Is the ability to identify deviations in multiple trajectories compromised by amblyopia?

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Amblyopia results in a severe loss of positional information and in the ability to accurately enumerate objects (V. Sharma, D. M. Levi, & S. A. Klein, 2000). In this study, we asked whether amblyopia also disrupts the ability to track a near-threshold change in the trajectory of a single target amongst multiple similar potential targets. In the first experiment, we examined the precision for detecting a deviation in the linear motion trajectory of a dot by measuring deviation thresholds as a function of the number of moving trajectories (T). As in normal observers, we found that in both eyes of amblyopes, threshold increases steeply as T increases from 1 to 4. Surprisingly, for T = 1–4, thresholds were essentially identical in both eyes of the amblyopes and were similar to those of normal observers.

In a second experiment, we measured the precision for detecting a deviation in the orientation of a static, bilinear “trajectory” by again measuring deviation thresholds (i.e., angle discrimination) as a function of the number of oriented line “trajectories” (T). Relative to the nonamblyopic eye, amblyopes show a marked threshold elevation for a static target when T = 1. However, thresholds increased with T with approximately the same slope as in their preferred eye and in the eyes of the normal controls.

We conclude that while amblyopia disrupts static angle discrimination, amblyopic dynamic deviation detection thresholds are normal or very nearly so.

Keywords: amblyopia, tracking, multiple-object tracking, attention, motion, angle discrimination, deviation detection

Introduction

Amblyopia is a developmental disorder of spatial vision usually associated with the presence of strabismus, anisometropia, or form deprivation early in life (Ciuffreda, Levi, & Selenow, 1991). A long-standing question is the site of damage in amblyopia. Current opinion places the earliest functional physiological abnormalities in cortical area V1 (for recent reviews, see Barrett, Bradley, & McGraw, 2004; Kiorpes, 2006; Levi, 2006), where amblyopia results in profound alterations. Amongst the earliest changes in V1 is increased binocular suppression, which appears to originate at a site beyond where information from the two eyes is first combined (Zhang et al., 2005).

Very much less is known about the physiological effects of amblyopia on visual areas downstream from V1. Brain-imaging studies (PET and fMRI) show a clear deficit in V1 (Barnes, Hess, Dumoulin, Achtman, & Pike, 2001; Goodyear, Nicolle, Humphrey, & Monen, 2000; Muckli et al., 2006), and several studies have also found deficits in other areas (e.g., V2). However, it is difficult to discern whether these downstream losses are simply a pass-through effect from V1 or whether the V1 losses are amplified downstream. One imaging study, using stimuli that were matched in perceived contrast in the two eyes, suggests that the deficits occur exclusively downstream of V1 in V2 but not in V1 (Imamura et al., 1997), and Lerner et al. (2003) suggest a selective abnormality in higher-order representations of objects in occipitotemporal cortex. Specifically, they report that face-related cortical areas show a severe disconnection from the amblyopic eye, while building-related regions remain essentially normal. The recent study of Muckli et al. (2006) provides the most complete picture to date, showing that the responses of the amblyopic eye are progressively reduced in higher areas (V3a/VP, V4/V8, and LOC) and suggests that transmission of activity from the amblyopic eye is increasingly impaired as it is relaid to higher processing levels.

A number of recent psychophysical studies are consistent with the idea that the abnormalities in V1 are amplified in V2 and possibly beyond. These studies show losses in second-order detection (Mansouri, Allen, & Hess, 2005; Wong & Levi, 2005; Wong, Levi, & McGraw, 2001; 2005), global form and motion integration (Mansouri et al., 2005; Simmers & Bex, 2004; Simmers, Ledgeway, & Hess, 2005; Simmers, Ledgeway, Hess, & McGraw, 2003), complex motion detection (Simmers, Ledgeway, Muckli, Hutchinson, & Hess, 2006), symmetry detection (Levi & Saarinen, 2004), and counting (Sharma, Levi, & Klein, 2000—discussed below).
When asked to count briefly presented stimuli, normal observers perform veridically. In contrast, strabismic amblyopes systematically undercount the number of features (Sharma et al., 2000). Moreover, amblyopes also undercount missing features (“holes” in a uniform texture of patches). A low-level deficit (e.g., reduced visibility) would predict overcounting of missing features (amblyopes would see fewer patches and therefore report more holes), so Sharma et al. concluded that there are likely to be high-level deficits in the amblyopic cortex and that undercounting in amblyopia may reflect a limit in the ability to select and attend to individual features amongst other features.

