inconsistencies.

The LAM also imposes some limitations on the theoretical interpretations of the TvC functions. This is reflected in the lack of stimulus-dependent internal noise in the model construct, as well as the paradoxical, decreased internal noise in amblyopia found in some of the conditions in Pelli et al. (2004). In fact, many studies have concluded that the LAM is an inadequate observer model for human performance (Burgess & Colborne, 1988; Chung et al., 2005; Eckstein et al., 1997; Lu & Dosher, 1999; Lu, Lesmes, & Dosher, 2002; Pelli, 1985; Tjan, Chung, & Levi, 2002): (1) the LAM does not include any stimulus-dependent noise, consistently found in double-pass experiments (Burgess & Colborne, 1988; Gold et al., 1999; Levi & Klein, 2003); (2) the LAM cannot adequately model the slope of psychometric functions (Lu & Dosher, 1999; Pelli, 1985); (3) although the LAM can provide an adequate description of TvC functions at a single performance level, a different set of model parameters is required to model TvC functions at each performance level, and the LAM provides no systematic relationship between the different sets of parameters (Chung et al., 2005; Lu & Dosher, 2004). (4) The LAM-based theory generated an apparently paradoxical account of perceptual learning in grating orientation/identification in fovea (Lu & Dosher, 2004): improved calculation efficiency, yet increased (dis-improved) additive internal noise.[1]

Lu and Dosher (1999) elaborated the LAM in order to provide a more general theoretical framework to model a wider range of experimental data for which the LAM does not adequately account, including all the four points outlined in the previous paragraph. The Perceptual Template Model, or PTM (Lu & Dosher, 1999), consists of five components: (1) a perceptual template, (2) a non-linear transducer function, $\|\cdot\|^{\gamma}$, (3) a Gaussian internal noise whose standard deviation is proportional (with a factor of N_{mul}) to the total energy in the stimulus after the non-linear transformation, (4) an additive internal noise whose amplitude (N_{add}) is independent of the stimulus strength, and (5) a decision process (see Lu & Dosher, 1999 for the formal development and quantitative tests for the form of the PTM). In the PTM, threshold signal contrast at a particular performance level (i.e.,

d') is expressed as a function of external noise contrast N_{ext}:

$$c_{\tau} = \frac{1}{\beta} \left[\frac{\left(1 + N_{mul}^2\right) N_{ext}^{2\gamma} + N_{add}^2}{\left(1/d'^2 - N_{mul}^2\right)} \right]^{\frac{1}{2\gamma}}. \qquad (2)$$

In contrast to the LAM, the PTM provides an excellent account of threshold versus contrast functions at multiple performance levels and full psychometric functions across a wide range of external noise levels with a single set of parameters (Lu & Dosher, 1999).

The PTM framework allows us to compare amblyopic and normal observers in terms of the gain of the perceptual template, the magnitude of internal additive noise, and the proportional constant of multiplicative noise. The different choice of model framework—LAM or PTM—could also have substantial consequences in the interpretation of the underlying mechanisms of amblyopia. For example, attributing amblyopia to lower sampling efficiency in the LAM leads to very strong constraints on the relative magnitudes of amblyopic deficits in high and low external noise levels: the threshold ratio between the amblyopic and fellow/normal eyes should be the same in high and low external noise conditions. Additional deficits in equivalent internal noise would lead to higher threshold ratios in low external noise conditions than in high noise conditions. Any observation of lower threshold ratio in low external noise conditions (as compared to high external noise conditions) would lead to the paradoxical conclusion that amblyopes have lower sampling efficiency but reduced internal noise. In contrast, the PTM accommodates independent mechanisms of amblyopia in high and low external noise levels. Detailed theoretical analyses of various external noise methods and observer models, including the LAM and the PTM, have been presented in conferences (Lu et al., 2002) and are in preparation (Lu & Dosher, 2006).

In this study, we investigated mechanisms of amblyopia using the PTM framework. To constrain the PTM (Lu & Dosher, 1999), TvC functions were measured at two different performance criterion levels. In Experiment 1, 12 normal and 10 amblyopic subjects identified the orientation of Gabors at a single spatial frequency. Their TvC functions were measured and modeled with the PTM. In Experiment 2, four amblyopic subjects performed the same task at three different Gabor spatial frequencies. The aims were (1) to identify the mechanisms of amblyopic deficits, and (2) to evaluate systematic changes of the mechanisms across Gabor spatial frequencies.

2. Methods

2.1. Observers

Twelve normal and 10 amblyopic observers, nine anisometropic and one strabismic/anisometropic amblyopes, participated in this study. The type of amblyopia, optical correction, and corrected visual acuity of the amblyopic observers were characterized by an ophthalmologist. The

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[1] Though mathematically possible, such paradoxical accounts render the theory much less parsimonious, and additionally would require an explanation of why practice increases the level of internal additive noise.

Table 1
Visual characteristics of the amblyopic observers

Subject	Sex	Age	Type	Optical correction		Visual acuity (MAR)
CC	M	20	A	AE	$+4.75/0.75 \times 80$	5.0
				FE	-1.00	1.0
HH	F	18	A	AE	$+6.00$	5.0
				FE	Plano	0.7
WQ	M	19	A	AE	$+3.50$	1.7
				FE	Plano	0.8
WZ	M	22	A	AE	$+3.00$	2.5
				FE	Plano	1.0
GZ	M	20	A	AE	$+3.50$	3.3
				FE	Plano	1.0
HC	F	20	A	AE	$+6.00/+2.00175$	4.0
				FE	-1.50	1.0
SY	F	19	A	AE	$+4.00/+1.50100$	3.3
				FE	Plano	1.0
XY	F	20	A	AE	$+6.75$	5.0
				FE	Plano	1.0
LH	M	23	A	AE	$+2.50$	1.3
				FE	Plano	1.0
ZQ	M	22	S/A	AE	$+1.00/+2.00170$	10.0
				FE	-1.75	0.7

F, female; M, male; A, anisometropic amblyopia; S, strabismic amblyopia; AE, amblyopic eye; FE, fellow eye; MAR, minimum angle of resolution, assessed with the Chinese Tumbling E Chart. The observers in gray area were tested at 1.5, 2.3, and 4.6 c/d. The others were only tested at SF 2.3 c/d.

results are listed in Table 1. All the normal observers had normal or corrected-to-normal vision. The average age of the amblyopic observers was 20.3 ± 0.5 years, and that of the normal observers was 22.1 ± 0.6 years.

2.2. Apparatus

All experiments were programmed using Matlab 6.1 with Psychtoolbox extensions (Brainard, 1997; Pelli, 1997), and run on a P4 1.7G PC computer with a Sony G220 monitor at a 160 Hz refresh rate. A special circuit was used to combine two 8-bit output channels of the video card to produce 14 bits of gray levels. Luminance calibration was performed using a psychophysical procedure in combination with a photometer (Li, Lu, Xu, Jin, & Zhou, 2003). The background luminance of the display was set to 50 cd/m².

2.3. Stimuli

All displays were viewed monocularly with the appropriate optical corrections; an opaque eye patch covered the un-used eye. Observers were asked to identify the orientation of a Gabor embedded in white external noise. The Gabors were tilted either $+12°$ or $-12°$ from vertical. They were rendered on a 50×50 pixel grid and displayed in the center of the computer screen. Three viewing distances were used to create Gabors of different spatial frequencies[2]: at 60.3 cm, the Gabors extended $2.31° \times 2.31°$ with a spatial frequency of 1.5 c/d; at 90.4 cm, the Gabors extended $1.54° \times 1.54°$ at 2.3 c/d; At 180.6 cm, the Gabors extended $0.77° \times 0.77°$ at 4.6 c/d.

