On the effective number of tracked trajectories in amblyopic human vision

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We estimated the effective number of trajectories that amblyopic observers could track with their amblyopic eyes and their non-amblyopic eyes using stimuli and methods described in S. P. Tripathy, S. Narasimhan, and B. T. Barrett (2007). The stimuli consisted of dots moving along straight-line trajectories. In Experiment 1, one of the trajectories (the target) deviated clockwise or counterclockwise by \( \pm 19^\circ, \pm 38^\circ, \text{ or } \pm 76^\circ \), halfway through the trajectory. In Experiment 2, \( D \) of the \( T \) trajectories deviated, all in the same direction and with the same magnitude of direction change. In both experiments, we varied \( T \) and the angle of deviation. In Experiment 2, we also varied \( D \). Amblyopic observers reported the direction of deviation of the target trajectories and, for each eye, the effective number of tracked trajectories was estimated. This number increased systematically with increasing magnitude of deviation of the targets. On average, the effective numbers of tracked trajectories were approximately 15\% smaller for the amblyopic eyes for each of the three magnitudes of deviation. A comparison with data previously published for normal eyes failed to reveal any deficit in the effective number of trajectories tracked by the non-amblyopic eyes of amblyopic observers for the current task.

Keywords: attention, tracking, memory, amblyopia, strabismus, anisometropia


Introduction

Pylyshyn and Storm (1988) showed that human observers could use attentional resources to reliably track up to 4 moving items at the same time. Since that initial study many others have confirmed that human observers can indeed use attention to track several moving objects at a time (Allen, McGeorge, Pearson, & Milne, 2004, 2006; Bahrami, 2003; Oksama & Hyona, 2004; Scholl & Pylyshyn, 1999; Scholl, Pylyshyn, & Franconeri, 1999; Tripathy, Narasimhan, & Barrett, 2007; Viswanathan & Mingolla, 2002; Yantis, 1992). In the current study, we investigate whether this ability to attentively track multiple moving objects is compromised in amblyopic human observers. For the purposes of the current study, “tracking” refers to the ability of the observers to attentively monitor, with or without eye-movements, properties of moving objects and does not refer to the ability of observers to keep objects foveated with the use of smooth pursuit eye-movements.

Various explanations have been proposed for the number of trajectories that can be tracked at a time. Pylyshyn and colleagues postulated that there are a fixed number of visual indices that the visual system assigns to moving objects, and once assigned, these move with the objects (e.g., Pylyshyn, 1989, 2000, 2001; Pylyshyn et al., 1994; Pylyshyn & Storm, 1988). Other explanations include performance limitations based on attentional resolution (Alvarez & Franconeri, 2007), working memory (Allen et al., 2006; Fougnie & Marois, 2006), and sensory memory (Narasimhan, 2006; Narasimhan, Tripathy, & Barrett, 2006; Narasimhan, Tripathy, & Barrett, 2007). Each of these is a potential explanation of the limits to human tracking performance and if these attentional, memory, or indexing systems are affected by amblyopia, this could result in a drop in the tracking performance of amblyopic observers. Additionally, tracking performance in amblyopic observers might be compromised if mechanisms of spatial localization or mechanisms of form perception or mechanisms of motion perception are compromised.

Amblyopia is a developmental abnormality that results in a broad range of neural, perceptual, and clinical abnormalities (for recent reviews, see Kiorpes, 2006; Levi, 2006; Barrett, Bradley, & McGraw, 2004). Below we consider how these abnormalities relate to tracking multiple objects.

There is abundant evidence that mechanisms of spatial localization are compromised in amblyopic vision (e.g., Levi & Klein, 1985; Wang, Levi, & Klein, 1998), and several studies have reported that the mechanisms of form perception are compromised in amblyopia (Hess & Demanins, 1998; Kovács, Polat, Penmefather, Chanda, &...
Hess & Jacobs, 1979; Levi & Klein, 1985 reflect have found no amblyopic deficit in the retina or the LGN compromised on account of losses in the retina or the amblyopic vision if the signals arriving at the cortex are amblyopia. The ability to track might be compromised in physiological and the anatomical changes that accompany attentional deficits. 