Multiple-object tracking (MOT) is a task widely thought to require attentional selection and pursuit (e.g., Scholl, 2001). In the “standard” MOT task, a number \( T \) of identical objects move in random directions. At the start of a trial, a subset of these is identified as “target” items (e.g., by a change in color or a flash). The observer’s task is to track the target items for a fixed time (e.g., 7 to 15 s). Pylyshyn and Storm (1988; and, subsequently, many other studies) showed that normal observers can reliably track up to five items. To date, there is only one report of MOT in amblyopia (Ho et al., 2006). Ho et al. tested 18 children (9–17 years of age) and reported that compared to an age-matched control group who could track \( \approx 5 \) objects, the amblyopic children were able to track fewer objects (on average, 4 with their preferred eyes and 3.7 with their amblyopic eyes). They also reported abnormalities in a single-object tracking task. These results are surprising given early reports that the motion system is spared in amblyopia (Kubova, Kuba, Juran, & Blakemore, 1996—but see the Discussion section), and Ho et al. interpreted their results to suggest high-level deficits in the posterior parietal cortex. It is interesting to note that children with Williams syndrome, a genetic disorder accompanied by severe spatiotemporal impairment and a high incidence of strabismus, amblyopia, and loss of stereopsis (Atkinson et al., 2001), also show abnormalities in tracking multiple moving objects (O’Hearn, Landau, & Hoffman, 2005).

In the standard MOT experiment, the trajectories of the moving objects are well above threshold, and the observer is only required to know the current positions of target items. The prior positions of the target items (beyond the information needed to update the target positions) are largely irrelevant. Tripathy and Barrett (2004) recently developed a rigorous new method in which the histories of the object paths are highly relevant to the task performed by the observer. They measured thresholds for detecting deviations in linear trajectories while varying the number of trajectories; detecting deviations in trajectories requires integrating information over substantial portions of the trajectories. The present paper uses this method to measure thresholds for detecting deviations in linear trajectories in observers with amblyopia, both for moving (Experiment 1) and static (Experiment 2) trajectories. The following paper uses a suprathreshold method to estimate the number of trajectories that amblyopes can attend to (Tripathy & Levi, 2006b).

Attention and/or memory have been proposed to limit performance in the current task (Tripathy & Barrett, 2004). Amblyopia has not been clearly linked to deficits in either attention or memory; however, amblyopes do show abnormal crowding (see Levi, 2006), and crowding has been proposed to be the spatial resolution limit of attention (He, Cavanagh, & Intriligator, 1996). Thus, it has been suggested that amblyopes show deficits in the spatial resolution of attention (Sharma et al., 2000). If attention is the primary limiting factor in our task, then we would expect amblyopes to show poor performance. If, on the other hand, amblyopes do not show deficits in our tracking task, then attention is probably not the primary limiting factor. Indeed, visual sensory memory has been proposed to be the primary limiting factor in the current task (Narasimhan, Tripathy, & Barrett, 2006). To our knowledge, visual sensory memory has not been studied in amblyopia. If sensory memory is the primary limiting factor in our task and if amblyopic performance is normal, we may infer that sensory memory is spared in amblyopia, and conversely, if amblyopic performance is poor, we may infer that sensory memory is compromised.

**General methods**

Our methods were largely identical to those of Tripathy and Barrett (2004) and will be described only in brief.

**Stimuli**

These consisted of bright dots or lines presented on a dark background on an ADI Microscan monitor with a 60-Hz frame rate. We used a chin and forehead rest to minimize head movements. At the viewing distance of 1.1 m, each pixel subtended 1° in the horizontal and vertical directions, and the monitor screen consisted of 800 \( \times \) 600 pixels.