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[2] Because spatial frequency was manipulated by changing the viewing distance, the spectral relationship between the signal and the external noise remained the same in all the spatial frequency conditions. This allows us to attribute the differences in different spatial frequency conditions to the observer, not to changes of the spectra relationship between the signal and the external noise.
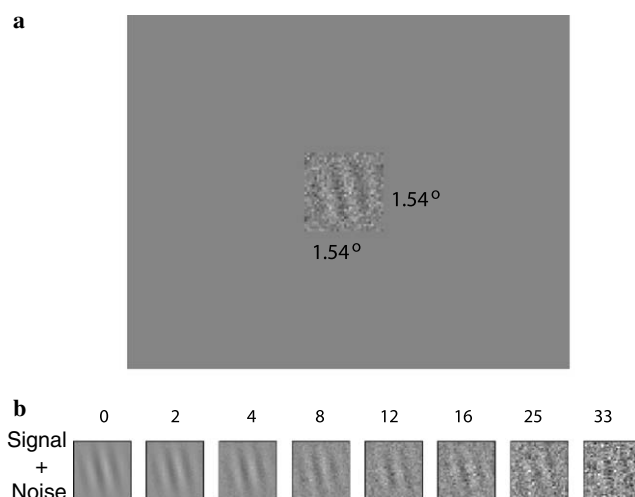
Fig. 1. (a) Layout of the displays. Observer identified the orientation of Gabor signals embedded in external noise. (b) Oriented Gabor signals embedded in external noise. Contrast thresholds for orientation identification were estimated at each of eight levels of external noise.

External noise images of identical size to the signal images were generated using 2×2 pixel patches. The contrast of each pixel patch was sampled from a Gaussian distribution with mean 0 and one of eight standard deviations: 0, 0.02, 0.04, 0.08, 0.12, 0.16, 0.25, and 0.33. The visual angle extended by the external noise images changed with viewing distance. The spatial layout of the display and samples of the external noise images are shown in Fig. 1.

2.4. Procedure

Each trial began with a 275 ms fixation display, followed by a sequence of five image frames (noise, noise, signal, noise, and noise), each lasting 31.3 ms. Signal contrasts were determined by staircase procedures. The four external noise images were independently sampled from identical distributions, and the standard deviation of the contrasts of the external noise images was randomly chosen from one of the eight levels.

Observers identified the orientation of the Gabor with a key press. Auditory feedback followed each response. For each external noise condition, contrast thresholds at two different performance criterion levels were tracked through two staircases: a 3/1 staircase that required three successive correct responses to reduce contrast by 10% or 0.91 dB and one error to increase contrast by 10% or 0.82 dB, and a 2/1 staircase requires two successive correct responses to reduce contrast by 10% or 0.91 dB and one error to increase contrast by 10% or 0.82 dB. The 3/1 and 2/1 staircases track 79.3% and 70.7% correct, respectively, corresponding to 1.634 and 1.089d′.

For each staircase, the threshold for Gabor orientation identification in an external noise condition was estimated from the reversals of the corresponding staircase. A reversal results when the staircase changes its direction (changing from increasing to decreasing contrast or vice versa). Following the standard practice in psychophysics, we excluded the first three (if the number of total reversals were odd) or four (if even) reversals. The average contrast of the remaining reversals was taken as the contrast threshold for Gabor orientation identification.

2.5. Design

Each 1-h session consisted of eight external noise conditions, with 100 trials per 3/1 staircase and 80 trials per 2/1 staircase in each condition, for a total of 1440 trials. All external noise conditions and staircases were randomly intermixed.
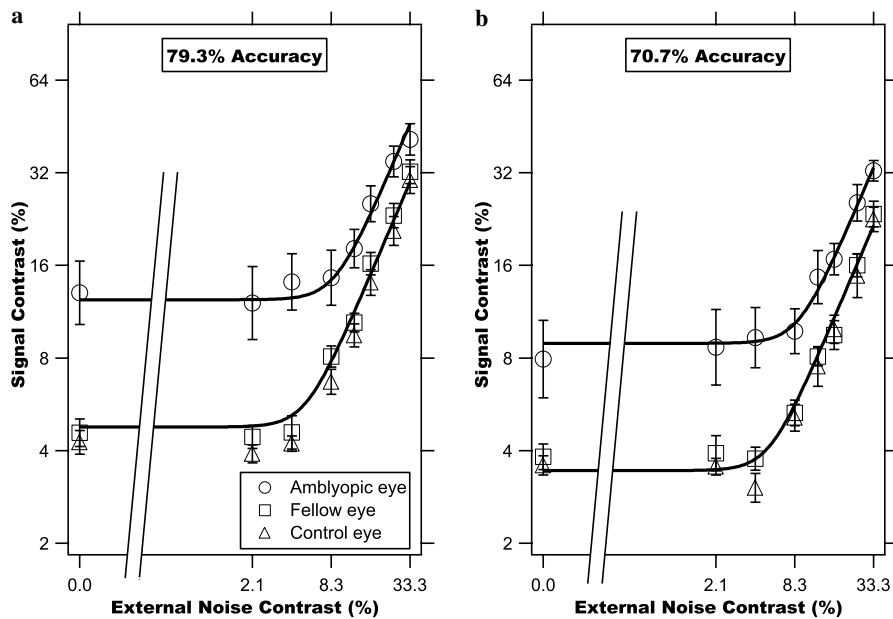
Fig. 2. Averaged signal contrast thresholds as function of external noise levels, for all amblyopic, fellow and normal control eyes at Gabor spatial frequency 2.3 c/d. The curves represents the predictions of the best-fitting PTM model. Circles: amblyopic eyes; squares: fellow eyes; triangles: normal control eyes. (a) TvC functions at 79.3% correct (3/1 staircase, 79.3% accuracy, $d' = 1.634$). (b) TvC functions at 70.7% correct (2/1 staircase, 70.7% accuracy, $d' = 1.089$). Error bars indicate ± 1 standard error.

All observers ran two sessions per eye with Gabors at 2.3 c/d. The order of measurements was randomly assigned. In addition, eight observers, four normal and four amblyopic, were also tested with Gabors at 1.5 and 4.6 c/d.

2.6. PTM model analysis

A least square procedure was used to fit the PTM to the threshold versus external noise contrast functions:

$$c_\tau = \frac{1}{\beta} \left[\frac{(1 + (A_m N_m)^2)(A_f N_{ext})^{2\gamma} + (A_a N_a)^2}{1/d'^2 - (A_m N_m)^2} \right]^{\frac{1}{2\gamma}}, \qquad (3)$$

in which N_a denotes the standard deviation of internal additive noise, N_{ext} denotes the standard deviation of external noise, N_m denotes the proportional constant of multiplicative noise, β denotes the gain of the perceptual template, and γ denotes the exponent of the non-linear transducer. For the fellow and normal eyes, $A_a = A_f = A_m = 1.0$. For the amblyopic eyes, the A's are model parameters.

Our fitting procedure was implemented in Matlab 7.0 with the curvefit toolbox extension. The sum of the squared differences (sqdiff = $[\log(c_{\tau theory}) - \log(c_\tau)]^2$) between the measured log thresholds and the model-predicted log thresholds was minimized.[3] The goodness of fit for each model was determined by:

$$r^2 = 1.0 - \frac{\sum \text{sqdiff}}{\sum \{\log(c_\tau) - \text{mean}[\log(c_\tau)]\}^2}. \qquad (4)$$

An F statistic was used to compare nested models:

$$F(df_1, df_2) = \frac{(r^2_{full} - r^2_{reduced})/df_1}{(1 - r^2_{full})/df_2}, \qquad (5)$$

where $df_1 = k_{full} - k_{reduced}$ and $df_2 = N - k_{full}$; N is the number of predicted data points.

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[3] The log approximately equates the standard error over large ranges in contrast thresholds, corresponding to weighted least squares, an equivalent to the maximum likelihood solution for continuous data.

The standard deviation of each model parameter for the best-fitting model was estimated using a resampling method (Lu & Dosher, 1999; Maloney, 1990). For a given external noise level, the contrast threshold was assumed to have a Gaussian distribution with its mean equal to the mean threshold of all the observers and the standard deviation estimated from the inter-subject variability. For the amblyopic eyes, a pair of TvC functions, one corresponded to the 3/1 staircase and the other to the 2/1 staircase, were then generated by sampling each of the threshold Gaussian distributions once. Repeating this process 1000 times, we generated 1000 pairs of theoretically resampled TvC functions for the amblyopic eyes. The same procedure was used to generate 1000 pairs of theoretically resampled TvC functions for the fellow eyes. Fitting the PTM model to one pair of TvC functions from the amblyopic eyes and the other pair from the fellow eyes at a time, we obtained one set of best-fitting PTM model parameters for each of the 1000 sets of resampled TvC functions. This allowed us to compute the mean and standard deviation of the best-fitting model parameters (Maloney, 1990).

