Characterizing the mechanisms of improvement for position discrimination in adult amblyopia

Roger W. Li
School of Optometry and Helen Wills Neuroscience Institute, University of California, Berkeley, CA, USA

Dennis M. Levi
School of Optometry and Helen Wills Neuroscience Institute, University of California, Berkeley, CA, USA

Adult amblyopes can improve positional acuity through practice; however, the neural mechanisms underlying this improvement are still not clear. In this study, seven adult amblyopes repeatedly practiced a position discrimination task in the presence of positional noise. We found that six of the seven showed systematic and significant improvements in position acuity that were both eye and orientation specific. Using a position-averaging model, we were able to parse the improvement in performance with practice into two factors: improvement in sampling efficiency and reduction of equivalent input noise. Three of the seven showed improved efficiency with no change in equivalent noise, two showed a significant reduction in equivalent noise with no change in efficiency, and one showed both improved efficiency and reduced equivalent noise. Interestingly, all observers showed substantial improvement in visual acuity, and one observer showed substantial improvement in stereoscopic. Three observers were also tested on a counting task, and all three improved after practicing positional discrimination. Our results reveal the mechanisms underlying perceptual learning in amblyopic vision, and may provide a basis for developing more effective and efficient strategies for the treatment of amblyopia.

Keywords: perceptual learning, amblyopia, occlusion therapy, visual acuity, stereoacuity, counting

Introduction

Extensive studies have shown that adults can improve performance in a wide range of visual tasks through practice (for a review, see Fine & Jacobs, 2002). We are particularly interested in positional acuity, for several reasons: (1) under ideal conditions, it represents the finest spatial grain of the visual system (Westheimer, 1967); (2) more importantly for our purposes, position acuity may be markedly degraded in amblyopia (Levi & Klein, 1983; Levi & Klein, 1985; Levi, Klein, & Yap, 1987); and (3) there is a close connection between position acuity and Snellen acuity (Enoch, Essock, & Williams, 1984; Levi & Klein, 1982; Levi & Klein, 1985; McKee, Levi, & Movshon, 2003).

There is a good deal of evidence that repetitious practice can significantly improve positional acuity (Fahle & Edelman, 1993; Fahle, Edelman, & Poggio, 1995; Li, Levi, & Klein, 2004; Poggio, Fahle, & Edelman, 1992), even in adults with amblyopia (Levi & Polat, 1996; Levi, Polat, & Hu, 1997). Our recent results suggest that in normal observers practice enhances the observer’s use of stimulus samples by retuning the observer’s decision template (Li et al., 2004) (i.e., by changing the weightings of inputs from basic visual mechanisms).

Perceptual learning could be a useful approach to improving visual performance in amblyopes. Amblyopia is a developmental disorder that occurs during a period of neural plasticity in childhood and leads to poor acuity in the amblyopic eye (Levi & Carkeet, 1993). Amblyopes have reduced performance in a wide range of visual tasks, from low-level tasks such as contrast sensitivity to high-level tasks such as counting (Asper, Crewther, & Crewther, 2000; Ciuffreda, Levi, & Selenow, 1991; Sharma, Levi, & Klein, 2000). Two major hypotheses suggested to explain this visual loss are spatial undersampling (decrease in neural sampling density or efficiency) and spatial uncertainty (spatial scrambling and/or an upward shift in the size of spatial filters) (Hess & Field, 1994; Levi & Klein, 1990; Wang, Levi, & Klein, 1998; Watt & Hess, 1987). The standard treatment for amblyopia since Buffon (1743), cited in (Ciuffreda et al., 1991), has consisted of penalizing the dominant eye through patching. The functional visual loss in amblyopia is often described as irreversible after a critical period; thus, occlusion therapy is not always undertaken to treat amblyopia after the age of 12. On the other hand, a number of clinical studies suggest that older children and adults can improve following treatment (Levi et al., 1997; Simmers & Gray, 1999). Moreover, Levi and his coworkers reported that adults with amblyopia show marked improvement in a Vernier task following intensive practice (Levi & Polat, 1996; Levi et al., 1997).