For Experiment 1, the stimuli (Figure 1, inset) consisted of \( T (T = 1−4) \) highly visible bright dots (squares of side, 5 arcmin; 44.1 cd/m\(^2\)) on a background, the luminance of which was adjusted (5.0 cd/m\(^2\)) so that traces of the moving stimuli were not noticeable. The dots moved from left to right at 4°/s for 850 ms (51 frames) along straight lines. At the halfway mark (Frame 26), which was reached by all dots at the same instant, the dots were vertically aligned perfectly and in line with the two vertical markers, after which one (and only one) dot changed its trajectory (each trajectory was \( \approx 3.4° \) long). Mean orientation of the trajectories was 0° (horizontal), with the individual trajectories randomly and uniformly jittered over \( \pm 80° \) about the horizontal; that is, the direction of a single element was randomly drawn from a uniform distribution of \( \pm 80° \). To minimize the effects of crowding, the vertical separation between dots at the midline was 60′(±5′).
For Experiment 2, the stimuli (Figure 5, inset) consisted of $T (T = 1–4)$ highly visible bright lines on a dark background. Each line was constructed from 51 dots, with each dot being similar to the dots used in Experiment 1. The lines were similar to the trajectories in Experiment 1, but here, all of the dots were presented simultaneously for the duration of a single frame (16.66 ms). The lines were $3.4^\circ$ long when the viewing distance was 1.1 m. At the halfway mark (indicated by two vertical markers), one line (and only one) changed its orientation. As before, the separation between dots at the midline was $60^\circ (\pm 5^\circ)$. For Experiment 2, we also varied the viewing distance (keeping the stimuli on the screen the same), enabling us to assess the role of spatial scale (line length and width and interline separation).

**Task and procedure**

The observer’s task on each trial was to decide whether the target trajectory deviated clockwise or anticlockwise, and auditory feedback was provided following each trial. To measure thresholds for detecting a change in trajectory, we used a method of constant stimuli with nine deviations that spanned the psychometric function (based on preliminary trials). Each block consisted of 180 trials. Thresholds ($d^' = 1$) were estimated from four separate blocks (720 trials). Prior to data collection, each observer was given extensive practice (more than a thousand trials).

**Observers**

We tested five amblyopes (one anisometropic, three strabismic, and one with both; see Table 1) and three normal control observers (including the authors). Three of the amblyopic observers participated in Experiment 1 and all five took part in Experiment 2. All observers were tested monocularly, normals with their preferred eye (the exception was S.T. whose data were obtained under binocular viewing conditions—reproduced from Figure 6 of Tripathy & Barrett, 2004) and amblyopes with their amblyopic and nonamblyopic eye separately.

<table>
<thead>
<tr>
<th>Observer</th>
<th>Age (years)</th>
<th>Gender</th>
<th>Type</th>
<th>Strabismus (at 6 m)</th>
<th>Eye</th>
<th>Refractive error</th>
<th>Line letter acuity (single-letter acuity)$^a$</th>
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<tr>
<td>J.S.</td>
<td>22</td>
<td>F</td>
<td>Strabismic</td>
<td>L EsoT 6–8$^A$ &amp; L Hyper 4–6$^A$</td>
<td>R</td>
<td>+1.25</td>
<td>20/16</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+1.00</td>
<td>20/40 (20/32$^{+1}$)</td>
</tr>
<tr>
<td>A.P.</td>
<td>19</td>
<td>F</td>
<td>Strabismic</td>
<td>L EsoT 4$^A$ &amp; L Hyper 2$^A$</td>
<td>R</td>
<td>$-1.50/-0.50 \times 180$</td>
<td>20/12.5$^{-2}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$-0.75/-0.25 \times 5$</td>
<td>20/50 (20/32$^{+1}$)</td>
</tr>
<tr>
<td>J.T.</td>
<td>52</td>
<td>F</td>
<td>Strabismic</td>
<td>L EsoT 5$^A$</td>
<td>R</td>
<td>$-1.00/-0.50 \times 10$</td>
<td>20/16$^{-2}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$-0.75/-0.50 \times 80$</td>
<td>20/63$^{-1}$ (20/25$^{-2}$)</td>
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<td>S.C.</td>
<td>27</td>
<td>M</td>
<td>Anisometropic</td>
<td>None</td>
<td>R</td>
<td>+0.50</td>
<td>20/16$^{-2}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$+3.25/-0.75 \times 60$</td>
<td>20/63$^{-2}$ (20/63$^{-2}$)</td>
</tr>
<tr>
<td>J.D.</td>
<td>19</td>
<td>M</td>
<td>Strabismic &amp; anisometropic</td>
<td>L EsoT 3$^A$</td>
<td>R</td>
<td>+2.50</td>
<td>20/16</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+5.00</td>
<td>20/125 (20/125$^{-2}$)</td>
</tr>
</tbody>
</table>