3. Results

3.1. Gabor center spatial frequency: 2.3 c/d

The average performance of the amblyopic eyes, the fellow eyes of the amblyopic subjects, and the left and right eyes of the normal controls are plotted as log threshold versus log external noise contrast (TvC) functions in Fig. 2, with thresholds at 79.3% and 70.7% correct in separate panels. The shapes of all the TvC functions were consistent with those documented in the literature: at low levels of external noise, thresholds were nearly independent of external noise; at high levels of external noise, log thresholds increased linearly with log external noise contrast (Ahumada & Watson, 1985; Barlow, 1956; Burgess et al., 1981; Lu & Dosher, 1999; Nagaraja, 1964; Pelli, 1981).

The contrast thresholds of the amblyopic eyes were significantly higher than those of the fellow eyes ($F(1,9) = 22.518$, $p < 0.001$) and normal eyes ($F(1,20) = 23.522$, $p < 0.001$), across all the external noise conditions and the two criterion performance levels. The contrast thresholds in the fellow eyes of the amblyopic subjects were not significantly different from those of the normal eyes ($F(1,20) = 1.183$, $p > 0.25$).

The threshold difference between the amblyopic eyes and the fellow/normal eyes depended on the external noise condition. There was significant interaction between external noises and (amblyopic and fellow) eyes in the within-subject design analysis of variance for the amblyopic group ($F(7,63) = 6.098$, $p < 0.001$), and significant interaction between external noises and (amblyopic and normal) eyes in the between-subject design analysis of variance of both groups of observers ($F(7,140) = 4.672$, $p < 0.001$). In the three lowest external noise conditions, the average threshold in the amblyopic eyes was $169 \pm 9\%$ higher than that of the fellow/normal eyes. In the three highest external noise conditions, the average threshold in the amblyopic eyes was $56 \pm 3\%$ higher than that of the fellow/normal eyes. This result is inconsistent with the efficiency account of amblyopia (Pelli et al., 2004), which predicts equal threshold increases in the amblyopic eyes across all external noise levels.

The threshold ratio between the two performance criterion levels (79.3% and 70.7% accuracy) for a given external noise condition did not depend on the external noise levels for all three types of eyes ($F(7,203) = 1.736$, $p > 0.10$). Averaged across external noise conditions, the ratio was 1.42 ± 0.06 for the amblyopic eyes, 1.35 ± 0.05 for the fellow eyes, and 1.30 ± 0.04 for the normal eyes. The results are very similar to the observations in the literature (Lu & Dosher, 2006).

Following Dosher and Lu (1999), we also computed the threshold ratio between the amblyopic and the fellow eyes in each external noise condition at each performance criterion level. Across external noise levels, the ratio was virtually the same at the two criterion performance levels ($F(1,144) = 0.331$, $p > 0.50$): The ratio was 2.88 ± 0.33 at 79.3% correct and 2.25 ± 0.31 at 70.7% correct for lowest three noise levels, and 1.44 ± 0.10 at 79.3% correct and 1.57 ± 0.12 at 70.7% correct for highest three noise levels. These results imply that the non-linear transducer and contrast-gain control in the perceptual template model were not affected by amblyopia (Dosher & Lu, 1999; Lu & Dosher, 1999).

The PTM model (Eq. (3)) was fit to the data of individual subjects.[4] For the amblyopic subjects, A_a, A_f, and A_m were set to 1.0 in the fellow eyes, but free to vary in the

amblyopic eyes. For all the amblyopic subjects, the best-fitting model consisted of a mixture of two mechanisms: increased internal noise and increased impact of external noise. This model is statistically equivalent to the most saturated model with three mechanisms (all $p > 0.10$) and is superior to all its reduced models (all at $p < 0.05$). For normal subjects, A_a, A_f, and A_m were all set to 1.0.

The parameters of the best-fitting PTM model for all the subjects are listed in Table 2. There was no significant difference between the amblyopic and normal subjects in a number of PTM parameters: N_m ($t(20) = 0.4665$, $p > 0.60$), N_a ($t(20) = 0.1893$, $p > 0.85$), β ($t(20) = 0.3467$, $p > 0.70$), and γ ($t(20) = 0.5441$, $p > 0.50$). Note that these "base" parameters characterize the fellow eyes of the amblyopes. That they are statistically equivalent to those of the normal observers is consistent with the observation that the corresponding TvC functions were statistically equivalent. The average ratio of internal additive noise between the amblyopic and fellow eyes (A_a) was 6.29 ± 1.37. The average ratio of the gain to external noise between the amblyopic and fellow eyes (A_f) was 1.53 ± 0.17. A_a was much greater than A_f ($t(9) = 3.535$, $p < 0.01$), indicating greater deficits in low external noise conditions than in high external noise conditions.

We also fit the PTM to the average TvC functions of the amblyopic eyes, fellow eyes, and the normal eyes. Because there was no significant difference between the average normal eyes and the average fellow eyes, we collapsed them in the PTM analysis. Again, the best-fitting PTM model consisted of a mixture of two mechanisms: increased internal noise and increased impact of external noise. This model is statistically equivalent to the most saturated model with three mechanisms (all $p > 0.20$) and is superior to all its reduced models (all at $p < 0.01$). The best-fitting PTM curves are plotted in Fig. 2. Note that a single curve in each panel of Fig. 2 fit the data in the fellow eyes and normal eyes. For the best-fitting model, A_a was 6.13; A_f was 1.54, comparable to the average of the individual subjects'.

3.2. Gabor center spatial frequency: 1.5, 2.3, and 4.6 c/d

Four amblyopic and four normal subjects were tested with Gabors at 1.5 and 4.6 c/d in addition to Gabors at 2.3 c/d. Their average TvC functions are plotted in Fig. 3, separated by Gabor spatial frequency, eye, and criterion performance level.

Within each type of eye, the threshold ratio between 79.3% and 70.7% correct was nearly constant across all the external noise levels ($F(2,18) = 2.502$, $p > 0.10$): 1.30 ± 0.07 for the amblyopic eyes, 1.27 ± 0.07 for the fellow eyes, and 1.23 ± 0.06 for the normal eyes at 1.5 c/d; 1.49 ± 0.11, 1.37 ± 0.08, and 1.38 ± 0.08 at 2.3 c/d; and 1.42 ± 0.13, 1.27 ± 0.06, and 1.39 ± 0.08 at 4.6 c/d.

At all three Gabor spatial frequencies, the contrast thresholds of the amblyopic eyes were significantly higher than those of the fellow eyes across all external noise conditions and the two criterion performance levels

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[4] One referee (S. Klein) suggested that we test a version of the PTM that has no multiplicative noise ($N_m = 0$). We found that the $N_m = 0$ model did provide statistically equivalent fits to the data of a subset (six out of eight) of observers. However, it is rejected by data from two individuals as well as the average of all the observers.

Table 2
PTM parameter estimates for amblyopic and normal observers at Gabor center frequency 2.3c/d

