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The response of the amblyopic visual system to noise

Dennis M. Levi *, Stanley A. Klein, Inning Chen

University of California, Berkeley, School of Optometry and The Helen Wills Neuroscience Institute, Berkeley, CA 94720-2020, USA

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Abstract

Visual perception is limited by both the strength of the neural signals, and by the noise in the visual nervous system. Here we use one-dimensional white noise as input, to study the response of amblyopic visual system. We measured the thresholds for detection and discrimination of noise contrast. Using an *N*-pass reverse correlation technique, we derived classification images and estimated response consistency.

Our results provide the first report of the sensitivity of the amblyopic visual system to white noise. We show that amblyopes have markedly reduced sensitivity for detecting noise, particularly at high spatial frequencies, and much less loss for discriminating suprathreshold noise contrast. Compensating for the detection loss almost (but not quite) equates performance of the amblyopic and normal visual system.

The classification images suggest that the amblyopic visual system contains adjustable channels for noise, similar to those found in normal vision, but "tuned" to slightly lower spatial frequencies than in normal observers. Our *N*-pass results show that the predominant factor limiting performance in our task in both normal and amblyopic vision is internal random multiplicative noise. For the detection of white noise the raised thresholds of the amblyopic visual system can be attributed primarily to extra additive noise. However, for the discrimination of suprathreshold white noise contrast, there is surprisingly little additional deficit, after accounting for the visibility of the noise.

Keywords: White noise; Psychophysics; Amblyopia; Classification images; Reverse correlation; Double-pass; Internal noise

1. Introduction

Visual perception is limited by both the strength of the neural signals, and by the noise in the visual nervous system (Barlow, 1957; Dosher & Lu, 1999; Eckstein, Ahumada, & Watson, 1997; Levi, Klein, & Chen, 2005; Pelli, 1990; Pelli & Farell, 1999). Indeed, internal noise is explicitly or implicitly incorporated into all extant models of spatial vision, and has been extensively quantified and modeled by measuring performance on a background of white noise [i.e., random fluctuations in luminance over space, time, or both] (Dosher & Lu, 1999; Eckstein et al., 1997; Pelli, 1990; Pelli & Farell, 1999).

Humans with naturally occurring amblyopia have marked abnormalities in spatial vision (see Kiorpes, 2006; Levi, 2006 for recent reviews). These abnormalities include reduced visual acuity, contrast sensitivity, position acuity and extensive crowding (Ciuffreda, Levi, & Selenow, 1991; McKee, Levi, & Movshon, 2003). Importantly, a number of recent studies have used stimuli either added to (e.g., Huang, Tao, Zhou, & Lu, 2007; Kiorpes, Tang, & Movshon, 1999; Levi & Klein, 2003; Levi, Waugh, & Beard, 1994; Pelli, Levi, & Chung, 2004; Xu, Lu, Qiu, & Zhou, 2006) or multiplied by (Mansouri, Allen, & Hess, 2005; Simmers, Ledgeway, Hess, & McGraw, 2003; Wong, Levi, & McGraw, 2001, 2005) background of white noise in order to try to estimate the factors limiting amblyopic vision. However, to date, almost nothing is known about what aspects of the input noise the amblyopic visual system

* Corresponding author. Fax: +1 510 642 7806.
E-mail address: dlevi@berkeley.edu (D.M. Levi).

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is sensitive to, i.e., what is the signal in noise delivered through the amblyopic eye?

Knowing about the sensitivity of the amblyopic visual system to white noise is important because white noise is broadband, containing a broad range of spatial frequencies with equal amplitude. An important study by Kersten (1987) suggests that humans with normal vision are quite efficient at detecting noise over a wide range of stimulus spatial frequencies (from 1 to 6 octaves in bandwidth—see also Levi et al., 2005; Taylor, Bennett, & Sekuler, 2003, 2004). Kersten's study is important because it raised questions about the now well-accepted multiple-channel model of visual detection. The multiple-channel model asserts that there are a number of narrow (1–2 octaves) bandwidth channels, each sensitive to a different range of spatial frequencies, and there is considerable evidence to support the existence of such channels for detection of simple patterns on a uniform background (see Graham, 1989 for a review). For detection of combinations of a few sinusoids the channels are combined inefficiently (Graham, 1989). However, Kersten's results seem to imply that visual noise is detected by an "adjustable" visual channel (i.e., a channel whose spatial frequency tuning is determined by the noise), just as auditory noise is detected by an adjustable auditory channel (Green, 1960). This notion has been confirmed using classification image methods to directly measure the observers' sensitivity to the components of the noise (Levi et al., 2005; Taylor et al., 2003, Taylor, Bennett, & Sekuler, 2004—discussed below). Thus the response of the visual system to white noise cannot be simply predicted on the basis of an observer's contrast sensitivity function (Jamar & Koenderink, 1985; Kersten, 1987). The classification images suggest that sensitivity to spatial noise in the normal visual system is not simply determined via passive filtering (i.e., it is not simply the input noise convolved with the observer's contrast sensitivity function). Rather, these results suggest that there must be active neural interactions. Are these interactions compromised by amblyopia? On a practical level it is also important to know which spatial frequencies within the white noise band the amblyopic visual system responds to in order to interpret the effect of the noise on the visibility of signals.

Finally understanding the amblyopic visual system's response to white noise is important because studies using white noise added to a stimulus have reached different conclusions. For example several studies have concluded that compared with normal observers, amblyopes have little or no elevation in internal noise (e.g., Pelli et al., 2004; Kiorpes' others), while others have suggested that amblyopes have increased internal noise (Levi & Klein, 2003; Xu et al., 2006). Typically these studies use a fixed (physical) noise contrast for both amblyopic and normal eyes, and it is not clear that the amblyopic visual system responds in the same way to the noise since the noise (or some components of the noise) may be less visible through the amblyopic eye. Thus it is important to understand the response function of the amblyopic visual system over a range of noise contrast levels.

In order to investigate these questions we asked amblyopic observers to discriminate differences in the strength of one-dimensional white noise. We measured their response consistency and classification images and compared the results with those of normal observers.

Our recent results and modeling show that in the normal visual system, detection and discrimination of noise is limited by three factors: a non-optimal template (i.e., the weighted combination of energy in each stimulus component) plus systematic noise (to be henceforth called consistent noise) in the form of higher order nonlinearities (like probability summation) among different spatial frequency channels, and by sources of random internal noise (Levi et al., 2005). Here we show that the amblyopic visual system has reduced sensitivity to noise, and we apply the N-pass response classification method to tracking down the factors that limit amblyopic performance.

2. Methods

Our methods are identical to those of Levi et al. (2005) and will only be described briefly.

2.1. Observers

Fifteen observers participated in these experiments; 10 amblyopic (4 anisometropic, 3 strabismic and 3 with both strabismus and anisometropia) and five normal control observers (from Levi et al., 2005) participated in this study. Details of the 10 amblyopic observers are provided in Table 1, and their results are color-coded according to their classification (anisometropic—green; strabismic—red; both—blue) in all of the figures. Viewing was monocular, with appropriate optical correction. All experiments were performed in compliance with the relevant laws and institutional guidelines.