There remain important questions about how the amblyopic brain learns to improve visual performance. In this study, we used noise to address some of these questions. Specifically, we measured positional acuity in noise to parse any changes during learning into two important factors: a change in equivalent input noise and/or an increase in the efficiency with which the stimulus information is used. Equivalent input noise is the noise that must be added to the stimulus to act like the limiting noise in the visual sys-
tem, and it largely reflects the amount of noise the observer’s visual system adds to the stimulus. Efficiency reflects the computation underlying the use of the information (samples) in the stimulus (Pelli, 1990). Because position discrimination relies on spatial relations, we use positional noise (i.e., perturbation of the positions of parts of the stimulus) to explore the underlying neural mechanisms.

Figure 1 illustrates three of the possible post-training outcomes (threshold vs. noise, TvN curves) based on an early noise model (Pelli, 1990; Zeevi & Mangoubi, 1984): (1) A pure improvement in efficiency would shift the curve downward. This type of improvement has been reported for learning faces and complex patterns (Gold, Bennett, & Sekuler, 1999), and we found that an efficiency shift completely accounts for the improvement in position discrimination in normally sighted adults (Li et al., 2004). A mostly downward shift also occurs for learning orientation discrimination in peripheral vision (Dosher & Lu, 1998; Dosher & Lu, 1999). (2) A pure decrease in equivalent input noise would shift the “knee” point of the curve down and to the left. (3) Another pattern of learning that has been found (Dosher & Lu, 1998; Dosher & Lu, 1999) for learning simple foveal discrimination tasks is a rightward shift of the curve, produced by a combination of improved efficiency and increased equivalent input noise. Dosher and Lu model this type of learning in terms of improved exclusion of external noise.

A better understanding of the limits, time course, and mechanisms of plasticity is essential to develop more effective and efficient strategies for the treatment of amblyopia, which is currently based almost entirely on occlusion of the fellow eye.

Methods

Design

In this study, observers practiced a position discrimination acuity task in which they had to judge which of three pairs of line segments was misaligned (i.e., top, middle, or bottom in Figure 2). Trial-by-trial feedback was provided.

We introduced positional noise by perturbing the positions of the individual patches of each segment according to a Gaussian probability function. We used positional noise to mimic the putative limiting noise for our positional discrimination task. Equivalent input noise and sampling efficiency were estimated by systematically manipulating the stimulus positional noise in each session. We also examined the specificity of learning to the trained orientation and eye. Because visual acuity of the amblyopic observers is highly correlated with Vernier acuity (Levi & Polat, 1996), we tested their visual acuities with a Bailey Lovie LogMAR chart, from session to session, while practicing position discrimination tasks.

![Figure 2. Stimuli in positional noise. The observer’s task was to indicate the position of the “test” stimulus (top, middle, or bottom). The top stimulus is misaligned: The right segment is higher than the left segment.](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/933515/)
Mathematical modeling

A positional averaging model (Zeevi & Mangoubi, 1984) was used to quantify the effects of external positional noise ($\sigma$) on the threshold ($\sigma_t$):

$$\sigma_{th}^2 = 2d^2 \left( \frac{1}{k} - \frac{1}{n} \right) \left( \sigma_e^2 + \sigma_i^2 \right),$$  

where $k$ denotes the number of samples extracted, $n$ is the total number of samples, and $\sigma_i$ is the equivalent input noise. The term $1/n$ is present in Equation 1 because of the zero mean adjustment of each line. In this study, each segment consisted of 8 Gabor light patches, and hence $n$ was equal to 8. For 66% correct-response probability, the detectability ($d'$) was 1.1 (Wickens, 2002). By measuring the thresholds in different external noise settings, both $\sigma_i$ and $k$ can be estimated by fitting a TvN curve on the basis of least-square computation.

Equivalent input noise is the noise that must be added to the stimulus to act like the limiting noise in the visual system, and it largely reflects the amount of noise the observer’s visual system adds to the stimulus. When external stimulus noise is small compared to equivalent input noise, threshold is determined mainly by equivalent input noise. As the stimulus noise increases and equals the equivalent input noise in magnitude, the threshold begins to rise in proportion to stimulus noise level. Sampling efficiency ($E$) reflects the computation underlying the use of the information (samples) of the stimulus (Pelli, 1990), and was defined as,

$$E = \frac{k}{n} \cdot 100\%$$  

Training protocol

Our training protocol was divided into three phases: (1) For the pretraining baseline measurements, position discrimination thresholds were measured in the amblyopic eye for both vertical and horizontal line orientations. Thresholds for the horizontal orientation were also measured in the fellow eye. (2) In the training phase, each observer’s amblyopic eye was trained with horizontal stimuli for another eight sessions while the fellow eye was occluded. (3) In the post-training phase, thresholds were measured in the trained eye again for both vertical and horizontal orientations, and for the horizontal orientation in the untrained fellow eye. The data collection was completed in about 6 weeks (two or three sessions in a week). Each observer had given more than 10,500 responses (learning plus transfer testing) at the end of the experiment.