Table 1. Observer characteristics. $^a$The acuities listed in this table were determined using a Bailey–Lovie chart, and we specify both the full line letter acuity and the single-letter acuity.
Results

Experiment 1: Moving trajectories

Amblyopic eyes show no obvious deficits in detecting deviations in moving trajectories when compared to their nonamblyopic eye. Figure 1 shows the psychometric functions of each eye of a strabismic amblyope (J.S.) for $T = 1$ (small symbols) and 4 (large symbols) trajectories. Specifically, Figure 1 shows the percentage of “anticlockwise” responses plotted as a function of the deviation magnitude. In order to quantify our results, we computed thresholds by fitting a cumulative normal function to the data, with the upper and lower asymptotes of the fit being fixed at 100% and 0%, respectively. The $SD$ of the normal fit was taken to be the empirical deviation threshold. This can be seen in Figure 1 as the deviation yielding a $d' = 1.0$, compared to the null stimulus, after correcting for response bias. In the absence of bias, a positive (negative) deviation of this size would correspond to an “anticlockwise” response on 84% (16%) of the trials (as indicated by the upper and lower dotted gray lines). Figure 1 shows clearly that (1) performance is strongly degraded when $T = 4$ and (2) the amblyopic (solid symbols) and dominant (open symbols) eyes are closely similar for both $T = 1$ and $T = 4$. This can be seen in both the raw data and in the threshold estimates shown by the corresponding symbols along the abscissa.

The nonamblyopic eyes of amblyopes show no obvious deficit in detecting deviations in moving trajectories when compared to the eyes of normal observers (Figure 2). Figure 2A summarizes the results of Experiment 1 for normal observers by plotting the threshold deviation for each observer as a function of $T$ using log–log coordinates. Threshold deviation increases more or less linearly with $T$ (Tripathy & Barrett, 2004). Tripathy and Barrett plotted their results in linear coordinates; however, there were indications that the increase of thresholds with increase in $T$ was slightly faster than linear. Therefore, we fit the data with a power function of the form: $Th_{dev} = Th_{T1}*T^k$, where $Th_{dev}$ is the deviation threshold, $Th_{T1}$ is threshold with $T = 1$ and $k$ is the slope of the best fitting line on log–log coordinates (the power function exponent). The fit shown in Figure 2A is the fit to the data of all three observers simultaneously. Figure 2B shows a similar fit to the thresholds of the combined data from the nonamblyopic eyes of the three amblyopes tested in this experiment. In both cases, the slopes appear to be qualitatively similar.

The observers’ amblyopic eyes also showed little deficit in detecting deviations in moving trajectories when compared to their nonamblyopic eyes and the eyes of normal observers. Figure 3A shows the deviation thresholds as a function of $T$ for the amblyopic eyes of the three amblyopic observers tested and the best fitting power function to their data. Figure 3B compares the best fitting power function to the amblyopic data with those fit to the data of the normal observers and to the data for the nonamblyopic eyes.

Figure 2. Experiment 1 (moving trajectories). Threshold deviation as a function of $T$. This graph summarizes the results of Experiment 1 by plotting the threshold deviation as a function of $T$ in log–log coordinates. (A) For each of the normal control observers. The line is the best fitting power function to the combined data. (B) For each of the nonamblyopic eyes. The line is the best fitting power function to the combined data of the three observers.
of the amblyopes. The thresholds in the three cases are very similar with minor differences in the slopes. Slopes were steepest for the normal observer and shallowest for the nonamblyopic eyes of the amblyopes (see below). Indeed, if anything, the thresholds of both eyes of the amblyopes were better than those of the normal observers for $T = 4$, perhaps reflecting an age effect since, on average, our normal observers were older than the amblyopes (Trick, Jaspers-Fayer, & Sethi, 2005; Trick, Perl, & Sethi, 2005); however, we note that our youngest normal observer (J.K., age 21) had higher thresholds than the oldest (D.L., age 58). The clustering of the slopes suggests that the detection of deviations in moving trajectories may be a low-resolution task and, therefore, robust to defocus. In order to assess this, we blurred the dominant eye of one of the amblyopic observers (S.C.) to match the acuity in his amblyopic eye ($\approx 20/60$) with a diffuser and repeated the experiment. His results, shown by the open triangles in Figure 3B, fall within the tight cluster of the normal eye, dominant eye, and amblyopic eye data and, indeed, were essentially unchanged from his data with no blur. We therefore conclude that our motion-tracking task mostly utilizes low spatial frequency information and is robust to both defocus and amblyopia.