	N_m	N_a	β	γ	A_a	A_f	r^2
Amblyopes							
GZ	0.12 ± 0.05	0.007 ± 0.002	1.42 ± 0.16	1.51 ± 0.27	2.97 ± 0.38	1.10 ± 0.10	0.9314
HC	0.35 ± 0.10	0.013 ± 0.007	1.06 ± 0.13	1.66 ± 0.25	13.55 ± 4.33	1.00 ± 0.10	0.9524
SY	0.49 ± 0.15	0.008 ± 0.005	1.72 ± 0.15	1.79 ± 0.32	2.56 ± 0.42	1.77 ± 0.13	0.9000
XY	0.50 ± 0.04	0.011 ± 0.005	2.31 ± 0.14	1.54 ± 0.20	9.16 ± 3.12	1.65 ± 0.11	0.9337
LH	0.47 ± 0.07	0.003 ± 0.004	1.71 ± 0.10	1.83 ± 0.21	1.00 ± 0.07	1.00 ± 0.01	0.9056
ZQ	0.25 ± 0.09	0.012 ± 0.006	1.56 ± 0.18	1.38 ± 0.19	8.25 ± 2.56	2.84 ± 0.31	0.9342
CC	0.12 ± 0.09	0.013 ± 0.005	2.16 ± 0.13	1.82 ± 0.10	9.43 ± 1.12	1.48 ± 0.09	0.9466
HH	0.32 ± 0.09	0.013 ± 0.003	1.83 ± 0.09	1.61 ± 0.14	4.64 ± 2.18	1.55 ± 0.11	0.9030
WQ	0.48 ± 0.06	0.006 ± 0.004	2.02 ± 0.08	1.60 ± 0.32	1.35 ± 0.23	1.27 ± 0.08	0.9126
WZ	0.30 ± 0.06	0.013 ± 0.003	1.67 ± 0.07	1.43 ± 0.08	9.96 ± 1.37	1.60 ± 0.07	0.9284
Controls							
DY	0.30 ± 0.10	0.019 ± 0.006	1.16 ± 0.12	1.20 ± 0.28			0.8713
MJ	0.23 ± 0.09	0.018 ± 0.004	1.27 ± 0.09	1.20 ± 0.21			0.9548
PZ	0.32 ± 0.08	0.019 ± 0.006	1.85 ± 0.15	1.31 ± 0.31			0.8382
HX	0.38 ± 0.07	0.002 ± 0.001	2.17 ± 0.14	2.02 ± 0.06			0.9447
ZB	0.19 ± 0.09	0.011 ± 0.002	1.69 ± 0.09	1.58 ± 0.13			0.9869
ZH	0.26 ± 0.08	0.011 ± 0.002	1.10 ± 0.09	1.20 ± 0.12			0.9327
ZX	0.45 ± 0.09	0.003 ± 0.004	1.74 ± 0.13	2.07 ± 0.24			0.9376
LG	0.40 ± 0.06	0.009 ± 0.005	2.38 ± 0.07	1.75 ± 0.12			0.8000
TY	0.58 ± 0.02	0.004 ± 0.004	3.13 ± 0.09	2.59 ± 0.17			0.8402
XP	0.29 ± 0.03	0.012 ± 0.001	1.52 ± 0.03	1.51 ± 0.03			0.9426

($F(1,3) = 17.983$, $p < 0.025$ at 1.5 c/d; $F(1,3) = 13.493$, $p < 0.05$ at 2.3 c/d; $F(1,3) = 34.042$, $p < 0.01$ at 4.6 c/d) and normal eyes ($F(1,6) = 9.165$, $p < 0.025$; $F(1,6) = 11.448$, $p < 0.025$; $F(1,6) = 26.850$, $p < 0.01$). The contrast thresholds in the fellow eyes of the amblyopic subjects were not significantly different from those of the normal eyes ($F(1,6) = 0.207$, $p > 0.50$; $F(1,6) = 0.237$, $p > 0.50$; $F(1,6) = 0.027$, $p > 0.50$).

Across Gabor spatial frequencies, the threshold difference between the amblyopic eyes and the fellow/normal eyes varied with external noise in different ways. At 1.5 c/d, the average threshold in the amblyopic eyes was $94 \pm 12\%$ higher than the fellow/normal eyes in low external noise, and $22 \pm 5\%$ higher in high external noise. At 2.3 c/d, the average threshold in the amblyopic eyes was $140 \pm 17\%$ higher in low external noise, and $65 \pm 5\%$ higher in high external noise. At 4.6 c/d, the average threshold in the amblyopic eyes was $358 \pm 34\%$ higher in low external noise, and $209 \pm 17\%$ higher in high external noise. As the spatial frequency of the Gabors increased, the threshold difference between the amblyopic eyes and the fellow/normal eyes in low and high external noise conditions became more and more similar.

The threshold difference between the amblyopic eyes and the fellow eyes was also virtually the same at the two criterion performance levels ($F(1,144) = 0.550$, $p > 0.40$): at 1.5 c/d, the ratios are 2.04 ± 0.39 and 1.85 ± 0.37 for 79.3% and 70.7% correct in the lowest three noise levels, 1.18 ± 0.06 and 1.32 ± 0.22 for 79.3% and 70.7% correct in the highest three noise levels; at 2.3 c/d, the ratios are 3.09 ± 0.49 and 1.97 ± 0.46 for 79.3% and 70.7% correct in the low noises, 1.42 ± 0.09 and 1.73 ± 0.16 for 79.3%

and 70.7% correct in the high noises; at 4.6 c/d, the ratios are 5.21 ± 1.12 and 4.09 ± 1.11 for 79.3% and 70.7% correct in the low noises, 2.84 ± 0.70 and 3.33 ± 0.82 for 79.3% and 70.7% correct in the high noises. Again, these results imply that the non-linear transducer and contrast-gain control of the PTM were not affected by amblyopia (Dosher & Lu, 1999; Lu & Dosher, 1999).

We plot the contrast threshold versus spatial frequency functions in Fig. 4. For the normal and fellow eyes, only contrast thresholds in low external noise increased with increasing spatial frequency; contrast thresholds in high external noise did not change as a function of spatial frequency. As Gabor frequency increased from 1.5 to 4.6 c/d, the average threshold in the three lowest external noise conditions increased $85 \pm 6\%$ ($F(1,7) = 44.389$, $p < 0.001$); the average threshold in the highest three external noise conditions changed $-9 \pm 3\%$ ($F(1,7) = 0.913$, $p > 0.35$). This is consistent with Chung, Levi, Legge, and Tjan (2002) who found that the CSF measured in high external noise was flat.

For the amblyopic eyes, contrast thresholds in both low and high external noise conditions increased with increasing spatial frequency. As Gabor frequency increased from 1.5 to 4.6 c/d, the average threshold in the three lowest external noise conditions increased $342 \pm 21\%$ ($F(1,3) = 216.675$, $p < 0.001$); the average threshold in the highest three external noise conditions increased $131 \pm 20\%$ ($F(1,3) = 21.756$, $p < 0.02$). This pattern of results is drastically different from that of the normals.

The PTM (Eq. (3)) was fit to the data of the individual subjects, separately at each Gabor spatial frequency. For the amblyopic subjects, A_a, A_f, and A_m were set to 1.0 in
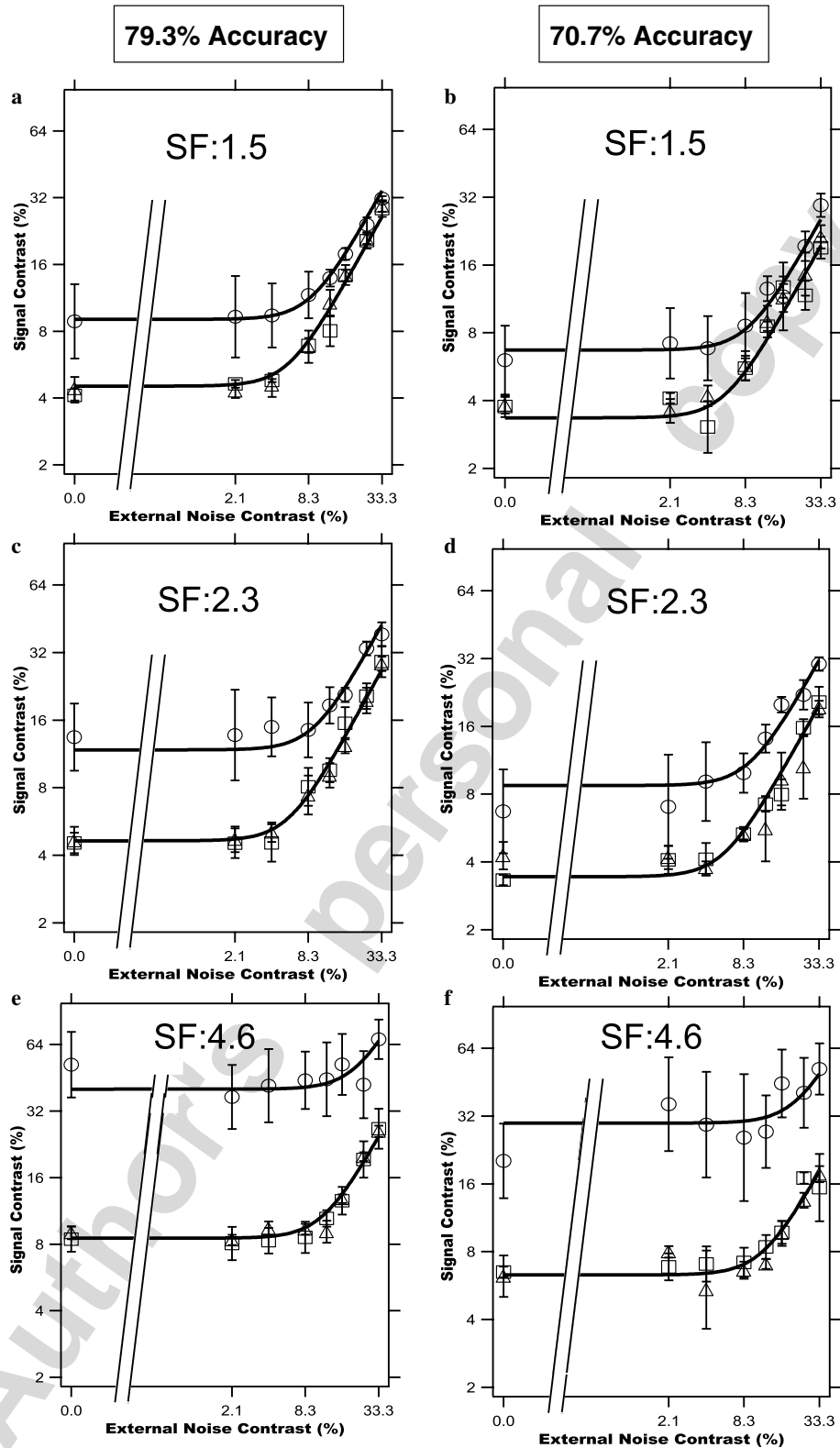
Fig. 3. Averaged contrast thresholds of four amblyopic, four fellow and four normal control eyes as functions of external noise levels for three Gabor spatial frequencies: 1.5, 2.3, 4.6 c/d. (a and b) TvC functions at 79.3% and 70.7% correct for Gabor spatial frequency 1.5 c/d. (c and d) TvC functions for 2.3 c/d. (e and f) TvC functions at 4.6 c/d. The curves present the predictions of the best-fitting PTM model. Circles, amblyopic eyes; squares, fellow eyes; triangles, normal control eyes. Error bars indicate ±1 standard error.