Seven adult observers with naturally occurring amblyopia were tested with full optical correction. The eye not being tested was occluded with a standard black eye patch. The clinical data are shown in Table 1. All observers were naive to the purpose of experiment and had no prior experience in psychophysical experiments. The experiments were undertaken with the understanding and written consent of each observer and all procedures were approved via institutional review.
Table 1. Clinical data. Note that the Bailey Lovie LogMAR chart was used for the visual acuity measurement.

<table>
<thead>
<tr>
<th>Observer</th>
<th>Age (yrs)</th>
<th>Gender</th>
<th>Type</th>
<th>Strabismus</th>
<th>Eye</th>
<th>Refractive error</th>
<th>Letter acuity (Snellen)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PD</td>
<td>48</td>
<td>M</td>
<td>Strabismic</td>
<td>L ExoT 30</td>
<td>R</td>
<td>Plano</td>
<td>20/20^2^</td>
</tr>
<tr>
<td>SL</td>
<td>20</td>
<td>M</td>
<td>Strabismic &amp; meridional</td>
<td>Alt. ExoT 7</td>
<td>R</td>
<td>+5.50/-5.00x95</td>
<td>20/32</td>
</tr>
<tr>
<td>AR</td>
<td>42</td>
<td>M</td>
<td>Anisometropic</td>
<td>None</td>
<td>R</td>
<td>+0.50</td>
<td>20/16</td>
</tr>
<tr>
<td>MS</td>
<td>55</td>
<td>F</td>
<td>Strabismic &amp; anisometropic</td>
<td>Alt. ExoT 18</td>
<td>R</td>
<td>+2.75/-1.28x135</td>
<td>20/16^2^</td>
</tr>
<tr>
<td>DH</td>
<td>22</td>
<td>F</td>
<td>Strabismic</td>
<td>R ExoT 40</td>
<td>R</td>
<td>-4.75/-0.25x120</td>
<td>20/32</td>
</tr>
<tr>
<td>JT</td>
<td>52</td>
<td>F</td>
<td>Strabismic</td>
<td>L EsoT 5</td>
<td>R</td>
<td>-1.25/-1.00x14</td>
<td>20/32</td>
</tr>
<tr>
<td>KT</td>
<td>21</td>
<td>M</td>
<td>Anisometropic</td>
<td>None</td>
<td>R</td>
<td>Plano</td>
<td>20/10^2^</td>
</tr>
</tbody>
</table>

Table 2. Slope (a) of learning curve (Th = Th0 + a ln x).

Results

Position discrimination learning

Generally, position discrimination performance gradually improved across sessions for all positional noise settings. But for observers JT and DH, little or no learning was observed for high noise settings, and for KT, no learning was observed for all noise settings. Figure 3 illustrates the thresholds specified as a Weber fraction (i.e., threshold/gap size) for the five noise settings across sessions. It should be noted that observer AR was tested at higher noise levels than the others because of his much reduced visual acuity. The function $Th = Th_0 + a \ln x$ was used to fit the data where $Th$ is discrimination threshold, $Th_0$ is the initial threshold, and $x$ is the training session; Table 2 shows the slope (a) of the learning curve for each noise level. On average, threshold improvement of about 30% was observed for zero noise and 20% for the highest noise level. Asymptotic performance was obtained in about six to seven sessions.