Cavanagh, & Intriligator, 1996; Intriligator & Cavanagh, 2001). Based on this explanation, it is plausible that the missing features are undercounted in amblyopic vision (e.g., Kiorpes, Kiper, O’Keefe, Cavanaugh, & Movshon, 1998), reduced metabolic activity within amblyopic ocular dominance columns (Wong, Burkhalter, & Tychsen, 2005), reduced contrast sensitivity for neurons driven by the amblyopic eye (e.g., Movshon et al., 1987), increased amblyopic suppression (e.g., Smith et al., 1997), reduced binocularity (e.g., Crawford, Harwerth, Chino, & Smith, 1996; Crawford, Harwerth, Smith, & von Noorden, 1996; Zhang et al., 2003), abnormal horizontal connectivity (e.g., Löwel & Singer, 1992; Tychsen, Wong, & Burkhalter, 2004), reduced fMRI activity for stimuli presented to the amblyopic eye (Barnes, Hess, Dumoulin, Achtman, & Pike, 2001), and slower and attenuated MEG responses for the amblyopic eye (Anderson, Holliday, & Harding, 1999). The anomalous responses in V1 for stimuli presented to the amblyopic eye could compromise tracking performance for the following reasons.

The computation in V1 might be compromised. Many complex motion tasks involve low-level motion processing in V1 followed by high-level integration of motion information in MT and MST. Moreover, signals from V1 to higher cortical areas that might be involved in tracking (e.g., area MT that might be involved in integrating motion information and parietal areas that might be involved in the processing of attention) might be attenuated. The behavioral studies discussed above suggest that all of the amblyopic losses cannot be explained by abnormalities in V1 alone, and several studies suggest that extrastriate areas of the cortex might also be compromised in amblyopia. In cats, amblyopia can result in reduced numbers of neurons in extrastriate cortex being driven by the affected eye, with greater deficits being found along the ventral pathway than along the dorsal pathway (Schröder, Fries, Roelfsema, Singer, & Engel, 2002). In humans, even when perceived contrast was matched in the two eyes, amblyopic deficits were still found in V2 (Imamura et al., 1997). Lerner et al. (2003) reported abnormal processing in the occipitotemporal cortex for faces presented to the amblyopic eye. Muckli et al. (2006) reported that gratings presented to amblyopic or fellow eye evoked strong fMRI activity in V1/V2, but activation by the amblyopic eye dropped progressively along the


With regard to motion processing, deficits in amblyopia the results from previous studies are mixed. Some studies have failed to find deficits in low-level motion processing, beyond that predicted by deficits in contrast sensitivity (Hess & Anderson, 1993; Hess, Mansouri, Dakin, & Allen, 2006; Kubová, Kuba, Juran, & Blakemore, 1996; Kiorpes, Tang, & Movshon, 2006; Qiu, Xu, Zhou, & Lu, 2007). Even in the complex tasks of detecting biological motion, amblyopic vision has been reported to be normal (Neri, Luu, & Levi, 2007). Other studies have reported substantial amblyopic deficits in motion processing. These include a reduced motion aftereffect (Hess, Demaninis, & Bex, 1997) and deficits in all of the following: oscillatory motion processing (Buckingham, Watkins, Bamsal, & Bamford, 1991; Kelly & Buckingham, 1998), following moving targets using pursuit eye-movements (Bedell, Yap, & Flom, 1990; Schor & Levi, 1980a, 1980b), global motion processing (Ellemberg, Lewis, Maurer, & Brent, 2000; Ho & Giaschi, 2006; Mansouri & Hess, 2006; Simmers, Ledgeway, & Hess, 2005; Simmers, Ledgeway, Hess, & McGraw, 2003), depth perception from motion parallax (Thompson & Nawrot, 1999), and complex motion processing (Simmers, Ledgeway, Mansouri, Hutchinson, & Hess, 2006). In addition, deficits have been reported in the ability of the fellow eye to process motion information (Giaschi, Regan, Kraft, & Hong, 1992; Ho et al., 2005; Kelly & Buckingham, 1998). In contrast to these findings, a few studies have reported amblyopic eyes to be more tolerant to motion than control eyes when detecting offsets in moving vernier stimuli (Chung & Levi, 1997; Fahle & Bachmann, 1996).