The results of the power function fits are summarized in Figure 4, and it is clear that both the thresholds for $T = 1$ (Panel A) and the slopes (Panel B) are remarkably similar in amblyopic and normal eyes. Thus, we conclude that the ability of the amblyopic eye to track a single trajectory, either on its own or in the presence of distractors, is not compromised relative to nonamblyopic eyes or the eyes of normal observers.

It has been suggested that the motion stream is spared by amblyopia (Kubova et al., 1996), so we performed a second experiment with static trajectories to probe the amblyopic visual system further.

**Experiment 2: Static “trajectories”**

While our amblyopes show no deficit in detecting deviations in a single moving trajectory, four of our five amblyopes do show deficits in detecting deviations in a single static trajectory (Figure 5). Figure 5 shows orientation deviation thresholds as a function of $T$ for the five amblyopic eyes tested and the best fitting power function to each eye’s data. Also shown are the mean thresholds for the nonamblyopic eyes and for the normal eyes as a function of the number of trajectories. Data are shown at the three different viewing distances tested. The static task is essentially detection of a change in orientation (inset in Figure 5), and it has been documented that amblyopes show deficits in orientation discrimination with short lines or high-contrast, high spatial frequency gratings (Skottun, Bradley, & Freeman, 1986; Venverloh, 1983; but see Hess & Malin, 2003), so it is not altogether surprising that they also show deficits in angle judgments (change in orientation) of this sort and that the deficits increase with increasing...
viewing distance. Figure 6 shows the parameters of our power function fits to the data in Figure 5 and illustrates clearly that thresholds for $T = 1$ trajectories increase with viewing distance when viewing with the amblyopic eye and that the slopes are only marginally higher in the amblyopic eye at the largest viewing distance (3.3 m). There are several points of interest in Figures 5 and 6.

First, for the 1.1 m viewing distance, although thresholds for $T = 1$ are elevated, the slopes of the best fitting power functions for the amblyopic eyes do not appear to be
markedly steeper than those for the nonamblyopic or normal eyes, and this is confirmed in Figure 6B. Second, while increasing viewing distance has little effect on the performance of the normal and nonamblyopic eyes, for several of the more severe amblyopes (J.D., A.P., and S.C.), thresholds for $T = 1$ increase with viewing distance. We believe that this is an effect of line length since increasing viewing distance reduces the line length from $3.4^\circ$ at 1.1 m to $1.7^\circ$ at 2.2 m and $1.1^\circ$ at 3.3 m (line width is also proportionally decreased). To test the effect of line length, we measured J.D.’s threshold for $T = 1$ trajectory at a viewing distance of 1.1 m with a “half-length” line ($1.7^\circ$). Figure 7 shows that his threshold with the short line 1.1 m away is considerably higher than with the long line and that it is comparable to his threshold at 2.2 m (as it should be if line length is an important limiting factor in the amblyopic eye).

Third, the slopes of the power function fits of the amblyopic eyes show a tendency to increase with increasing viewing distance. Indeed, J.D. was unable to perform the task with $T = 4$ at 3.3 m (indicated by the arrow). We attribute this to crowding, which is extensive in amblyopic vision (e.g., Hariharan, Levi, & Klein, 2005; Levi, Hariharan, & Klein, 2002). Doubling the minimum separation between lines (from $20^\circ$ to $40^\circ$) brings the threshold into line (rightmost solid circle in the right-hand panel).

Fourth, unlike the motion task, static tracking is highly sensitive to defocus. Blurring S.C.’s preferred eye at 3.3 m (open black inverted triangles in Figure 5) increases distance. We believe that this is an effect of line length since increasing viewing distance reduces the line length from $3.4^\circ$ at 1.1 m to $1.7^\circ$ at 2.2 m and $1.1^\circ$ at 3.3 m (line width is also proportionally decreased). To test the effect of line length, we measured J.D.’s threshold for $T = 1$ trajectory at a viewing distance of 1.1 m with a “half-length” line ($1.7^\circ$). Figure 7 shows that his threshold with the short line 1.1 m away is considerably higher than with the long line and that it is comparable to his threshold at 2.2 m (as it should be if line length is an important limiting factor in the amblyopic eye).