<table>
<thead>
<tr>
<th>Observer</th>
<th>Noise (gap)</th>
<th>Slope x10^3</th>
<th>se x10^-3</th>
<th>t</th>
<th>p</th>
<th>Sig</th>
</tr>
</thead>
<tbody>
<tr>
<td>PD</td>
<td>0</td>
<td>-5.2</td>
<td>1.7</td>
<td>-3.03</td>
<td>0.016</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.01</td>
<td>-4.3</td>
<td>1.2</td>
<td>-3.48</td>
<td>0.008</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>-10.4</td>
<td>2.9</td>
<td>-3.63</td>
<td>0.007</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.03</td>
<td>-16.6</td>
<td>5.3</td>
<td>-3.15</td>
<td>0.014</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.04</td>
<td>-17.7</td>
<td>4.9</td>
<td>-3.60</td>
<td>0.007</td>
<td>s</td>
</tr>
<tr>
<td>SL</td>
<td>0</td>
<td>-1.7</td>
<td>1</td>
<td>-1.71</td>
<td>0.125</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>0.01</td>
<td>-3.2</td>
<td>1</td>
<td>-3.05</td>
<td>0.016</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>-4.3</td>
<td>1.4</td>
<td>-3.11</td>
<td>0.014</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.03</td>
<td>-1.8</td>
<td>2.2</td>
<td>-0.85</td>
<td>0.419</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>0.04</td>
<td>-5.3</td>
<td>5</td>
<td>-1.06</td>
<td>0.32</td>
<td>ns</td>
</tr>
<tr>
<td>AR</td>
<td>0</td>
<td>-6.8</td>
<td>2</td>
<td>-3.40</td>
<td>0.009</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>-8.8</td>
<td>3</td>
<td>-2.98</td>
<td>0.018</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.04</td>
<td>-12.5</td>
<td>3.5</td>
<td>-3.63</td>
<td>0.007</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.06</td>
<td>-13.3</td>
<td>5.5</td>
<td>-2.40</td>
<td>0.043</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.08</td>
<td>-13.9</td>
<td>4.2</td>
<td>-3.32</td>
<td>0.011</td>
<td>s</td>
</tr>
<tr>
<td>MS</td>
<td>0</td>
<td>-13.2</td>
<td>3.6</td>
<td>-3.64</td>
<td>0.007</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.01</td>
<td>-10.4</td>
<td>3.2</td>
<td>-3.21</td>
<td>0.012</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>-7.9</td>
<td>3.4</td>
<td>-2.34</td>
<td>0.048</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.03</td>
<td>-9.2</td>
<td>2.9</td>
<td>-3.24</td>
<td>0.012</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.04</td>
<td>-11.7</td>
<td>5.7</td>
<td>-2.04</td>
<td>0.076</td>
<td>ns</td>
</tr>
<tr>
<td>DH</td>
<td>0</td>
<td>-4.8</td>
<td>1.2</td>
<td>-3.89</td>
<td>0.005</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.01</td>
<td>-8.7</td>
<td>1.7</td>
<td>-5.07</td>
<td>0.001</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>-5.5</td>
<td>2.5</td>
<td>-2.22</td>
<td>0.057</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>0.03</td>
<td>-1.5</td>
<td>3</td>
<td>-0.52</td>
<td>0.615</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>0.04</td>
<td>-4.7</td>
<td>2.6</td>
<td>-1.78</td>
<td>0.113</td>
<td>ns</td>
</tr>
<tr>
<td>JT</td>
<td>0</td>
<td>-10.1</td>
<td>1.8</td>
<td>-5.45</td>
<td>0.001</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.01</td>
<td>-8.1</td>
<td>2.4</td>
<td>-3.39</td>
<td>0.01</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>-3.7</td>
<td>3.1</td>
<td>-1.18</td>
<td>0.273</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>0.03</td>
<td>-6.6</td>
<td>2.8</td>
<td>-2.38</td>
<td>0.045</td>
<td>s</td>
</tr>
<tr>
<td></td>
<td>0.04</td>
<td>-0.8</td>
<td>2.9</td>
<td>-0.28</td>
<td>0.79</td>
<td>ns</td>
</tr>
</tbody>
</table>
To compare position discrimination learning in amblyopic to normal observers, we replotted the mean data of 10 normal observers from our recent study (Li et al., 2004) in the bottom right panel (Figure 3). Initially, most of the amblyopic observers (PD, AR, MS, and JT) showed degraded performance for all noise settings when compared with mean normal performance. With practice, performance was generally improved to near the pretraining levels of normal observers. Observers DH and KT showed about the same performance, in terms of “gap” units, when compared with mean normal performance. Surprisingly, observer SL showed substantially better performance than even the post-training thresholds of normal observer. SL has high astigmatism and hence meridional amblyopia, which reduces his acuity and contrast sensitivity in the vertical meridian. We speculate that his “super” position thresholds might be a consequence of the neural blur in the vertical meridian – the meridian corresponding to the offset cue.