the fellow eyes, and were free to vary in the amblyopic eyes at each Gabor spatial frequency. For all the amblyopic subjects, the best-fitting model consisted of a mixture of

two mechanisms: increased internal noise and increased impact of external noise. This model is statistically equivalent to the most saturated model with three mechanisms
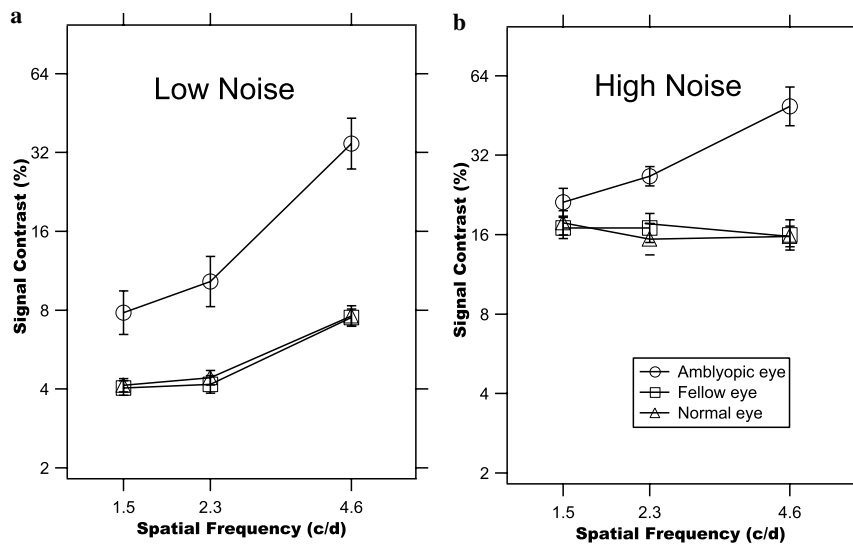
Fig. 4. Average threshold versus spatial frequency functions in low (a) and high (b) external noise conditions for amblyopic, fellow, and normal eyes. Data from the lowest three (contrast standard deviation = 0.0, 0.02, and 0.04) and the highest three (0.16, 0.25, and 0.33) external noise conditions were averaged to create the plots in (a) and (b), respectively.

(all $p > 0.10$) and is superior to all its reduced models (all at $p < 0.05$). For the normal subjects, A_a, A_f, and A_m were all set to 1.0.

The parameters of the best-fitting PTM model for all the subjects are listed in Table 3. There was no significant difference between the amblyopic and normal subjects in a number of PTM parameters: N_m ($t(6) = 0.482$, $p > 0.60$ at 1.5 c/d; $t(6) = 0.217$, $p > 0.50$ at 2.3 c/d; $t(6) = 1.414$, $p > 0.20$ at 4.6 c/d), N_a ($t(6) = 0.155$, $p > 0.50$ at 1.5 c/d;

$t(6) = 1.635$, $p > 0.15$ at 2.3 c/d; $t(6) = 1.401$, $p > 0.20$ at 4.6 c/d), β ($t(6) = 0.647$, $p > 0.50$ at 1.5 c/d; $t(6) = 0.651$, $p > 0.50$ at 2.3 c/d; $t(6) = 0.553$, $p > 0.50$ at 4.6 c/d), and γ ($t(6) = 1.356$, $p > 0.20$ at 1.5 c/d; $t(6) = 1.122$, $p > 0.25$ at 2.3 c/d; $t(6) = 2.052$, $p = 0.09$ at 4.6 c/d). Note that these "base" parameters describe the fellow eyes of the amblyopic observers. That they are statistically equivalent to those of the normal observers is consistent with the observation that the corresponding TvC functions were statistically

Table 3
PTM parameter estimates for amblyopic (shaded) and normal observers at Gabor center frequency 1.5, 2.3 and 4.6 c/d

Frequency		N_m	N_a	β	γ	$A_a^{(1.5c/d)}$	$A_f^{(1.5c/d)}$	r^2
1.5 c/d	CC	0.29 ± 0.04	0.011 ± 0.005	1.83 ± 0.07	1.61 ± 0.11	1.20 ± 0.62	1.02 ± 0.03	0.8715
	HH	0.26 ± 0.06	0.010 ± 0.002	2.03 ± 0.05	1.65 ± 0.12	5.25 ± 0.07	1.32 ± 0.01	0.8488
	WQ	0.13 ± 0.04	0.010 ± 0.004	2.10 ± 0.08	1.66 ± 0.14	1.14 ± 0.15	1.64 ± 0.05	0.9455
	WZ	0.10 ± 0.03	0.008 ± 0.004	1.45 ± 0.04	1.62 ± 0.14	10.62 ± 2.10	1.12 ± 0.04	0.9617
	LG	0.22 ± 0.03	0.008 ± 0.001	1.86 ± 0.03	1.58 ± 0.01			0.9050
	TY	0.28 ± 0.02	0.010 ± 0.001	1.80 ± 0.03	1.68 ± 0.02			0.9418
	XP	0.10 ± 0.07	0.010 ± 0.003	1.24 ± 0.04	1.52 ± 0.10			0.9735
	QZ	0.32 ± 0.03	0.009 ± 0.001	1.95 ± 0.09	1.57 ± 0.04			0.9441
2.3 c/d	CC	0.12 ± 0.09	0.013 ± 0.005	2.16 ± 0.13	1.82 ± 0.10	9.43 ± 1.12	1.48 ± 0.09	0.9466
	HH	0.32 ± 0.09	0.013 ± 0.003	1.83 ± 0.09	1.61 ± 0.14	4.64 ± 2.18	1.55 ± 0.11	0.9030
	WQ	0.48 ± 0.06	0.006 ± 0.004	2.02 ± 0.08	1.60 ± 0.32	1.35 ± 0.23	1.27 ± 0.08	0.9126
	WZ	0.30 ± 0.06	0.013 ± 0.003	1.69 ± 0.07	1.43 ± 0.08	9.96 ± 1.37	1.60 ± 0.07	0.9284
	LG	0.40 ± 0.06	0.009 ± 0.005	2.38 ± 0.07	1.75 ± 0.12			0.8000
	TY	0.58 ± 0.02	0.004 ± 0.004	3.13 ± 0.09	2.59 ± 0.17			0.8402
	XP	0.29 ± 0.03	0.012 ± 0.001	1.52 ± 0.03	1.51 ± 0.03			0.9426
	QZ	0.06 ± 0.02	0.006 ± 0.001	1.67 ± 0.08	1.74 ± 0.15			0.9869
4.6 c/d	CC	0.45 ± 0.03	0.027 ± 0.017	2.55 ± 0.20	1.67 ± 0.06	7.30 ± 1.01	2.64 ± 0.54	0.8088
	HH	0.03 ± 0.02	0.205 ± 0.027	3.80 ± 1.32	1.25 ± 0.71	11.40 ± 2.78	4.80 ± 1.31	0.8865
	WQ	0.52 ± 0.01	0.006 ± 0.002	1.52 ± 0.04	2.27 ± 0.11	3.13 ± 0.26	1.01 ± 0.03	0.8916
	WZ	0.09 ± 0.04	0.056 ± 0.025	2.12 ± 0.94	1.22 ± 0.54	19.99 ± 8.90	3.19 ± 1.43	0.9697
	LG	0.56 ± 0.01	0.008 ± 0.002	2.50 ± 0.07	1.94 ± 0.09			0.8154
	TY	0.46 ± 0.01	0.013 ± 0.001	2.33 ± 0.04	2.43 ± 0.04			0.9385
	XP	0.35 ± 0.03	0.014 ± 0.001	1.77 ± 0.06	1.90 ± 0.04			0.9221
	QZ	0.46 ± 0.04	0.006 ± 0.003	2.27 ± 0.06	2.70 ± 0.24			0.8043