2.2. Stimuli

Each noise stimulus was presented for 0.75 s, with a mean luminance of 42 cd/m^2 and a dark surround. The noise is a one-dimensional grating consisting of 11 harmonics (either 0.5–5.5, 1–11 or 2–22 c/deg) with phases and amplitudes randomized. The stimuli can be seen in the inset of Fig. 1. We varied the range of harmonics by varying the viewing distance. For the lowest range (0.5–5.5 c/deg) with $f = 0.5$ c/deg, the noise appeared in a 2.2 degree square field. Slightly more than one cycle of the fundamental was displayed. At the higher ranges, (1–11 or 2–22 c/deg), the field size was proportionally smaller.

2.3. Psychophysical methods

We used a rating-scale signal detection method of constant stimuli to measure the observers' performance.

The stimulus pattern, $P_k(x)$, for the kth trial is given by

$$P_k(x) = N_k \sum_m n_{k,m} \cos(2\pi m f x + \phi_{k,m}) \quad (1)$$

where m is summed from 1 to 11, f is 0.5, 1, or 2 c/deg, $\phi_{k,m}$ is a random number with a uniform distribution from 0 to π and $n_{k,m}$ is a random number centered at zero with a Gaussian distribution and unity standard deviation. The overall component contrast is set by N_k, the "intended" rms stimulus contrast that takes on one of three levels for discrimination and four levels for detection. Note that the actual component contrast differs from N_k because of the Gaussian noise $n_{k,m}$. For a fixed value of N_k

Table 1
Observer characteristics

Observer	Age (yr)	Gender	Strabismus (at 6 m)	Eye	Refractive error	Line letter acuity (single letter acuity)[a]
Strabismic						
MR	22	F	L EsoT 14^{Δ}	R	$-3.25/-2.50 \times 175$	$20/20^{+2}$
				L	$-3.25/-3.25 \times 175$	$20/32^{-1}$
JT	52	F	L EsoT 5^{Δ}	R	$-1.00/-0.50 \times 10$	$20/16^{+2}$
				L	$-0.75/-0.50 \times 90$	$20/63^{-1}$ $(20/25^{-2})$
SF	20	F	L EsoT $6–8^{\Delta}$	R	$-2.75/-0.25 \times 90$	$20/20^{+2}$
				L	-2.00	20/50 $(20/40^{-1})$
Anisometropic						
JW	22	F	None	R	$+1.75$	$20/80^{-2}$ $(20/80^{+1})$
				L	-2.00	20/20
SC	27	M	None	R	$+0.50$	$20/16^{+2}$
				L	$+3.25/-0.75 \times 60$	$20/50^{+2}$ $(20/40^{-2})$
VG	31	M	None	R	$+4.25/-4.00 \times 03$	$20/50^{+2}$
				L	$-0.25/-1.50 \times 177$	$20/20^{+2}$
MLR	44	F	None	R	$+4.00/-1.00 \times 31$	$20/125^{-2}$ (20/100)
				L	$+0.75$	20/20
Strab & aniso						
SM	55	F	Alt. ExoT 18^{Δ}	R	$+2.75/-1.25 \times 135$	20/40 $(20/25^{+1})$
				L	-2.00	$20/16^{-2}$
JD	19	M	L EsoT 3^{Δ}	R	$+2.50$	20/16
				L	$+5.00$	20/125 (20/125+2)
AW	22	F	R EsoT $4\text{-}6^{\Delta}$ & hypoT 4^{Δ}	R	$+2.75/-1.00 \times 160$	$20/80^{-1}$ $(20/50^{-1})$
				L	$-1.00/-0.50 \times 180$	$20/16^{-1}$

[a] The acuities listed in the table were determined using a Bailey–Lovie chart, and we specify both the full line letter acuity and the single letter acuity when available.

the intended rms contrast of the kth stimulus would be: $c = \text{sqrt}(11/2)\ N_k$ when averaged over many trials. The factor of 1/2 is because the average value of $\cos^2$ is 1/2.

For noise contrast *discrimination*, on each trial the expected value of the noise contrast, c, was chosen from one of three suprathreshold stimulus levels. That is, the observer responded by rating the noise contrast by giving numbers from 1 [lowest perceived contrast] to 5 [highest perceived contrast]. The three levels were chosen to be just discriminable ($d' \approx 1$) on the basis of preliminary experiments. Observers were given auditory feedback following each trial. The feedback was based on the intended stimulus contrast, c, rather than the actual contrast that was randomly distributed around c. There were more response categories (5) than stimulus categories (3) since the perceived contrast is a continuous variable, able to be subdivided into five categories by using four criteria. Feedback was helpful in stabilizing the criteria.

For noise contrast *detection* either a blank (noise contrast = 0) or one of three near-threshold stimuli were shown and the observer responded with numbers from 1 (confident the stimulus was a blank) to 4 (highest perceived contrast). Observers were given auditory feedback following each trial.

Data were collected in runs of 410 trials, preceded by 20 practice trials. Each classification image is based on the results averaged over either 3 or 4 separate runs (1230–1630 trials). As noted below, each run was an identical replica (with scrambled order) of the first run. We used the consistency of responses from run to estimate internal noise as discussed below.

2.4. Ideal observer

It is relatively straightforward to calculate the ideal observer's discrimination threshold. For this purpose it is convenient to rewrite Eq. (1) for a single stimulus presentation as

$$P(x) = N \sum_m a_m \cos(2\pi m f x) + b_m \sin(2\pi m f x) \tag{2}$$

where a and b are zero mean unit variance Gaussian random numbers and the summation goes from $m = 1$ to 11. The total energy of this stimulus is given by

$$E = \int_0^1 P^2(x)\mathrm{d}x = N^2 K/2 \tag{3}$$

where

$$K = \sum_{m=1}^{11} \left(a_m^2 + b_m^2\right) \tag{4}$$

The quantity K is a random number with a chi-square distribution with 22 degrees of freedom. The mean and standard deviation of K over many stimuli is

$$K \approx 22 \pm \sqrt{2 * 22} \tag{5}$$

The d' for the task of discriminating a contrast of $N + \Delta/2$ from $N - \Delta/2$ could be written in terms of discriminating the two energies corresponding to these two contrasts

$$\begin{aligned} d' &= (E_+ - E_-)/\text{std}(E) \\ &= \left((N+\Delta/2)^2 - (N-\Delta/2)^2\right)\ \text{mean}(K)/N^2\text{std}(K) \\ &= 2N\Delta(22)/N^2\ \text{sqrt}(44) \end{aligned} \tag{6}$$

If threshold is defined to be the contrast shift Δ that gives $d' = 1$ then Eq. (6) can be solved for Δ to give the threshold, th

$$\text{th} = \Delta = N/(2\ \text{sqrt}(11)) \tag{7}$$

This surprisingly simple result shows that the Weber fraction for noise discrimination equals 1/2 divided by the square root of the number of frequency components. For 11 frequency components the Weber fraction is $1/\text{sqrt}(44) = 0.15$. For detection the ideal observer's threshold would be zero since the ideal observer has no intrinsic noise.