To explore the mechanisms underlying perceptual learning, thresholds were replotted as a function of positional noise throughout training (Figure 4), and a positional averaging model (see “Methods”) was used to fit the

![Graphs showing position discrimination thresholds for different positional noise settings across sessions for seven observers. Note that observer AR and the others were tested with 2.5 and 5 cpd stimuli, respectively. The mean data of normal observers were plotted in bottom right panel from our recent studies (Li et al., 2004).](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/933515/)
data (TvN curves). Different observers showed different learning patterns: (1) The TvN curves for observers PD (strab), SL (strab & meridional), and AR (aniso) gradually shifted downward across sessions. About the same proportional decrease in thresholds was observed for all noise settings. (2) In contrast, observers JT (strab) and DH (strab) showed strong learning effects in low noise, but little or no learning in high noise. The “knee” points of their curves gradually shifted to the left in successive sessions. (3) The learning pattern of observer MS (strab & aniso) seems to be a mixture: the curves gradually displaced downward and the knee points shifted to the left across the measurements. Note that KT did not show any significant improvement in positional discrimination, and thus his TvN curves are not shown in Figure 4.

The improvement in performance reflects increased sampling efficiency and/or reduced equivalent input noise (shaded area in Figure 5). Observers SL, PD, and AR showed substantial improvement in efficiency (38%, 77%, and 60%, respectively) after learning, but no significant changes in equivalent input noise. In contrast, the improved performance for observers JT and DH was mainly the result of lowered equivalent input noise (37% and 32%, respectively); no significant changes in efficiency were observed. On the other hand, observer MS showed both a significant decrease in equivalent input noise (43%) and an increase in efficiency (24%). Observer KT showed no improvement in performance and no change in either equivalent input noise or efficiency.

Figure 4. TvN curves for different learning mechanisms. (a). Observers PD, SL, and AR show a downward shift of TvN curves across sessions. (b). Observers JT and DH show a leftward shift of knee points with practice, with little improvement at high positional noise. (c). Observer MS shows both a downward curve shift and a leftward knee point shift. For comparison, the mean data of normal observers are replotted here from our recent studies (Li et al., 2004).
For comparison, we included the post-training data of normal observers (Li et al., 2004) in Figures 3 and 4. These observers completed eight training sessions with the same task; they had better than 20/20 vision and were tested with higher spatial frequency (10 cpd) stimuli. Generally, the post-training thresholds of amblyopic eyes were higher than those of normal observers (Figure 4). Even after training, two amblyopic observers (AR and KT) showed elevated equivalent input noise, in terms of gap units, when compared to the mean normal data, and four observers showed lower efficiency (Figure 5). It should be noted that the viewing distance was different for normal and amblyopic observers. However, data of a highly experienced observer (author RL) show that equivalent input noise and efficiency are essentially unchanged over the entire range of viewing distances (1-4 m). It is therefore appropriate to compare the equivalent input noise for individual observers using gap units.

Learning specificity

We examined the specificity of visual learning (i.e., whether improvement transfers to a different orientation, eye, etc.) to further explore the possible mechanisms for the plasticity. To test whether the visual learning effects transfer to the untrained stimulus orientation, we compared pre- and post-training measurements of thresholds with vertical stimuli. To examine whether the specificity of the visual learning transfers to the trained eye, we performed pre- and post-training measurements with horizontal stimuli in the untrained fellow eye.

Figure 6 shows the percentage improvement in thresholds across all noise settings for individual observers; positive values mean that the post-training performance is better than the pretraining performance and vice versa. The mean of the last three sessions was used as the asymptotic post-training threshold. The mean percentage change in thresholds for five observers is also provided in the figure (large open symbol).

In general, there was a small but not significant decrease in thresholds for vertical stimuli after training with horizontal stimuli. Moreover, the learning effects were not significantly transferred to the fellow untrained eye. The pre- and post-training measurements with horizontal targets in the untrained eye revealed no significant changes in thresholds for most of the noise settings. It is important to recognize that there are substantial variations between observers.