equivalent. The average ratio of internal additive noise between the amblyopic and fellow eyes (A_a) was 4.55 ± 2.23 at 1.5 c/d, 6.34 ± 2.05 at 2.3 c/d, and 10.46 ± 3.60 at 4.6 c/d; the average ratio of the gain to external noise between the amblyopic and fellow eyes (A_f) was 1.28 ± 0.14 at 1.5 c/d, 1.48 ± 0.07 at 2.3 c/d, and 2.91 ± 0.78 at 4.6 c/d.

We also fit the PTM model to the average TvC functions of the amblyopic eyes, fellow eyes, and the normal eyes, separately at the three Gabor spatial frequencies. Because there was no significant difference between the average normal eyes and the fellow eyes, we collapsed them in the PTM analysis. Again, the best-fitting PTM model consisted of a mixture of two mechanisms: increased internal noise and increased impact of external noise. This model is statistically equivalent to the most saturated model with three mechanisms (all $p > 0.15$) and is superior to all its reduced models (all at $p < 0.02$). The best-fitting PTM curves are plotted in Fig. 4. For the best-fitting model, A_a was 3.53 at 1.5 c/d, 4.86 at 2.3 c/d, and 8.72 at 4.6 c/d; A_f was 1.12 at 1.5 c/d, 1.42 at 2.3 c/d, and 2.57 at 4.6 c/d. All these are comparable to those of the average from individual subjects.

3.3. Relationship between mechanisms of amblyopia and visual acuity

We have identified two mechanisms of amblyopia in our study: increased additive internal noise and deficient perceptual template. Thanks to the suggestion of an anonymous referee of an earlier version of the manuscript, we generated two scatter plots to illustrate the relationship between the two mechanisms and visual acuity in Figs. 5 and 6.
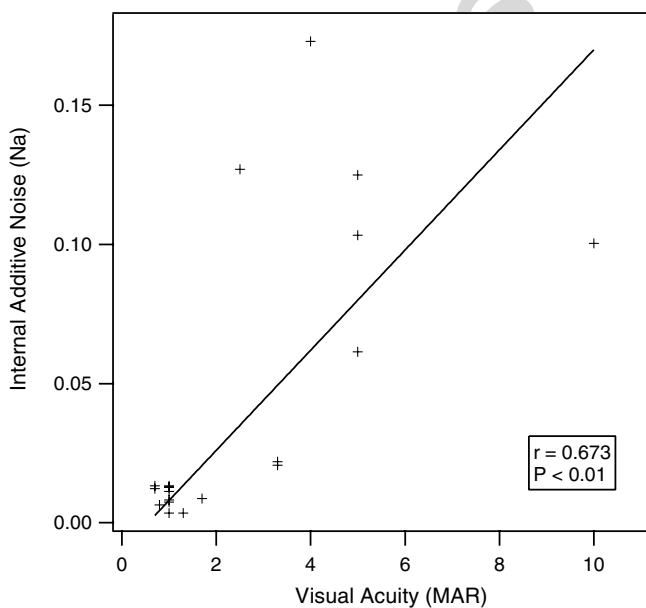
Fig. 5. Internal additive noise (N_a) versus visual acuity. The amblyopic and fellow eyes of the 10 subjects in the 2.3 c/d condition are included.
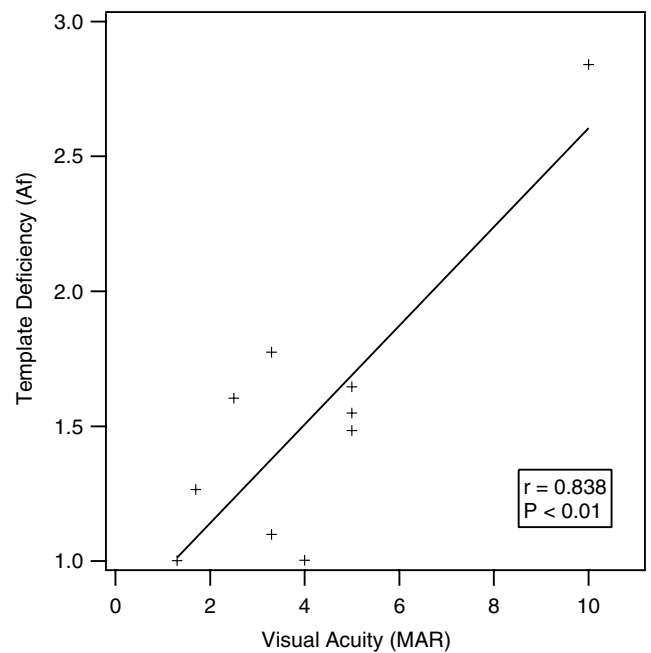
Fig. 6. Template deficiency (A_f) versus visual acuity. The amblyopic eyes of the 10 subjects in the 2.3 c/d condition are included.

In Fig. 5, internal additive noise (N_a) is plotted against visual acuity for both amblyopic and fellow eyes of all the subjects in the 2.3 c/d Gabor condition. Consistent with Pelli et al. (2004), we found a high degree of correlation between internal additive noise and visual acuity ($r = 0.673$, $p < 0.01$). In Fig. 6, template deficiency (A_f) is plotted against visual acuity for the amblyopic eyes of all the subjects in the 2.3 c/d Gabor condition. Again, we found a high degree of correlation between template deficiency and visual acuity ($r = 0.838$, $p < 0.01$). These strong correlations were expected because visual acuity is determined by internal noise and the quality of perceptual template.

4. Discussion

In this study, we applied the external noise method and the PTM framework to identify mechanisms underlying performance deficits in amblyopia. We found that amblyopic deficits can be attributed to two independent factors: (1) increased additive internal noise, and (2) deficient perceptual templates. Whereas increased additive noise underlay performance deficits in all spatial frequencies, the degree of perceptual template deterioration increased with the spatial frequency of the Gabor stimuli. In fact, in the lowest spatial frequency tested (1.5 c/d), the perceptual template was almost normal. In addition, we found that amblyopia did not affect the non-linear transducer and multiplicative noise.

The external noise and the observer model approach has provided many new insights into the mechanisms underlying amblyopia (Kersten et al., 1988; Kiorpes &

McKee, 1999; Levi & Klein, 2003; Mansouri, Allen, Hess, Dakin, & Ehrt, 2004; Nordmann et al., 1992; Pelli et al., 2004; Wang et al., 1998). There have been some inconsistencies both in terms of the relative degree of deficits in high and low external noise conditions and in terms of the theoretical interpretation. To search for a resolution for the empirical inconsistencies in the literature, we measured TvC functions for Gabor orientation identification over a range of Gabor spatial frequencies in the same groups of amblyopic and normal observers. The different dependency of threshold deficits on spatial frequency in low external noise and high external noise conditions suggests that amblyopic deficits in these different noise conditions are uncoupled. The apparent inconsistencies in the literature may be due to the interaction between the characteristics of the subjects and the spatial frequency used in different studies. For the same amblyopic observers, there might be a trend for increased deficit in high external noise conditions as the test spatial frequency increases. Research employing stimuli with a wider range of spatial frequencies is necessary to further test this hypothesis.