2.5. General response model for noise targets

In order to clarify our approach for distinguishing random from consistent noise, we now present a review of the formalism developed in Methods and Appendix of Levi et al. (2005). We have altered the notation

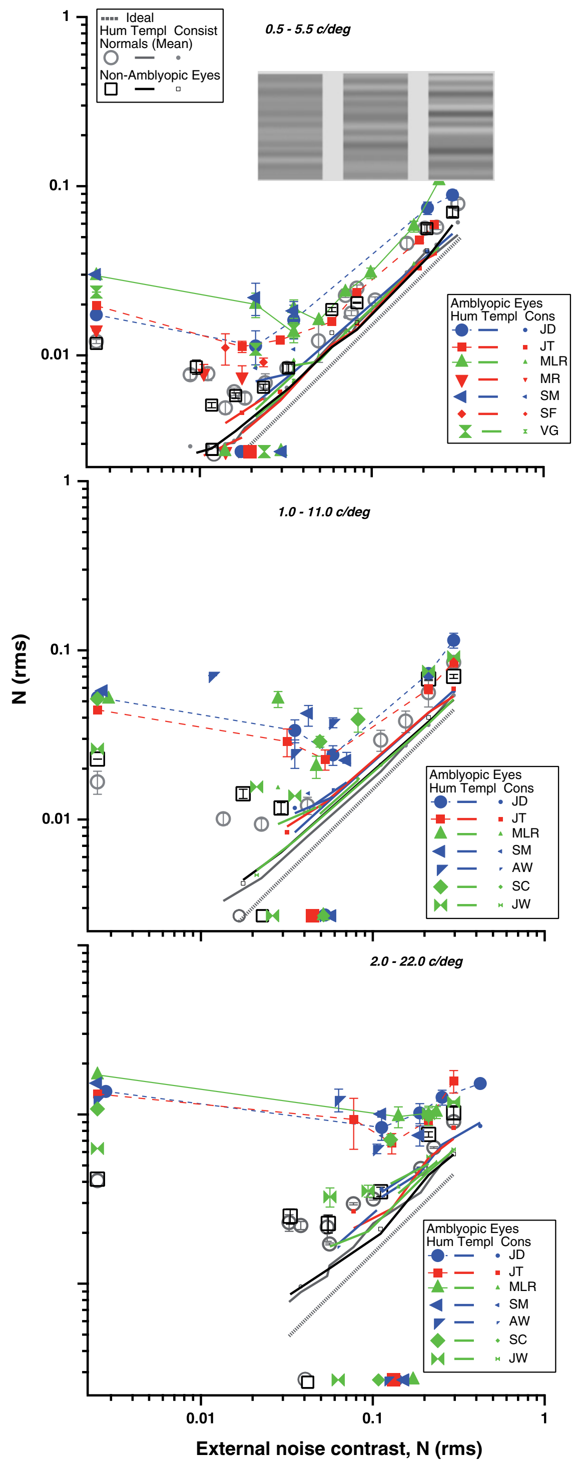

Fig. 1. Noise discrimination thresholds (ΔN) as a function of external noise contrast (N). Each panel shows a different noise spatial frequency range. For human observers (Hum—large symbols). Predictions are also shown for the ideal observer (gray dotted line), the "template" observer (Temp—lines) and for the consistent noise (cons—small symbols). Symbols near the abscissa in the bottom panel show the observers' thresholds for detecting the noise. Note that in this and all other figures, gray circles indicate normal control observers, black squares, non-amblyopic eyes, and solid symbols, amblyopic eyes color-coded according to classification (anisometropic—green; strabismic—red; both—blue). The inset shows examples of our stimuli: one-dimensional white noise shown at low (left) medium (middle) and high (right) contrast.

slightly for greater clarity. The starting point is to divide the subject's internal response for the kth trial of the pth pass, $r_k(p)$, into a consistent response, rc_k, and a random response, $\mathrm{rr}_k(p)$

$$r_k(p) = \mathrm{rc}_k + \mathrm{rr}_k(p) \tag{8}$$

Our goal will be to estimate the magnitude of the random internal noise rr and to subdivide the consistent internal noise into three parts: the ideal observer part, the additional noise due to a non-ideal template and a part due to higher order nonlinearities.

When we calculate both the classification image (the template) and the ratio of random to consistent noise we will do the calculations separately for each stimulus level. In order to emphasize this point, Eq. (1) will be rewritten by removing the factor N_k

$$P_k(x) = \sum_m n_{k,m} \cos(2\pi m f x + \phi_{k,m}) \tag{9}$$

where $n_{k,m}$ are zero mean Gaussian random numbers with a fixed standard deviation that can differ from unity (the intended noise contrast N_k of Eq. (1) has been incorporated into $n_{k,m}$) and the other variables are the same as in Eq. (1).

The consistent noise, rc_k, can be subdivided into two parts, a template term representing a linear weighting of the energy at each frequency (combining the ideal observer's noise and the noise from a mismatched template) plus a consistent error containing higher order nonlinearities, h_k plus a possible dependence on previous stimuli $p_{<k}$ (the reason for the $<k$ subscript).

$$\mathrm{rc}_k = \sum_{m=1}^{11} t_m n_{k,m}^2 + h_k + p_{<k} \tag{10}$$

A template factor, t_m, has been introduced. The ideal observer would use a matched filter given by $t_m = 1$ since the matched filter has equal weighting of all the frequencies. The next section examines how to estimate t_m for a real observer. The method for estimating the higher order nonlinear consistent noise, h_k will be taken up in the forthcoming discussion of response consistency. The present paper will henceforth ignore $p_{<k}$ since we randomize the order of presentation so any consistent order effects would get shifted to the random noise, rr_k component of the response (see Klein, 2006; Levi et al., 2005) for a detailed discussion of this point.

2.6. Classification images

We used the response classification method to assess what stimulus information our observers used to judge the contrast of the noise. Response classification provides an important new tool for learning about what information an observer uses to make perceptual decisions (Eckstein & Ahumada, 2002). By keeping track of both the pattern of noise and the observer's responses on each trial it is possible to compute the correlation between the noise and the observer's response. The result is a classification image that shows which aspects of the noise influence the observer's performance. Thus, the classification image may be thought of as a behavioral receptive field (Gold, Murray, Bennett, & Sekuler, 2000) and this method provides an important new tool for measuring the "template" an observer uses to accomplish the visual tasks (Neri & Levi, 2006).

In order to measure the classification image for our noise discrimination task we used linear regression to compute the classification coefficients, as described by Levi and Klein (2002, 2003).