Few studies have directly investigated potential attentional deficits in amblyopia. Compared to normal observers, amblyopic observers undercount briefly presented features when viewing with their amblyopic eye; even missing features are undercounted in amblyopic vision suggesting a reduction in the ability to select and to attend to individual features (Sharma, Levi, & Klein, 2000). Indirect evidence for attentional deficits in amblyopia can be found in crowding studies. Crowding, according to one explanation, is the spatial resolution limit of attention (He, Cavanagh, & Intriligator, 1996; Intriligator & Cavanagh, 2001). Based on this explanation, it is plausible that the abnormally large crowding effects observed in amblyopic foveal vision (e.g., Flom, Weymouth, & Kahneman, 1963; Hess & Jacobs, 1979; Levi & Klein, 1985) reflect attentional deficits.

Much work has been done to try to understand the physiological and the anatomical changes that accompany amblyopia. The ability to track might be compromised in amblyopic vision if the signals arriving at the cortex are compromised on account of losses in the retina or the lateral geniculate nucleus (LGN). However, most studies have found no amblyopic deficit in the retina or the LGN (DeLint, Berendschot, & van Norren, 1998; Hendrickson et al., 1987; Movshon et al., 1987; however, see Miki, Liu, Goldsmith, Liu, & Haselgrove, 2003, who found reduced fMRI activity in human LGN and V1 for motion stimuli presented to the amblyopic eye of an anisometropic observer). In contrast, a host of studies in cats, monkeys, and humans have reported amblyopic abnormalities in primary visual cortex. These reports include: reduced widths in the ocular dominance columns in the input layers of V1 that are controlled by the amblyopic eye (Crawford & Harwerth, 2004; Goodyear, Nicolle, & Menon, 2002; Löwel, 1994; but see Horton, Hocking, & Kiorpes, 1997; Murphy et al., 1998; Schmidt, Singer, & Galuske, 2004; Tychsen & Brukhalter, 1997), reduced proportion of cells driven by the amblyopic eye (e.g., Kiorpes, Kiper, O’Keefe, Cavanagh, & Movshon, 1998), reduced metabolic activity within amblyopic ocular dominance columns (Wong, Burkhalter, & Tychsen, 2005), reduced contrast sensitivity for neurons driven by the amblyopic eye (e.g., Movshon et al., 1987), increased amblyopic suppression (e.g., Smith et al., 1997), reduced binocularity (e.g., Crawford, Harwerth, Chino, & Smith, 1996; Crawford, Harwerth, Smith, & von Noorden, 1996; Zhang et al., 2003), abnormal horizontal connectivity (e.g., Löwel & Singer, 1992; Tychsen, Wong, & Burkhalter, 2004), reduced fMRI activity for stimuli presented to the amblyopic eye (Barnes, Hess, Dumoulin, Achtman, & Pike, 2001), and slower and attenuated MEG responses for the amblyopic eye (Anderson, Holliday, & Harding, 1999). The anomalous responses in V1 for stimuli presented to the amblyopic eye could compromise tracking performance for the following reasons.

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visual pathway, through V3a/VP, V4/V8, and LOC. A similar drop in activation in higher levels of the visual cortex on account of amblyopia has also been reported in Lerner et al. (2006). In normal human observers, attending or not attending to moving stimuli results in modulation of the fMRI activity at the V1/V2 border and in areas V3a and the MT-MST/V5 complex (Büchel et al., 1998; Friston & Büchel, 2000; O’Craven, Rosen, Kwong, Treisman, & Savoy, 1997; for attentional modulation of motion-sensitive neurons in primate MT-MST, also see Treue & Maunsell, 1996). Bonhomme et al. (2006) reported that strong activation of areas V3 and MT/V5 were observed in normal control observers stimulated with motion stimuli to either eye, whereas anisometropes exhibited less activation in these areas for amblyopic eye stimulation. Interestingly, Culham et al. (1998) measured cortical fMRI responses while observers tracked multiple bouncing balls and found that actively tracking the balls resulted in enhanced fMRI activity compared to passively viewing the balls; enhancements in activity were absent in early visual areas, weak in the MT/V5 complex, and very strong in parietal and frontal cortex. Jovicich et al. (2001) used a similar stimulus as in the Culham et al. study but examined how fMRI responses in the different cortical regions changed as the attentional load (the number of bouncing balls) was changed; a linear increase in cortical activity with increasing attentional load was observed primarily in the posterior parietal areas. Similar attention-load-dependent activities were reported in parietal and frontal areas of cortex by Culham, Cavanagh, and Kanwisher (2001). An amblyopic deficit in tracking could result if any of the areas identified in the Culham et al. studies or the Jovicich et al. study were to be compromised in amblyopia. This is very likely given the findings of Muckli et al. (2006) that amblyopic eye activity is progressively attenuated at higher levels along the visual pathway.