Visual acuity and counting

One of the most interesting aspects of our findings is that visual acuity improves while practicing position discrimination; all amblyopic observers showed significant and substantial improvements ranged from 28% to 37% (mean 32.6%; SD 3.0%) in letter acuities (percent improvement shown in Figure 6, raw data in Figure 7a). Note that for all observers except AR, sessions 2 and 12 were pre- and post-training measurements with vertical stimuli. Acuity im-
proved by as much as two letter lines within seven training sessions. Observers JT and MS showed fast and strong improvements in the first three sessions, but for observers SL and AR visual acuity started to show improvement after only two or three sessions, and steep improvements occurred at the fifth and sixth sessions.

It may be argued that the improvement was mainly due to repeated testing or training of visual acuity. Therefore, in three amblyopic observers (DH, PD, and KT), only pre- and post-training visual acuity measurements were performed, with about six weeks in between these sessions. These three observers also showed substantial improvement of almost two chart lines from ∼1.5 arcm (Snellen 20/32−1) at the beginning to ∼1 arcm (= Snellen 20/20) at the end of the experiment. Interestingly KT showed no improvement in position thresholds. We speculate that because of low thresholds and high efficiency, his pretraining thresholds were at a floor (i.e., they could not be lowered further) due to anatomical and physiological limitations. Nonetheless, the effects of repetitious practice, making perceptual decisions with his amblyopic eye, evidently transferred to improve his visual acuity. This observer failed a Randot® stereotest (Stereo Optical, Chicago, USA), > 400 arcsec, before the start of learning experiment; we tested his stereoacuity once again at the end of the experiment and, surprisingly, found substantial improvement in stereoacuity (25 arcsec).

Strabismic amblyopes often show greater deficits in acuity when presented with a line of letters than when shown isolated letters. This is known as the crowding phenomenon. To examine the crowding phenomenon, we also tested our observers’ line acuities before and after practice. We found that all observers showed significant improvement in line acuity (Figure 7b), and there are also important individual differences. For example, observer JT showed a bigger improvement in line acuity (52% from Snellen 20/125−1 to 20/63−1), compared with a 37% improvement in letter acuity. The greater improvement in line than in letter acuity indicates that her crowding was reduced. Observer DH showed a bigger improvement in letter (34%) than line acuity (21%). On the other hand, three other observers showed similar improvements in line and letter acuity. Note that we do not have line acuity data for observers MS and KT; only their letter acuities are shown in Figure 7a.

Previous work show that strabismic amblyopes have difficulty in counting features and missing features, and point to a high-level deficit (Sharma et al., 2000). To test whether practice effects transfer to counting, we performed pre- and post-training measurements of counting performance in three amblyopic observers. Experimental details can be found in the previous studies by Sharma et al. (2000). In the present study, we asked observers to count the number of Gabor patches briefly presented on the monitor. Observer AR was tested with 5-cpd Gabor patches, and the others with 10 cpd. We found that the mean counting threshold of the amblyopic eyes increased by 52% from 2.8 to 4.3 patches (large filled circle in Figure 8a), whereas the mean thresholds of the preferred eyes were about the same for both pre- and post-training measurements (5.2 and 5.4 patches, respectively; large unfilled circle). For observer KT, the improved post-training performance was comparable to that of the fellow preferred eye. We also note that observer DH showed a small improvement in accuracy in post-training measurements. Before training, this observer markedly underestimated the number of patches when more than five patches were presented (Figure 8b), replicating the findings of Sharma et al. (2000). After training, the number of patches reported by DH was significantly closer to the number of patches presented (x) (one-tail Mann-Whitney test: for x = 7, p = .0395; for x = 10, p = .0112). The other two observers also markedly undercounted; however, although their counting thresholds improved, they did not show statistically significant changes in accuracy.
Our results show strong individual differences in the learning in amblyopia, enabling us to parse the improvements or reweighting of disordered visual mechanisms, enabling observers to sample the stimulus information more efficiently and to reduce the uncalibrated internal position jitter. Moreover, our amblyopic observers showed some improvement in higher level visual tasks while practicing position discrimination tasks. This provides evidence for cortical plasticity at higher cortical levels. It has been suggested that learning is mediated by synaptic plasticity (Ahissar et al., 1992; Brown, Kairiss, & Keenan, 1990; Zohary, Celebrini, Brittin, & Newsome, 1994); perhaps this forms the basis of cortical reweighting.