Eqs. (8) and (10) can be rewritten as

$$R_k(p) = \sum_m e_{k,m} t_m + h_k + \mathrm{rr}_k(p) + \mathrm{err}_k(p) \tag{11}$$

where the main change from Eq. (10) is that R_k is the observer's digital rating response rather than the internal analog response r_k. The analog to digital conversion is accomplished by the placement of criteria (see Appendix of Levi et al., 2005) and the error in this conversion is included in the error term $\mathrm{err}_k(p)$. The coefficient of the template, $e_{k,m} = n_{k,m}^2$, is the stimulus energy on the kth trial for the mth frequency. Since the classification image is part of the consistent aspect of the response the dependence on pass, p, can be ignored. The classification image will be averaged over the multiple passes.

Eq. (11), is the standard linear regression situation with hundreds of equations (one for each datum k) and a small number of parameters (the 11 t_m values). As was discussed, when calculating the classification image t_m we restrict the linear regression analysis to a single test contrast level. That is, only values of k corresponding to the same level are used for the linear regression. For the discrimination experiments a classification image is obtained for each of three levels (four for detection) and then averaged to produce the templates that will be shown in Section 3.

It is convenient to use a matrix method to implement linear regression to solve for the template in Eq. (11). In matrix notation Eq. (11) becomes,

$$R = E * T + \text{error} \tag{12}$$

where we have grouped the consistent noise term with the error term. Eq. (12) can be solved for T by first multiplying both sides of Eq. (12) on the left by the transpose of E

$$E' * R = (E' * E) * T + E' * \text{error} \tag{13}$$

and then solving for the template vector T

$$T_{\text{LinReg}} = \text{pinv}(E) * R \tag{14}$$

where the pseudoinverse of E is given by:

$$\text{pinv}(E) = \text{inv}(E' * E) * E'. \tag{15}$$

Eq. (14) is the matrix method for doing linear regression. If we had left off the inverse term (replacing $\text{inv}(E' * E)$ with unity) then Eq. (14) would have been

$$T_{\text{RevCor}} = E' * R \tag{16}$$

corresponding to the reverse correlation method for calculating classification images. The advantage of doing linear regression rather than reverse correlation is that it is more accurate, especially when the number of trials is relatively small. It is for that reason that we are able to obtain classification images with less than 500 trials.

These classification images enable us to infer the perceptual template that the observer uses for the task.

2.7. Response consistency

We used an N-pass method to determine our observers' response consistency (Burgess & Colborne, 1988; Gold, Bennett, & Sekuler, 1999; Levi & Klein, 2003; Levi et al., 2005). In this method, the experiment is repeated N times with identical stimuli (but with randomized presentation order), and the consistency of individual trials on each pass is used to provide an estimate of the observers' internal random noise (Ahumada & Lovell, 1971; Burgess & Colborne, 1988; Gold et al., 1999; Levi & Klein, 2003). The amount of response disagreement between the N tests allows the system's total noise (measured by the signal detection d') to be parsed into random noise that is independent across multiple presentations of the identical stimulus, and internal plus external noise that is consistent (100% correlated) across multiple presentations.

It is generally stated that the double-pass method measures the ratio of internal to external noise (e.g., Burgess & Colborne, 1988; Gold et al., 1999). However, we believe that the term "external noise" should be restricted to properties of the external noise that is independent of the observer. Therefore we use the term consistent noise and reserve the name external noise for a measure of the external noise that is independent of the human observer.

As discussed earlier the ideal observer calculates the rms stimulus contrast for making its decision. Random internal noise can be thought of as extra random noise added to the external noise. Consistent internal noise represents factors in the decision stage that would give consistent, but incorrect, responses on repeated presentations. One example of consistent noise is the use of a mismatched frequency domain template. As discussed in the preceding section we have separated out this type of consistent noise since it is readily measurable by calculating the classification image. Another example of consistent noise would be expected to be found for the detection runs where the observer must discriminate a stimulus from a blank screen. Rather than following the ideal observer strategy of integrating power across the full stimulus, human observers are likely to base their decision on a small patch of the stimulus that exceeds threshold. That type of behaviour would be expected from a system with band-pass detection mechanisms that do probability summation across the full stimulus rather than efficient energy summation.

In order to measure the amount of consistent internal noise, we saved the random seed from the initial run, and re-used it so that the noise was identical in either two (double-pass), three (triple pass) or four runs (quadruple pass). In the double-pass case, we ran two separate double passes. For triple and quadruple passes we analyzed and averaged all possible pairings. Although the same stimuli were presented in multiple runs the order of presentation was randomized across runs.

As discussed in Levi et al. (2005) we used two methods for estimating the correlation q^2 that is related to the ratio of consistent response variance to total response variance, where the consistent part is given in Eq. (10), and the total response is given by the human threshold as measured by our standard signal detection methods (Levi et al., 2005).

The first method, based on Eqs. (8) and (10) involves finding a best fit to the data in terms of the estimated d' values for the different stimulus levels and the placement of criteria. To estimate the correlation, q^2, we replaced the assumptions of independent Gaussian noise on each pass with bivariate Gaussian noise that was correlated across pairs of passes. The correlation was a free parameter that was varied to get the best fits to the double pass data. All pairings of multiple passes were examined and the q^2 from each pairing were averaged. The search for the optimal q^2 was done with the d' and criteria constrained to their best values.

The second method for estimating q^2 was much simpler. We simply calculated the standard correlations of the responses, $R_k(p)$ given in Eq. (11) for all pairs of passes, p. As discussed above, this analysis was done separately for each stimulus level. We found that the two methods gave similar estimates of q as shown in the inset to Fig. 5 of Levi et al. (2005). We also carried out simulations to validate the two methods. Although the two methods often gave small biases, the biases were often in opposite directions, so our estimates of the ratio of consistent to random noise are based on the average of the two methods.

Fig. 3 of Levi et al. (2005) illustrates our general model for noise discrimination in the normal visual system. Our working hypothesis here is that amblyopia could result in an inefficient template for noise, or increased random and/or systematic internal noise, each of which would elevate noise discrimination thresholds above those of the normal human observer. The current experiments were aimed at exploring this hypothesis.

3. Results

3.1. Detection and discrimination of noise

Fig. 1 shows both human (symbols) and ideal (dotted gray line) discrimination thresholds (ΔN) as a function of noise contrast (N) specified as the rms contrast of the noise. Note that N spans a large range from below the observers' noise detection threshold (shown by the symbols along the abscissa) to well above threshold. Each panel shows a different noise spatial frequency range. For now we will ignore the solid lines (which show the thresholds predicted for an ideal observer with the human observer's template) and small symbols (which show the thresholds predicted on the basis of the observers' consistent noise). We will discuss those predictions later.

Consider the top panel (0.5–5.5 cpd). For normal control observers (gray open symbols) noise thresholds follow the well-known "dipper" function of contrast discrimination

(Legge, 1981; Levi et al., 2005; Stromeyer & Klein, 1974), first falling as contrast increases, and then rising more or less in proportion to the noise contrast, indicating that noise discrimination is a more or less constant Weber fraction of the noise contrast once noise contrast reaches about three times the noise detection threshold (indicated by the open gray symbol along the abscissa). Similar results were obtained for the non-amblyopic eyes (mean data shown by the open black squares). Note that as the spatial frequency range of the noise increases (lower panels) the detection thresholds increase, and the dipper shifts to the right.