A more elaborated observer model, the PTM, was used in this study. The PTM is based on the LAM and can include the LAM as a special case when the exponent of the transducer function is 1.0 and the multiplicative noise is 0. Based on the PTM, we compared the amblyopic and fellow/normal eyes in terms of the gain of the perceptual template, the magnitude of internal additive noise, and the proportional constant of multiplicative noise. Importantly, the PTM accommodates independent mechanisms of expressions of amblyopia in high and low external noise levels, while the efficiency account based on the LAM suggests strong coupling of performance deficits in high and low external noise conditions. In this study, we found that the manifestation of the two mechanisms of amblyopia, increased internal additive noise and poorly matched perceptual template, depended on the signal spatial frequency in rather different ways. That larger template deficits were found in higher spatial frequencies is consistent with the observation that amblyopes have more profound deficits in tasks that require processing of high spatial frequencies (McKee et al., 2003).

In a letter identification task, Pelli et al. (2004) suggested that both anisometropic and strabismic amblyopes had a marked loss of efficiency; only strabismic amblyopes had increased equivalent internal noise. Their analysis was based on the LAM model, in which a loss of efficiency implicates equal amount of threshold elevation [in log] in all external noise conditions; increased equivalent noise results only when threshold elevations in low external noise conditions are higher than in high external noise conditions. Most of the amblyopic observers in the current study were anisometropic. We found a different pattern of results: these anisometropic observers exhibited larger threshold elevations in low external noise conditions than in high external noise conditions. Our results seem to be

more consistent with those of Wang et al. (1998), who found that, in a spatial position judgment task, spatial uncertainty (internal position noise) is elevated, but spatial sampling is normal for the anisometropic visual system, and both increased spatial uncertainty and spatial undersampling applied for the strabismic visual system. On the other hand, we don't have a good explanation of the differences between Pelli et al. (2004) and our results aside from differences in terms of tasks and subjects.

In this study, the same stimulus parameters were used to generate visual displays on the computer monitor; spatial frequency was manipulated only by changing the viewing distance. As a consequence, the spectral relationship between the signal and the external noise remained the same in all the spatial frequencies. This allows us to attribute the differences in different spatial frequency conditions to the observer, not to the change of the spectra relationship between the signal and the external noise. In contrast, Nordmann et al. (1992) used a "fixed" noise pixel size in terms of visual angles and varied the spatial frequency of the signal patterns by changing their spatial period on the monitor. They found that the impact of external noise reduced with signal spatial frequency. On the other hand, the power of external noise reduced with spatial frequency in their study. The difference in the characteristics of external noise might account for the different results.

Contrary to Levi and Klein (2003), we did not find increased multiplicative noise in the amblyopic eyes. One might attributed this difference to the different tasks used: Levi and Klein studied position discrimination of fuzzy bars; we investigated Gabor orientation discrimination in this study. Completely different perceptual processing might be involved in these two different tasks. A good explanation of the different results will require a direct comparison of the same observers in the two tasks.

Physiological recordings in monkeys with experimental amblyopia (Kiorpes et al., 1998) showed that amblyopia is usually associated with a modest reduction of effective input from the amblyopic eye. Such input reduction may be one physiological basis for increased internal noise in amblyopia—as shown by Lu and Dosher (1998), reduced stimulus input is mathematically equivalent to increased additive internal noise. Another possible physiological basis for increased internal noise in amblyopia might be increased variance of neuronal activities in the amblopic cortex (Shadlen & Newsome, 1998; Tolhurst, Movshon, & Dean, 1983). Our results suggest that this might be a worthwhile direction for future physiological investigations on amblyopia.

The perceptual template in the PTM represents the "receptive field" of the overall observer. Using the classification image technique, Levi and Klein (2003) found that some amblyopic observers had abnormal perceptual templates in both a position judgment task and a detection task, exhibiting a shift toward lower spatial frequencies, although the deficiencies in perceptual templates could

not account for all the observed performance deficits in the amblyopic eyes. A deficient perceptual template might be associated with mis-wiring of cortical neurons ("topographical jitter") in any or all of the many stages of visual processing (Hess, 1982; Hess & Field, 1994; Hess & Holliday, 1992). It is also possible that a deficient perceptual template is due to some form of down-weighting of high spatial frequency channels of the amblyopic eyes in the decision stage. Here, we can draw some interesting parallels to the perceptual learning literature, where representation change versus channel reweighting has been under much investigation (Dosher & Lu, 1998; Petrov, Dosher, & Lu, 2005). Much new research is necessary to distinguish these two possibilities.

Acknowledgments

References

Ahumada, A. J. (1987). Puing the visual system noise back in the picture. *Journal of the Optical Society of America, 4*, 2372–2378.

Ahumada, A. J., & Watson, A. B. (1985). Equivalent-noise model for contrast detection and discrimination. *Journal of the Optical Society of America A, 2*(7), 1133–1139.

Barlow, H. B. (1956). Retinal noise and absolute threshold. *Journal of the Optical Society of America, 46*, 634–639.

Barnes, G. R., Hess, R. F., Dumoulin, S. O., Achtman, R. L., & Pike, G. B. (2001). The cortical deficit in humans with strabismic amblyopia. *The Journal of Physiology, 533*(Pt. 1), 281–297.

Brainard, D. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*(4), 433–436.

Burgess, A. E., & Colborne, B. (1988). Visual signal detection. IV. Observer inconsistency. *Journal of the Optical Society of America A, 5*(4), 617–627.

Burgess, A. E., Shaw, R., & Lubin, J. (1999). Noise in image processing. *Journal of the Optical Society of America A [Special Issue]*(16).

Burgess, A. E., Wagner, R. F., Jennings, R. J., & Barlow, H. B. (1981). Efficiency of human visual discrimination. *Science, 214*(4516), 93–94.

Chung, S. T., Levi, D. M., Legge, G. E., & Tjan, B. S. (2002). Spatial-frequency properties of letter identification in amblyopia. *Vision Research, 42*(12), 1571–1581.

Chung, S. T. L., Levi, D. M., & Tjan, B. (2005). Learning letter identification in peripheral vision. *Vision Research, 45*(11), 1399–1412.

Ciuffreda, K., Levi, D. M., & Selenow, A. (1991). *Amblyopia: Basic and clinical aspects*. Boston: Butterworth–Heinemann.

Crewther, D. P., & Crewther, S. G. (1990). Neural site of strabismic amblyopia in cats: spatial frequency deficit in primary cortical neurons. *Experimental Brain Research, 79*(3), 615–622.

D'Zmura, M., & Knoblauch, K. (1998). Spectral bandwidths for the detection of color. *Vision Research, 38*(20), 3117–3128.

Dao, D. Y., Lu, Z.-L., & Dosher, B. A. (2006). Mechanisms of adaptation. *Journal of Vision, 6*, 739–759.

Daw, N. (1998). Critical periods and amblyopia. *Archives of Ophthalmology, 116*, 502–505.

Dosher, B. A., & Lu, Z.-L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences of the United States of America, 95*(23), 13988–13993.

Dosher, B. A., & Lu, Z. L. (1999). Mechanisms of perceptual learning. *Vision Research, 39*(19), 3197–3221.

Dosher, B. A., & Lu, Z.-L. (2000a). Mechanisms of perceptual attention in precuing of location. *Vision Research, 40*(10-12), 1269–1292.

Dosher, B. A., & Lu, Z. L. (2000b). Noise exclusion in spatial attention. *Psychological Science, 11*(2), 139–146.

Eckstein, M. P., & Ahumada, A. J. Jr., (2002). Classification images: a tool to analyze visual strategies. *Journal of Vision, 2*(1), 1x.