Our study differs from the earlier work of Levi and colleagues (Levi & Polat, 1996; Levi et al., 1997) in that their stimulus was a pair of abutting thin lines (which are broadband in spatial frequency). Their Vernier alignment task is strongly dependent on stimulus visibility, so improvement in Vernier acuity could, in principle, have been a result of improved line visibility after practice, or due to a change in the spatial scale of analysis. In normal vision, abutting Vernier is thought to be limited by the response properties of contrast-sensitive filters (Levi, Klein, & Carney, 2000). The separated, band-limited (Gabor sample) stimulus used in the current study is not strongly dependent on visibility (halving the target contrast has almost no effect on threshold), but depends strongly on spatial relations, and is thought to be limited by positional uncertainty (Li et al., 2004).

Figure 8. (a). Counting performance before and after practicing a position discrimination task. (b). The number of patches reported is illustrated for observer DH. The shaded area illustrates the better post-training threshold over pretraining threshold.

### Discussion

In agreement with earlier studies (Levi & Polat, 1996; Levi et al., 1997), our results show that the adult amblyopic visual system retains a substantial degree of plasticity: repetitive practice can substantially improve position discrimination acuity. Our use of positional noise provides new insights into the mechanisms underlying perceptual learning in amblyopia, enabling us to parse the improvement in performance into two important factors: decreased equivalent input noise and increased sampling efficiency. Our results show strong individual differences in the mechanism by which adult amblyopes learn. With practice, three amblyopic observers improved mainly by increased sampling efficiency, one observer improved through a pure decrease in equivalent input noise, and one observer by both. The seventh observer (KT), who showed very low initial thresholds and high efficiency, failed to learn, perhaps due to a floor effect. In contrast, the learning effects in normal observers are mostly acquired through improved efficiency of about 35%, with equivalent input noise remaining almost unchanged (or very little changed) (Li et al., 2004). Our recent study (Li et al., 2004) further demonstrated that improved efficiency in normal observers was a consequence of retuning of the observer’s decision template.

Previous studies have shown that the amblyopic visual system has high levels of equivalent input noise in the visual system and fails to extract useful information efficiently (Hess & Field, 1993; Levi & Klein, 2003; Wang et al., 1998; Watt & Hess, 1987). Generally, our data (Figures 4 and 5) seem to support the notion that both strabismic and anisometropic amblyopes have increased spatial uncertainty. For an anisometropic observer (AR), the sampling efficiency was about the same or even better than normal observers. On the other hand, strabismic observers (PD, MS, DH, and JT) also suffered from spatial undersampling.

Our findings show that repetitive practice can lower the noise levels and/or boost the amblyopic brain's ability to use the relevant information more efficiently. We speculate that practice with feedback allows some sort of recalibration or reweighing of disordered visual mechanisms, enabling observers to sample the stimulus information more efficiently and to reduce the uncalibrated internal position jitter. Moreover, our amblyopic observers showed some improvement in higher level visual tasks while practicing position discrimination tasks. This provides evidence for cortical plasticity at higher cortical levels. It has been suggested that learning is mediated by synaptic plasticity (Ahissar et al., 1992; Brown, Kairiss, & Keenan, 1990; Zohary, Celebrini, Brittin, & Newsome, 1994); perhaps this forms the basis of cortical reweighting.

Transfer and specificity of learning

An alternative hypothesis is that the improvement in performance might have a more trivial explanation. For example, improvement might be in part attributed to high-level cognitive task learning [what Westheimer (2001) refers to as “instrument learning”]. Our 3AFC “odd man out” paradigm requires no memory and has little cognitive load (even a 4-year-old can do the task). Observers were given
unlimited time, and were instructed to carefully inspect each of the three positions before making a decision. If the improvement was the consequence of instrument learning, the improvement should also be generalized to the untrained orientation and fellow eye. The absence of transfer makes it difficult to fully explain the improvement on the basis of generalized cognitive learning. The absence of interocular transfer should be taken cautiously as the fellow eyes of amblyopic observers were tested with a higher spatial frequency (2-to-4-fold) than that in the amblyopic eye. We cannot completely rule out the possibility that transfer might have occurred had we used the same spatial frequency. Nonetheless, the absence of transfer is not compatible with generalized instrument learning. Moreover, the gradual improvement in thresholds across sessions indicates that the changes in sensitivity are genuine.

Another plausible (but uninteresting) explanation is that amblyopes learn to fixate and/or accommodate more accurately with their amblyopic eye. Improvement in fixation and/or accommodation is unlikely to account for the present results for several reasons: (1) Our task (separated horizontal line segments) is not strongly dependent on precise focus or fixation (Bedell & Flom, 1985; Schor & Hallmark, 1978; Williams, Enoch, & Essock, 1984), and we provided observers with unlimited time. (2) If the improvement in performance were due to improved fixation/focus, we would expect the improvement to transfer across orientations.