The amblyopic eye data (solid symbols) are qualitatively similar—exhibiting the characteristic dipper shape; however the noise detection thresholds are elevated (solid symbols along the abscissa), and the transition from falling to rising thresholds is shifted correspondingly (and more so as noise spatial frequency increases). Note that when compared to the normal controls, some of the amblyopic observers show very severe losses at low contrast levels (e.g., more than a log unit at an rms contrast of 0.04 in the lower right panel), and much smaller losses (≈ a factor of two) at the highest noise contrast levels.

These results are reminiscent of several previous studies showing that both contrast detection and discrimination thresholds for high spatial frequency grating patterns are elevated in the amblyopic eye (Bradley & Ohzawa, 1986; Ciuffreda & Fisher, 1987; Hess, Bradley, & Piotrowski, 1983; Levi, Klein, & Wang, 1994). Bradley and Ohzawa (1986) found that under a wide variety of conditions that influence contrast detection thresholds (luminance, spatial frequency and retinal locus, and amblyopia), the contrast discrimination function maintains its characteristic form. This seems to be largely the case too for noise discrimination. The data of Fig. 1 are re-plotted in Fig. 2, with both ΔN and N (the noise pedestal) specified in threshold units (i.e., both the ordinate and the abscissa were divided by the noise detection threshold). The effect of this operation is to almost (but not quite) superimpose all of the curves (dipping at approximately 1.3 NTU contrast), suggesting that the processes underlying noise discrimination are similar in amblyopic and normal vision, differing mainly by a "scale factor", i.e., the noise detection threshold. Interestingly, Legge and Kersten (1987) found that foveal and peripheral contrast discrimination functions also nearly superimpose when both the contrast increment and the contrast pedestal are specified in threshold units. The dipper is easily seen in this figure, where all points below an ordinate value of 1.0 are in the dipper regime.

In normal foveal vision, we (Levi et al., 2005) showed that human efficiency (defined as the ratio of ideal to human thresholds squared) for discriminating noise is lowest at low (near threshold) noise levels (≈3–4%), and increases to about 30% beyond the dipper regime, and that the efficiency loss can be attributed to three factors: (1) a poorly matched template, (2) high levels of internal noise and (3) higher order nonlinearities (consistent noise) not present in the transducer function. In the following sections

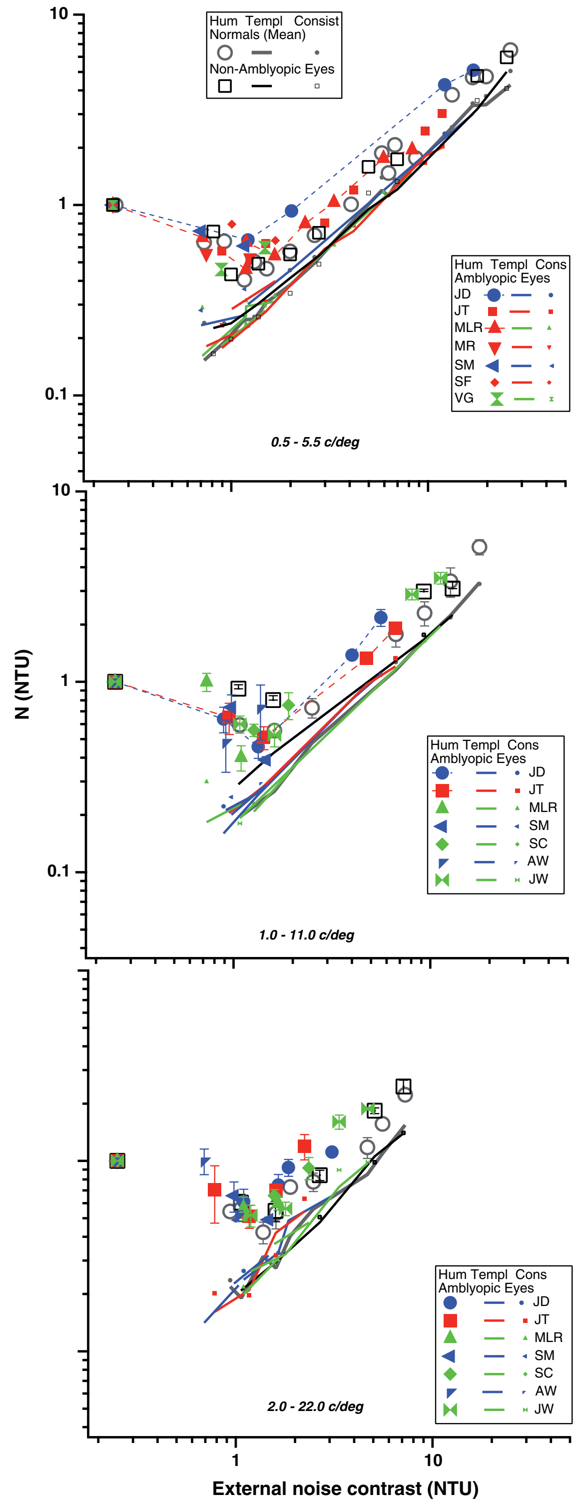

Fig. 2. Normalized noise discrimination thresholds (ΔN) as a function of external noise contrast (N). The data of Fig. 1 are re-plotted here with both axes divided by the observers' noise detection threshold. All other details as in Fig. 1.

we will ask how each of these to factors limits performance in the amblyopic visual system, and whether they might account for the failure to superimpose exactly.

One crucial factor that might limit human performance is the information that the observer uses to solve the task.

An ideal observer would use all of the information in the stimulus, equally weighted. However, human observers are more sensitive to certain spatial frequencies in the noise than to others, so their template for performing the task may be inefficient. Using linear regression, we showed that in normal observers, the classification image for noise is band-pass, and that it changes with noise frequency band by re-centering on the range of frequencies in the stimulus (Levi et al., 2005). Given the well-established loss of sensitivity to high spatial frequencies in the amblyopic visual system, it is of special interest to ask how amblyopia influences the classification image or template for noise.

Fig. 3 shows the classification images. Each panel represents a different spatial frequency range. The classification coefficients reveal that for each of the three frequency ranges the classification image for normal (open gray symbols), non-amblyopic (open black squares) and amblyopic (large solid symbols) is band-pass—it is more or less proportional to f for low frequencies, and there's a rapid drop in the coefficient amplitude at high frequencies. For all eyes, the classification plots are similar in shape, however, the amblyopic eyes are shifted to the left (to lower spatial frequencies). As noted above, for normal observers the template changes by re-centering on the range of frequencies in the stimulus. This is also true for amblyopic eyes. Fig. 4 plots the peak spatial frequency of the best-fitting Gaussian function versus the middle of the noise spatial frequency range for each observer.[1] For normal and non-amblyopic eyes, the peak shifts from ≈4.5 to 10 c/deg as the mid-spatial frequency shifts from 3 to 12 c/deg. On average (yellow line) the amblyopic eyes peaked at a spatial frequency about 50% lower, and all but one of the amblyopic eyes (JW) showed a peak-shift toward lower spatial frequencies. Levi et al. (1994) showed a similar (but larger) scale-shift when detecting a line in noise.