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thresholds substantially—to a level very similar to that of his amblyopic eye (solid green inverted triangles).

In summary, static deviation thresholds were more severely compromised by amblyopia than dynamic deviation thresholds, and these increased rapidly with viewing distance.

**Discussion**

**Tracking moving objects**

Amblyopes undercount features (and missing features—Sharma et al., 2000), have difficulty in performing high-level motion-tracking tasks both with their amblyopic and nonamblyopic eye (Ho et al., 2006), and are known to have deficits in pursuit eye movements (Bedell, Yap, & Flom, 1990; Schor & Levi, 1980a). Based on these findings, we anticipated that amblyopes would have difficulties in pursuing or tracking linear motion trajectories when monitoring several trajectories at the same time for deviations. Specifically, our prediction at the outset was that amblyopes would be unable to do the task and the stimuli would need to be scaled for reasonable performance; their thresholds with \( T = 1 \) would be elevated and the slopes of the power function fits to their deviation thresholds would be steeper than in normal observers (possibly with the preferred as well as the amblyopic eye). To our surprise (and embarrassment!), we found little evidence to support our prediction, even in an amblyope with an almost eightfold loss in acuity (J.D.). Although our stimuli were bright and easily visible, we did not scale either the size or the brightness of our stimuli for viewing with the amblyopic eye. Single trajectory deviation thresholds and slopes of the power functions in amblyopic eyes were comparable to those of nonamblyopic eyes and the eyes of normal observers. We found the ability of amblyopic eyes to track deviations in multiple trajectories to be essentially preserved compared to nonamblyopic eyes and the eyes of normal observers.

It is worth noting that tracking requires more than just motion processing. It involves attention, selection, pursuit (with eye movements and with attention), direction discrimination, and so forth. Surprisingly, it appears that all of these are intact in our amblyopic observers, at least to the extent required by our task.

Our results appear to be at odds with the very recent study of Ho et al. (2006), so it is worth considering how the two studies differ and how they overlap. Ho et al. actually performed four experiments on a large group of children (ages 9–17 years), 18 with amblyopia and 30 age-matched controls. We consider their single-object tracking tasks in this section (their other tasks will be considered later). In their single tracking task (their Experiment 3), the stimulus consisted of four large white discs on a gray background. The discs rotated around a circle with a radius of 9°. The observer’s task on any trial was to track one of the four discs (indicated by a color change at the start of the trial). At the end of the trial, one of the four dots turned red and the observers had to indicate whether that was the dot they had been asked to track; rotation speed was varied to determine an upper speed limit for tracking. This experiment is analogous to ours in that both studies required observers to track a single trajectory amongst distractors (in our study, the number of distractors was varied from zero to three, in the Ho study, it was always three). They found that the maximum rate at which their amblyopic observers could track a single disc was approximately 15°/s (0.274 rotations/s—1 rotation \( \approx 56.5\)°) compared with approximately 20°/s for the control group. We note that these rates are very slow compared with adult performance. For example, the observers of Verstraten, Cavanagh, and Labianca (2000), using similar stimuli and methods, were able to track at rates of 40–50°/s with four discs. Thus, it is possible that the ability to do this task in their population of children was still developing and that amblyopia slowed the time course of development, whereas attentive tracking had matured in our adult amblyopes. This developmental difference could also explain the failure to find a deficit in motion-defined form perception in amblyopic adults even though amblyopic children showed a large deficit in both amblyopic and fellow eyes (Giaschi, Regan, Kraft, & Hong, 1992). However, we note that although the average age of the two subject groups is very different (≈12 vs. 27 years), the oldest observers from Ho et al.’s study were almost 17 years while our youngest observers were 19 years.