Eckstein, M. P., Ahumada, A. J., Jr., & Watson, A. B. (1997). Visual signal detection in structured backgrounds: II. Effects of contrast gain control, background variations, and white noise. *Journal of the Optical Society of America, 14*(9), 2406–2419.

Eggers, H. M., & Blakemore, C. (1978). Physiological basis of anisometropic amblyopia. *Science, 201*(4352), 264–267.

Gegenfurtner, K. R., & Kiper, D. C. (1992). Contrast detection in luminance and chromatic noise. *Journal of the Optical Society of America A, 9*(11), 1880–1888.

Geisler, W. S. (1989). Sequential ideal-observer analysis of visual discriminations. *Psychological Review, 96*(2), 267–314.

Gold, J., Bennett, P. J., & Sekuler, A. B. (1999). Signal but not noise changes with perceptual learning. *Nature, 402*(6758), 176–178.

Hay, G. A., & Chesters, M. S. (1972). Signal-transfer functions in threshold and suprathreshold vision. *Journal of the Optical Society of America, 62*, 990–998.

Hess, R. F. (1982). Developmental sensory impairment: amblyopia or tarachopia? *Human Neurobiology, 1*(1), 17–29.

Hess, R. F., & Field, D. J. (1994). Is the spatial deficit in strabismic amblyopia due to loss of cells or an uncalibrated disarray of cells? *Vision Research, 34*(24), 3397–3406.

Hess, R. F., & Holliday, I. E. (1992). The spatial localization deficit in amblyopia. *Vision Research, 32*(7), 1319–1339.

Imamura, K., Richter, H., Fischer, H., Lennerstrand, G., Franzen, O., Rydberg, A., et al. (1997). Reduced activity in the extrastriate visual cortex of individuals with strabismic amblyopia. *Neuroscience Letters, 225*(3), 173–176.

Kersten, D., Hess, R. F., & Plant, G. T. (1988). Assessing contrast sensitivity behind cloudy media. *Clinical Vision Science, 2*, 143–158.

Kiorpes, L., Kiper, D. C., O'Keefe, L. P., Cavanaugh, J. R., & Movshon, J. A. (1998). Neuronal correlates of amblyopia in the visual cortex of macaque monkeys with experimental strabismus and anisometropia. *The Journal of Neuroscience, 18*(16), 6411–6424.

Kiorpes, L., & McKee, S. P. (1999). Neural mechanisms underlying amblyopia. *Current Opinion in Neurobiology, 9*, 480–486.

Legge, G. E., Kersten, D., & Burgess, A. E. (1987). Contrast discrimination in noise. *Journal of the Optical Society of America A, 4*(2), 391–404.

Levi, D. M., & Klein, S. A. (2003). Noise provides some new signals about the spatial vision of amblyopes. *The Journal of Neuroscience, 23*(7), 2522–2526.

Li, X., Lu, Z.-L., Xu, P., Jin, J., & Zhou, Y. (2003). Generating high gray-level resolution monochrome displays with conventional computer graphics cards and color monitors. *Journal of Neuroscience Methods, 130*(1), 9–18.

Lu, Z. L., & Dosher, B. A. (1998). External noise distinguishes attention mechanisms. *Vision Research, 38*(9), 1183–1198.

Lu, Z. L., & Dosher, B. A. (1999). Characterizing human perceptual inefficiencies with equivalent internal noise. *Journal of the Optical Society of America. A, Optics, Image Science and Vision, 16*(3), 764–778.

Lu, Z. L., & Dosher, B. A. (2001). Characterizing the spatial-frequency sensitivity of perceptual templates. *Journal of the Optical Society of America. A, Optics, Image Science and Vision, 18*(9), 2041–2053.

Lu, Z. L., & Dosher, B. A. (2004). Spatial attention excludes external noise without changing the spatial frequency tuning of the perceptual template. *Journal of Vision, 4*(10), 955–966.

Lu, Z. L., & Dosher, B. A. (2006). Characterizing observers using external noise and observer models, submitted for publication.

Lu, Z. L., Lesmes, L. A., & Dosher, B. A. (2002). Spatial attention excludes external noise at the target location. *Journal of Vision, 2*(4), 312–323.

Maloney, L. T. (1990). Confidence intervals for the parameters of psychometric functions. *Perception & Psychophysics, 47*(2), 127–134.

Mansouri, B., Allen, H. A., Hess, R. F., Dakin, S. C., & Ehrt, O. (2004). Integration of orientation information in amblyopia. *Vision Research, 44*(25), 2955–2969.

McKee, S. P., Levi, D. M., & Movshon, J. A. (2003). The pattern of visual deficits in amblyopia. *Journal of Vision, 3*(5), 380–405.

Movshon, J. A., Eggers, H. M., Gizzi, M. S., Hendrickson, A. E., Kiorpes, L., & Boothe, R. G. (1987). Effects of early unilateral blur on the macaque's visual system. III. Physiological observations. *The Journal of Neuroscience, 7*(5), 1340–1351.

Nagaraja, N. S. (1964). Effect of luminance noise on contrast thresholds. *Journal of the Optical Society of America, 54*(7), 950–955.

Nordmann, J. P., Freeman, R. D., & Casanova, C. (1992). Contrast sensitivity in amblyopia: masking effects of noise. *Investigative Ophthalmology and Visual Science, 33*(10), 2975–2985.

Pelli, D. G. (1981). *Effects of visual noise*. PhD dissertation. Cambridge, England: University of Cambridge.

Pelli, D. G. (1985). Uncertainty explains many aspects of visual contrast detection and discrimination. *Journal of the Optical Society of America A, 2*, 1508–1532.

Pelli, D. G. (1990). The quantum efficiency of vision. In C. Blakemore (Ed.), *Vision: Coding and efficiency* (pp. 3–24). Cambridge, UK: Cambridge University Press.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442.

Pelli, D. G., & Farell, B. (1999). Why use noise? *Journal of the Optical Society of America. A, Optics, Image Science, and Vision, 16*(3), 647–653.

Pelli, D. G., Levi, D. M., & Chung, S. T. (2004). Using visual noise to characterize amblyopic letter identification. *Journal of Vision, 4*(10), 904–920.

Petrov, A. A., Dosher, B. A., & Lu, Z. L. (2005). The dynamics of perceptual learning: an incremental reweighting model. *Psychological Review, 112*(4), 715–743.

Rose, A. (1948). The sensitivity performance of the human eye on an absolute scale. *Journal of the Optical Society of America, 38*, 196–208.

Schroder, J. H., Fries, P., Roelfsema, P. R., Singer, W., & Engel, A. K. (2002). Ocular dominance in extrastriate cortex of strabismic amblyopic cats. *Vision Research, 42*(1), 29–39.

Shadlen, M. N., & Newsome, W. T. (1998). The variable discharge of cortical neurons: implications for connectivity, computation, and information coding. *The Journal of Neuroscience, 18*(10), 3870–3896.

Sireteanu, R., Tonhausen, N., Muckli, L., Lanfermann, H., Zanella, F. E., & Singer, W. (1998). Cortical cite of the amblyopic deficit in strabismic and anisometropic subjects, investigated with fMRI. *Investigative Ophthalmology and Visual Science, 39*(4), s909.

Tanner, W. P., Jr., & Birdsall, T. G. (1958). Definitions of d' and n as psychophysical measures. *Journal of the Acoustical Society of America, 30*, 922–928.

Tjan, B. S., Braje, W. L., Legge, G. E., & Kersten, D. (1995). Human efficiency for recognizing 3-D objects in luminance noise. *Vision Research, 35*(21), 3053–3069.

Tjan, B. S., Chung, S., & Levi, D. (2002). Limitation of ideal-observer analysis in understanding perceptual learning. In *Twenty-seventh annual interdisciplinary conference. Jackson Hole, Wyoming.*

Tolhurst, D. J., Movshon, J. A., & Dean, A. F. (1983). The statistical reliability of signals in single neurons in cat and monkey visual cortex. *Vision Research, 23*(8), 775–785.

Van Meeteren, A., & Barlow, H. B. (1981). The statistical efficiency for detecting sinusoidal modulation of average dot density in random figures. *Vision Research, 21*(6), 765–777.

Wang, H., Levi, D. M., & Klein, S. A. (1998). Spatial uncertainty and sampling efficiency in amblyopic position acuity. *Vision Research, 38*(9), 1239–1251.