We can estimate the degree to which the observer's template limits performance by computing the performance of the human observer's template, and this is shown by the solid lines in Figs. 1 and 2. The normal human template is moderately efficient (template efficiency varies from about 50% at low noise levels to close to 80% at high—see Fig. 3 of Levi et al., 2005). After compensating for the detection loss (Fig. 2), the amblyopes' templates superimpose almost completely with that of the normal fovea, and are quite efficient. Thus performance must be limited by other factors, and we investigate those further using multiple runs with the identical stimuli intermixed in each run as discussed in Section 2.

By repeating the experiment several times with *identical* noise sequences shown in a randomized order, we are able to estimate the ratio of consistent to total internal noise (q).

[1] For most of the classification plots, the Gaussian provided an adequate fit (as indicated by the chi-square). However, in a few cases (e.g., VG) we had to use an iterative procedure, fitting one parameter at a time while holding the others constant, in order to achieve the best fit.

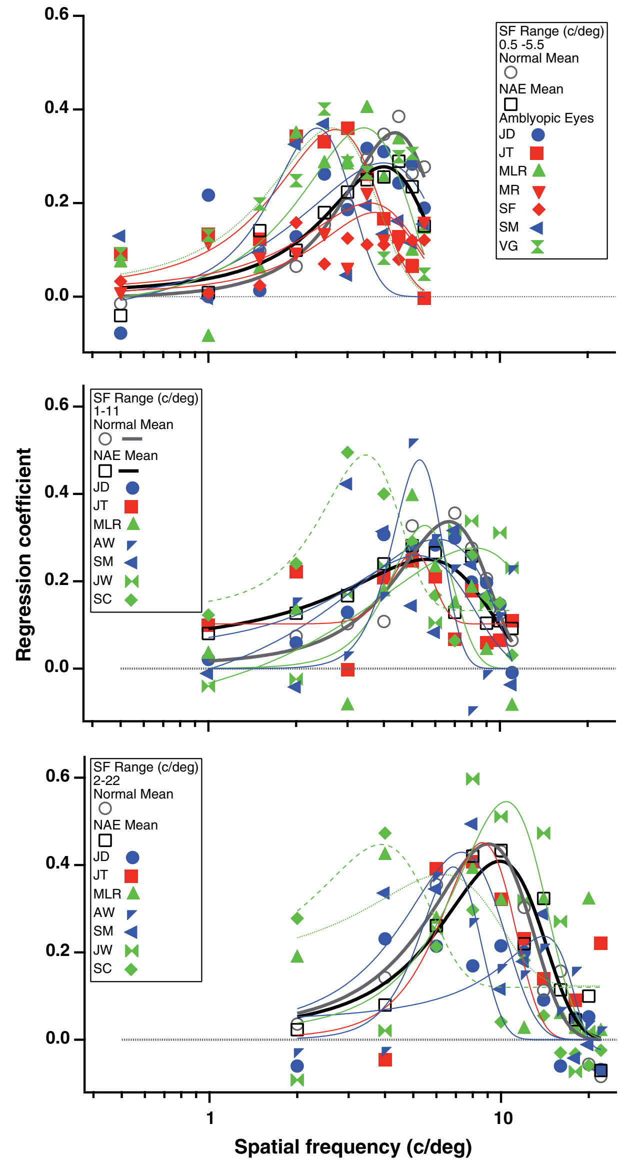

Fig. 3. Noise classification images: Classification images for noise levels of about three times threshold. The three panels represent three different noise ranges (top 0.5–5.5, middle 1–11 and bottom 2–22 c/deg). The open circles and squares are averaged across the normal observers and non-amblyopic eyes, respectively. The solid symbols are for individual amblyopic observers viewing with their amblyopic eye. Lines are Gaussians fit to the data.

Note that Levi et al. (2005) calculated q in two different ways (q_{Npass} and q_{bi}), which gave similar but not identical results. Here we simply averaged the two methods, and report the average value in Fig. 5.

For normal and non-amblyopic eyes, q increases rapidly from zero at low noise contrasts (near the noise detection threshold, NTU ≈1), to about 0.5 at ≈3 NTU, and then continues to increase more slowly up to about 0.6 (Fig. 5). Thus, not surprisingly, at low noise contrast random noise dominates, while at high noise contrast, consistent noise dominates. Note that for the non-amblyopic eyes, at the higher spatial frequency range q was lower

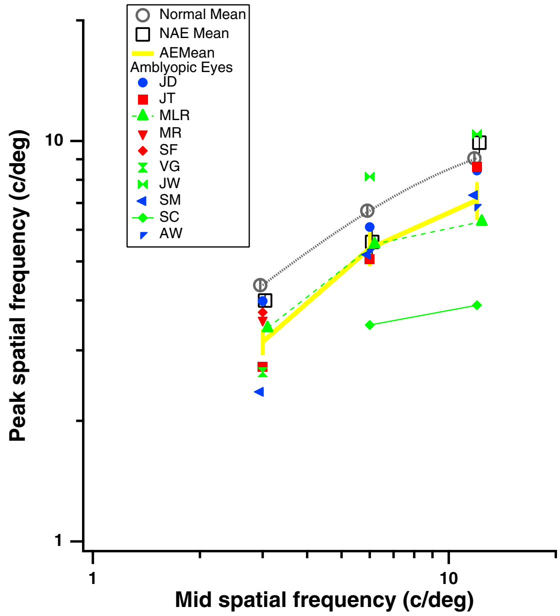

Fig. 4. Peak spatial frequency versus noise-band (as characterized by the middle of the spatial frequency of the noise—i.e., 3, 6 and 12 cpd for the ranges 0.5–5.5, 1–11 and 2–22 cpd, respectively). The peak frequencies are estimated by the Gaussian fits in Fig. 3. Open circles and squares are averaged across the normal observers and non-amblyopic eyes, respectively. The solid symbols are for individual amblyopic observers viewing with their amblyopic eye. The thick yellow line is the peak spatial frequency averaged across the amblyopic eyes.