Our Experiment 1 differed from Ho et al.’s in a number of ways, some obvious, and others more subtle. Ho et al. tested a large number of children, each performing a small number of trials (16 practice and 64 test trials). We tested a small number of adults, each performing a large number of trials (more than a thousand practice trials and almost 3000 experimental trials per eye). Both age and the amount of practice could be important (Tripathy & Barrett, 2004 reported large effects of practice; see Trick, Jaspers-Fayer, et al., 2005; Trick, Perl, et al., 2005 for the effects of age on tracking). Ho et al. used large stimuli that were confined to peripheral vision. We were interested in testing the ability to select and pursue stimuli in central vision (where the effects of amblyopia are thought to be most acute). Thus, the crucial information in our trajectories (the point of deviation) was at or very near the fovea. Another major difference is that Ho et al. varied the speed of their stimuli to obtain an upper speed limit while we held speed constant (at 4°/s) and varied the angular change in the trajectory to determine the change in orientation required for it to be detected. Thus, speed might be a crucial difference since our experiments were performed at a fixed (relatively) low speed, while Ho et al. increased speed until performance dropped. Thus, their deficits were seen at a fast speed (15°/s) while our stimuli were considerably slower (4°/s).
not clear, but global motion deficits have been reported at fast speeds (Ellemberg, Lewis, Maurer, & Brent, 2000; Simmers et al., 2003), while Ho et al. (2005) found close to normal global motion perception at a slow speed. Another difference is that in Ho et al.’s experiments, the trajectories of the moving objects were well above threshold and the observer was required to know only the current position of the target. The prior positions of the target items (beyond the information needed to update the target position) were largely irrelevant. In our experiments, the histories of the object paths were highly relevant to the task. Finally, it is possible that observers might have used eye movements to track in our experiments, but not in Ho et al.’s.

It is not clear which (if any) of the factors mentioned above explain the discrepancy in the results, and further work will be needed to sort this out. What is clear is that while the standard MOT task shows a significant loss in both eyes of amblyopic children (Ho et al., 2006), the current results show that the ability to track near-threshold deviations in a trajectory is quite robust to spatial factors (blur, amblyopia) and is thus not seriously degraded by amblyopia. Finally, it could be argued that our threshold paradigm is so difficult that even normal observers are at a floor (i.e., performance cannot be worse). We address this in the following paper and show that performance on a supra-threshold task is also normal or very nearly normal in amblyopic vision (Tripathy & Levi, 2006a, 2006b; Tripathy, Narasimhan, & Barrett, 2006).

Is the motion system spared in amblyopia? Amblyopia is generally considered to be a disorder of spatial vision; however, it is clear that the effects of amblyopia are not limited to deficits in spatial vision. Indeed, a number of studies have reported abnormalities in the performance of amblyopes on tasks involving detection of motion or temporal modulation, particularly for high spatial and low temporal frequencies (Ellemberg et al., 2000; Hess & Anderson, 1993; Hess, Howell, & Kitchin, 1978; Levi & Harwerth, 1977; Manny & Levi, 1982), direction selectivity (Schor & Levi, 1980b), velocity discrimination (Steinman, Levi, & McKee, 1988), displacement thresholds (Buckingham, Watkins, Bansal, & Bamford, 1991; Levi, Klein, & Aitsebaomo, 1984), and global motion detection (Simmers et al., 2003). It is likely that at least some of these deficits can be accounted for on the basis of the amblyopes’ reduced spatial vision (Chung & Levi, 1997; Hess et al., 1978; Steinman et al., 1988). Indeed, Kubova et al. (1996) reported that visually evoked potentials (VEPs) to motion onset were indistinguishable in both eyes of amblyopes while VEPs to pattern onset were quite different. They concluded that the motion system is spared by amblyopia.

However, it is now clear that there are aspects of motion perception in amblyopia that are not accounted for simply on the basis of the spatial deficits. Evidence for specific motion deficits comes from the reduced duration of motion aftereffects (Hess, Demanins, & Bex, 1997), abnormalities in the fellow eye (Giaschi et al., 1992; Ho et al., 2005, 2006; Simmers et al., 2003), and the use of second-order stimuli where the losses are not predictable from those with first-order stimuli (Giaschi et al., 1992; Simmers et al., 2003). Indeed, Ho et al. (2006) reported that children with amblyopia perform normally on global motion and apparent motion tasks but were impaired on “high-level” object tracking tasks in either eye. A very recent study of monkeys with experimental amblyopia (Kiorpes, Tang, & Movshon, 2006) showed that, consistent with human amblyopes (Steinman et al., 1988), motion sensitivity functions are shifted toward lower spatial scales, but importantly, they reported a specific deficit for long temporal offsets, suggesting an abnormality in temporal integration, possibly at a stage beyond the initial spatial filtering stage.