Our results show that practicing position discrimination does show transfer to two important tasks: Snellen acuity and counting. Levi and colleagues also reported that some of their observers showed transfer to a Snellen task. In the present study, all seven (including KT, who showed no significant improvement in position acuity) showed improvements in Snellen acuity. On average, acuity improved by approximately 32.6% for several mild amblyopes, resulting in single-letter acuity of 20/20 following practice. The close link between positional and visual acuities has been pointed out previously (Enoch et al., 1984; Levi & Klein, 1982; Levi & Klein, 1985; McKee et al., 2003). We note that 20/20 single letter acuity does not necessarily imply a “cure.” Many amblyopes display severe crowding (i.e., poorer acuity when letters are shown in a line, than for isolated letters) (Flom, Heath, & Takahashi, 1963; Giaschi, Regan, Kraft, & Kothe, 1993; Simmers, Gray, McGraw, & Winn, 1999a). For example, JT’s letter acuity improved from 20/32 to 20/20; however, although her line acuity also improved (by a factor of 2), she remains amblyopic (20/63⁻¹). Levi et al. (1997) have also reported two but not all of their mild amblyopes had normal crowded acuity after learning a Vernier task.

To evaluate long-term maintenance of visual acuity improvement, we again examined visual acuities of four observers 3 to 12 months after the last day of learning experiment. In agreement with a recent study, the improvement in visual acuity is essentially stable for a long time period (Figure 7) (Ohlsson, Baumann, Sjostrand, & Abrahamsson, 2002).

Our findings further revealed that when the vision in the amblyopic eye improves to a level that is comparable to that in the fellow eye, the recovery of stereopsis is possible in an adult anisometropic amblyopia (KT). However, no improvement in stereoaucuity was observed in the other “deep” anisometropic amblyope AR. This is probably because there remains a substantial difference in the visual acuity of the two eyes, and thus those signals from the amblyopic eye are mostly suppressed.

**Perceptual learning and treatment of amblyopia in adults**

It is often stated that the visual loss in adults with amblyopia cannot be treated. Generally, treatment for amblyopia is only undertaken for children (Bhartiya, Sharma, Biswas, Tandon, & Khokhar, 2002; Simmers, Gray, McGraw, & Winn, 1999b). However, there is now considerable evidence that treatment of amblyopia can be effective in adults (Levi et al., 1997; Simmers & Gray, 1999). In a case report, Simmers and Gray (1999) showed that occlusion therapy appeared to improve visual acuity and hyperacuity in an adult strabismic amblyope. There are also reports suggesting that some adult amblyopes recover vision in their amblyopic eye following loss of vision in their fellow (nonamblyopic) eye (El Mallah, Chakravarthy, & Hart, 2000; Rahi et al., 2002), and recent work suggests that there is substantial recovery of visual perception following long-term deprivation (Fine, Wade, Brewer, May, Goodman, Boynton, Wandell, & MacLeod, 2003).

Perceptual learning may be thought of as a form of “active” treatment; observers are engaged in making fine judgments near the limit of their performance, using their amblyopic eyes (with their preferred eye occluded), and they receive feedback. A forced-choice task such as ours is quite demanding. Observers have to compare all three stimuli very carefully before making decisions about subtle offsets, and the stimuli remained on the monitor until the observer response was obtained. In each of the training sessions, they were required to respond to more than 2,250 stimuli (more than 10 kilo-trials in all).

**Conclusions**

Our results show that perceptual learning is effective in improving visual performance and that the effects may transfer to visual acuity. The present study characterized the limits, time course, and mechanisms of improvement. These findings may be helpful in developing more effective and efficient treatment regimens for amblyopia. In our laboratory, the classification image technique is being used to study how the behavioral receptive fields of the amblyopic brain change with perceptual learning.
Acknowledgments

This work was supported by a National Eye Institute grant R01EY01728.

Commercial relationships: None.
Corresponding author: D. M. Levi.
Email: dlevi@berkeley.edu.
Address: School of Optometry and Helen Wills Neuroscience Institute, University of California-Berkeley, Berkeley, CA, USA.

References