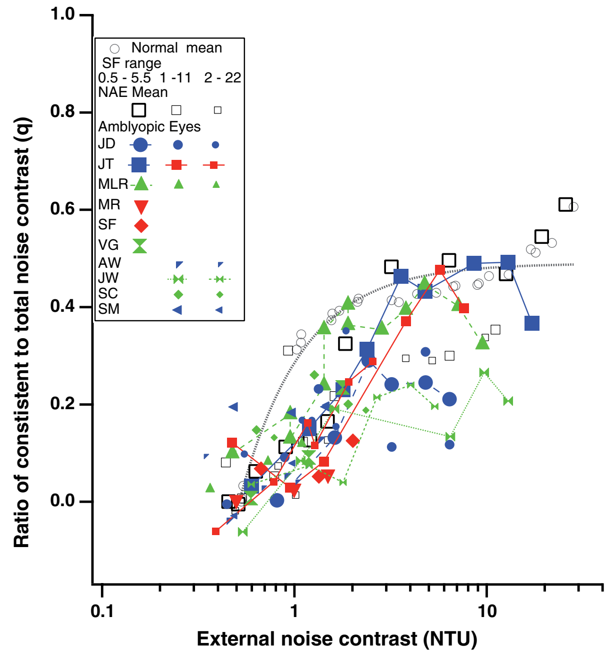

Fig. 5. Ratio of consistent to total noise (q) as a function of noise contrast (normalized to the observers' noise detection thresholds, i.e., in Noise Threshold units, NTU). Open circles and squares are averaged across the normal observers and non-amblyopic eyes, respectively. The solid symbols are for individual amblyopic observers viewing with their amblyopic eye. Noise spatial frequency range is coded by symbol size.

(only reaching ≈0.36 at 10 NTU). Interestingly, many (but not all) of the amblyopic eyes show a more gradual increase in q and fail to reach levels above ≈0.3 (e.g., JW, SF, JD and VG) even at noise contrast levels of more than 10 times threshold, indicating a greater proportion of random noise.

The small symbols in Figs. 2 and 3 show the contribution of consistent noise to human performance. We found only a small effect of consistent noise at low noise contrast levels in normal observers (Levi et al., 2005), whereas at high noise contrast, consistent noise results in little or no loss of efficiency beyond the mismatched template. As can be seen in Fig. 2 (small symbols), consistent noise predicts little or no loss beyond the template. At all noise levels above detection threshold, normal human discrimination thresholds are about 50% higher than the consistent noise prediction, so random noise reduces human efficiency by about a factor of 2.25 (1.5^2) over the approximately fortyfold range of noise levels tested. This random noise is stimulus dependent or multiplicative, consistent with the Weber's law dependence of noise thresholds on the noise pedestal. For some of the amblyopes, as noted above, this multiplicative random noise is higher, and this is reflected in the amblyopes' elevated noise thresholds. One surprising result of the present study is that amblyopic thresholds do not seem to be much elevated over normal thresholds in the high contrast regime where multiplicative noise would be visible.

4. Discussion

4.1. Detection and discrimination of noise

Our results provide the first report of the sensitivity of the amblyopic visual system to white noise. We show that amblyopes show markedly reduced sensitivity (elevated thresholds) for detecting noise, particularly at high spatial frequencies, and much less loss (smaller threshold elevation) for discriminating noise contrast (Fig. 1). Compensating for the detection loss (Fig. 2) almost (but not quite) equates performance of the amblyopic and normal visual system.

4.2. The template for noise

Our classification images reveal the signal in noise, showing which aspects of noise influence an observer's responses. Our results show that the amblyopic template for noise, like that of normal observers, is band-pass in shape *in each noise band*. It has sometimes been assumed that detection of noise occurs after filtering by the eye's contrast sensitivity function (Jamar & Koenderink, 1985; Kersten, 1987) and is therefore determined by passive filtering (i.e., it is simply the input noise convolved with the observer's contrast sensitivity function). We (Levi et al., 2005) developed a model for "adjustable" noise channels, consistent with Green's (1960) inference that the critical bands for auditory noise are adjustable, and the recent report that human observers can summate both spatial frequency (Taylor et al., 2003) and orientation information in noise over a very broad range of spatial frequency and orientation bandwidths (Taylor et al., 2004). Our new results suggest that similar adjustable channels appear to be operational in the amblyopic visual system, but are "tuned" to slightly lower spatial frequencies than in normal observers, even when the range of input spatial frequencies is quite low (0.5–5.5 cpd) as shown in the top panel of Fig. 3. This result is surprising. Our amblyopic observers show substantial losses in visual acuity (from 2- to 8-fold) thus one might have expected them to show substantial shifts in the tuning of their template for noise; however, as can be seen clearly in Fig. 6 the large acuity loss (abscissa) is not reflected in the small shift in tuning peak (ordinate).

Once the detection loss is taken into account, the amblyopes' template for noise is very similar in efficiency to that of normal observers. We note that unlike the linear template for detecting or discriminating the position of a bar (Levi & Klein, 2003), the noise template is a nonlinear energy template. Our results show that any loss of performance in discriminating the noise energy in amblyopia is not due to a mis-matched template.

4.3. Internal noise and response consistency

We used an N-pass method (Burgess & Colborne, 1988; Gold et al., 1999; Green, 1964; Levi et al., 2005) to estimate the ratio of random to consistent noise in the observers' visual system. Our results show that the predominant factor limiting performance in our task in both normal and amblyopic vision is internal random multiplicative noise. A surprising outcome of the current study is that for the discrimination of suprathreshold white noise in the high visibility range, there is surprisingly little deficit after accounting for the visibility of the noise. Our previous work, using signals known exactly in fixed contrast noise, shows that increased random noise is a critical factor limiting amblyopic performance in detecting and discriminating the position of signals in noise (Levi & Klein, 2003).

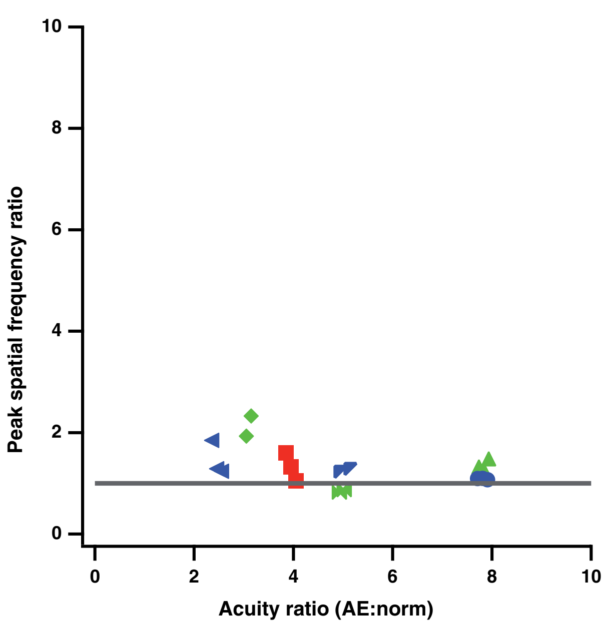

Fig. 6. Shift in peak spatial frequency (amblyopic eye relative to normal—from Fig. 4, lower panel) plotted against the shift in visual acuity (the amblyopic eye acuity relative to normal). Note that the symbols and color coding are as in Fig. 1.