The preceding discussion makes it clear that there are aspects of visual motion processing that are not spared by amblyopia, even after taking into account the spatial deficits. Our results show that there is no deficit in the ability of the amblyopic visual system to select and track a moving object amongst other similar moving objects. How do we reconcile this with the preceding discussion? It has been suggested that the bottleneck for our task might reside in visual sensory memory (Narasimhan et al., 2006). The current findings in amblyopes would be consistent with this suggestion. If this is true, our results suggest that visual memory is not impaired in the amblyopic visual system. In our second experiment, entire trajectories were presented in a single shot, reducing the load on visual sensory memory. We discuss this experiment below.

### Tracking static objects

Our goal in undertaking Experiment 2 was to test MOT under conditions where the amblyopic deficit is in evidence with a single trajectory. It is worth pointing out that while our motion stimulus is very sparse, our static stimulus is more dense, and it could be that crowding (because of the dense static stimulus) might explain why thresholds were higher for amblyopes with \( T = 1 \) with static stimuli. However, an added benefit of our static task was that it reduces the need to remember the trajectory prior to the deviation (since the entire trajectory is shown in a single shot). Of course, if the observer has to search for the target and if the memory trace is decaying, this will impair performance as the number of trajectories increases.

Four of our five amblyopes showed deficits in detecting a single static deviation, and these deficits increased with viewing distance (due to a decrease in the line length). Interestingly, the threshold for \( T = 1 \) trajectories at 3.3 m is closely related to the observers’ line visual acuity (Figure 8). Most importantly, we found that the power function slopes were only minimally affected by amblyopia (and only at the largest viewing distance), suggesting that the static-tracking task may be limited by spatial factors (acuity and crowding) rather than by high-level factors related to individualization, selection, or attention.
Relation to other studies

A number of recent studies point to high-level (beyond V1) deficits in the amblyopic visual pathway. These studies show losses in second-order detection (Mansouri et al., 2005; Wong & Levi, 2005; Wong et al., 2001, 2005), global form and motion integration (Mansouri et al., 2005; Simmers & Bex, 2004; Simmers et al., 2003, 2005, 2006), symmetry detection (Levi & Saarinen, 2004), and undercounting of features and missing features (Sharma et al., 2000). Indeed, the fact that amblyopes undercount features and missing features led us to suspect that amblyopia would compromise the ability to select and track a single object amongst similar objects. We note that counting deficits in amblyopia were most evident when the number of features exceeded four and the features themselves were suprathreshold, and we examine the ability of amblyopes to select, attend to, and track multiple suprathreshold objects elsewhere (Tripathy & Levi, 2004). However, we note that some of Sharma et al.’s observers showed deficits in counting the number of missing or different features when they were as few as two or when there was no poststimulus mask.

Since amblyopic performance was comparable to normal on our task, the primary factor limiting performance is unlikely to be attention. If visual sensory memory is the primary limiting factor, our findings suggest that this memory is not compromised in amblyopia.

The surprising result of our study is that performance in our motion-tracking task is normal or nearly so in amblyopia. One possible explanation is that our task might be accomplished not by tracking the trajectory but rather by the detection of a change in the response of motion detectors. Consider that these motion detectors produce a sustained response for 850 ms as long as the stimulus does not change orientation. The dot that changes orientation (after 425 ms) produces transient on and off responses in some motion detectors. The larger the size of the deviation from the original trajectory, the more separate will be the pools of neurons activated. Under this scenario, thresholds would be expected to increase with the number of trajectories because for detection, the transient should be stronger than the local transients of the sustained response to the motion of the distracter dots. If the deficit in amblyopia is primarily in local acuity and in spatial selection (individual), then, given the discussion above, our paradigm does not pose any problem in selection or individuation because the observers do not have to mark the deviating trajectory, only to detect any change and identify its direction. If this analysis is correct, then it is not surprising that no deficit was found. This may also help to explain the discrepancy between our results and those of Ho et al. (2006). It may also help to explain the apparent discrepancy with the undercounting results of Sharma et al. (2000). This possible explanation needs further investigation, and such investigations are in progress. We note that this explanation cannot easily account for our static-tracking task, where the stimuli are presented in a very brief snapshot, unless the visual system instantaneously computes changes in angle.

Conclusions

Taken together, our experiments suggest that the ability to select and track an object (moving or static) amongst similar distractors is not compromised in adults with amblyopia. Amblyopes, like individuals with normal vision, are able to effectively monitor approximately one near-threshold trajectory (Tripathy & Barrett, 2004).

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