We do not yet understand the origin of the high fraction of random noise in the amblyopic visual system. Earlier we (Levi & Klein, 2003) suggested the increased fraction of random noise in the amblyopic cortex might be a consequence of a variable or noisy template (McIlhagga & Paakkonen, 1999). Noisy templates can be achieved in a variety of ways, e.g., by including randomly selected, but irrelevant, neurons (Shadlen, Britten, Newsome, & Movshon, 1996) or by uncertainty (Pelli, 1990) in which a multiplicity of mechanisms (e.g., shifted templates) are monitored. We pointed out that a multiplicity of shifted templates would lead to a broader template, would degrade the bar position discrimination task more than the bar detection task, and, importantly, would lead to an increased proportion of internal noise.

As noted in Section 1, a large number of previous studies have used external noise in an attempt to better understand the internal noise that limits performance in the amblyopic visual system (Levi & Klein, 2003; Nordmann, Freeman, & Casanova, 1992; Watt & Hess, 1987; Pelli et al., 2004; Wang, Levi, & Klein, 1998; Xu et al., 2006). In most of these studies external noise was added to a stimulus, and the observer's task was to detect or identify the stimulus. In some studies (e.g., Xu et al., 2006) the amount of external noise was varied; however, ours is the first study to determine the visibility of the noise, and to use noise as the stimulus. Below we discuss why these points are important, and how our results relate to previous work.

4.4. Noise visibility

Somewhat surprisingly, the amblyopic visual system shows reduced sensitivity to white noise, even when the components of the noise are within the pass-band of the amblyopic eye. It's surprising because, as shown by the classification images, amblyopic observers show a shift in spatial scale (toward lower spatial frequencies) that could, in principle, preserve high sensitivity to noise. Consider for example the lower panel of Fig. 1. Several of the amblyopic observers have noise detection thresholds elevated by a factor of 4–5 relative to the normal controls (symbols along the abscissa). Moreover, their noise discrimination thresholds are elevated by a factor of ≈ two at high noise levels. Consider the effect of using a single fixed rms noise contrast (e.g., 0.1) as done in many previous studies (Levi & Klein, 2003; Pelli et al., 2004). The visibility of the noise would be different for normal and amblyopic observers and would vary amongst observers depending on the degree of amblyopia. As noted in Fig. 5 the ratio of consistent to total noise depends strongly on noise visibility. If the external noise were close to the observer's threshold, one might mistakenly conclude that they had high degrees of random noise relative to normal observers for whom the noise is highly visible (Levi & Klein, 2003). Indeed, several of our observers show values of q (ratio of consistent to total noise) that are normal or near normal at high external noise visibility levels; however some (e.g., JD and JW) appear to saturate and never approach normal levels, particularly for high spatial frequencies. As we discuss below, none of the extant studies that have used white noise in amblyopes have taken into account the visibility of the noise.

4.5. Why Noise?

It is commonly assumed that visual perception is limited by both the strength of the neural signals, and by the noise in the visual nervous system (Barlow, 1957; Dosher & Lu, 1999; Eckstein et al., 1997; Levi et al., 2005; Pelli, 1990; Pelli & Farell, 1999). Indeed, internal noise is explicitly or implicitly incorporated into all extant models of spatial vision, and has been extensively quantified and modeled by measuring performance on a background of white noise [i.e., random fluctuations in luminance over space, time, or both] (Dosher & Lu, 1999; Eckstein et al., 1997; Pelli, 1990; Pelli & Farell, 1999).

A number of studies (discussed below) have used white external input noise to infer the amount and type of noise in the amblyopic visual system. The new results presented here show the sensitivity of the amblyopic visual system to white noise and importantly, which spatial frequencies within the noise the amblyopic visual system responds to best.

Another advantage of noise is that our noise discrimination task relies only on noise energy, so position uncertainty (and shifted templates) would not be expected to have any impact on performance. As noted above, a multiplicity of shifted templates could lead to a broader template, which would degrade the detection of a bar, and would further degrade bar position discrimination as shown by Levi and Klein (2003) leading to an increased proportion of internal noise. However, increased internal noise for our noise discrimination task cannot be simply explained on the basis of noisy templates (McIlhagga & Paakkonen, 1999).

4.6. Relationship to previous studies

A large number of studies have applied the noise paradigm to exploring internal noise in amblyopia. Here we focus on those that have used white luminance or pixel noise (Nordmann et al., 1992; Kersten, Hess, & Plant, 1988; Kiorpes et al., 1999; Pelli et al., 2004) as opposed to, for example, positional noise (Watt & Hess, 1987; Wang et al., 1998).

An influential model treats internal noise as if it were a low level of noise added to the screen display (equivalent input noise—Barlow, 1957; Pelli & Farell, 1999). Because the equivalent input noise is additive, it limits performance at detection threshold and at low noise levels, but not at high external noise levels, where the external noise is dominant. Previous studies of grating contrast sensitivity (Nordmann et al., 1992; Kersten et al., 1988; Kiorpes et al., 1999) and letter recognition (Pelli et al., 2004) and position acuity (Levi & Klein, 2003) have reported small or no increases in equivalent input noise and large reductions in efficiency in amblyopes. However, in a detailed vision model, noise need not be additive (Dosher & Lu, 1999; Eckstein et al., 1997). Indeed, there is strong physiological evidence that in cortical neurons noise increases in proportion to the signal strength (Shadlen et al., 1996). This signal-dependent intrinsic noise is not made explicit in the standard additive noise model (it is factored into the efficiency loss).

Two studies have applied more detailed models that incorporate multiplicative noise and the observers' decision template. Levi and Klein (2003) used the double-pass method, which provides an estimate of all of the intrinsic noise, whether it is additive or multiplicative, early or late. The intrinsic noise that they reported was primarily *multiplicative* noise, since it is evident over a range of target contrast levels (both near threshold and suprathreshold). Importantly, their measurements and modeling allowed them to parse the intrinsic noise into two components: consistent noise, and random noise, and revealed that the amblyopic brain has high levels of random intrinsic noise for detecting a local stimulus (a bar) and for discriminating it's position. Their measurements revealed that amblyopes have a coarse template (classification image) for position, with severe high frequency attenuation.

Xu et al. (2006) measured orientation discrimination in white noise, and applied the PTM model of Dosher and Lu (1998, 1999). In agreement with Levi and Klein (2003) they concluded that amblyopes have deficient perceptual templates for their task. However, they also suggest that they have raised levels of additive internal noise. This is consistent with the elevated thresholds for noise detection. Future work with signals in noise will be needed to further clarify the relationship between Xu et al.'s raised additive noise and Levi and Klein's multiplicative noise.

4.7. Summary and conclusions

Our results show that amblyopes have reduced sensitivity (elevated thresholds) for detecting noise, particularly at high spatial frequencies, and much less loss (smaller threshold elevation) for discriminating noise contrast. Compensating for the detection loss almost (but not quite) equates performance of the amblyopic and normal visual system. Combining threshold measurements with trial-by-trial analysis (Green, 1964) allows us a unique way of dissecting the sources of noise in the visual nervous system that limit amblyopic vision.

Competing interests statement

The authors declare that they have no competing financial interests.

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