Only two studies have investigated the deficits in tracking multiple objects in amblyopic observers psycho-physically. Ho et al. (2006) used a range of tracking tasks, including the multiple-object tracking task of Pylyshyn and Storm (1988) to test 18 amblyopic children and 30 age-matched controls. They found deficits in tracking in the amblyopic and fellow eyes of the amblyopic observers when compared to the control observers. Levi and Tripathy (2006) used the paradigm of Tripathy and Barrett (2004) to estimate thresholds for detecting a deviation in a bilinear target trajectory in the presence of linear distractor trajectories. They found that thresholds for detecting deviations in trajectories were similar in amblyopic eyes, fellow eyes, and control eyes. The mixed results obtained from the two studies targeting amblyopic deficits in tracking may be a consequence of the different nature of the tasks employed in the two studies. The Pylyshyn and Storm (1988) paradigm used by Ho et al. (2006) requires the observers to track multiple objects for durations of about 10 seconds, but at any instant only the current positions of the targets are of relevance for performing the task; the previous positions of the targets (say, 250 ms earlier) are of little relevance to the task of continuing to track the targets. In the paradigm used in Levi and Tripathy (2006), the objects are tracked for less than a second, but monitoring the previous positions of the dots (say, 250 ms before the deviation occurred) is very important for determining the direction of deviation of the targets. Different tracking tasks may involve memory and attention to different extents, and understanding amblyopic deficits in multiple object tracking requires quantification of these deficits in a variety of tracking tasks.

In the current experiments, we estimated the effective number of trajectories tracked by amblyopic observers by studying their ability to track deviations in linear trajectories (Tripathy & Barrett, 2004; Tripathy, Narasimhan, et al., 2007). Tripathy and Barrett (2004) showed that thresholds for detecting deviations in a bilinear target trajectory were severely compromised when additional linear distractor trajectories were simultaneously presented and that observers were unable to track more than a single trajectory when this threshold paradigm was used. Tripathy, Narasimhan, et al. (2007) extended the earlier study to investigate stimuli with substantially suprathreshold deviations and introduced techniques for estimating the effective number of trajectories tracked by the observers. They showed that the effective number of trajectories tracked depends on the angle of deviation of the target trajectories and that as many as 3 or 4 trajectories can be tracked simultaneously if the angle of deviation is large. We used the methods of Tripathy, Narasimhan, et al. (2007) to estimate the effective number of trajectories tracked by amblyopic observers with their amblyopic and fellow eyes and to compare the performance in the two eyes. We found small but consistent differences between the effective numbers of trajectories tracked by amblyopic and fellow eyes. A comparison of the performance of the fellow eyes with the previously published performance of normal observers (Tripathy, Narasimhan, et al., 2007) did not reveal any deficit in the ability of the fellow eyes to track multiple trajectories. The ability to track multiple trajectories in the current task appears to be largely preserved in amblyopic observers.

Methods

Equipment

The stimuli were generated on a personal computer clone and were displayed on an ADI Microscan monitor (a Vivitron 1776 monitor at Bradford) with a frequency of 60 Hz, yielding a frame duration of 16.67 ms. The monitor consisted of 800 × 600 pixels, each pixel subtending 1 × 1 arcmin at the viewing distance of 1.1 m (1.29 m at Bradford). Chin and forehead rests were used to minimize head movements during the experiment. The room was lit...
normally using fluorescent lights to prevent the persistence of the trajectory traces on the screen from being noticeable.

Stimulus and procedure

Our stimuli and procedure were almost identical to those of Experiments 1 and 2 of Tripathy, Narasimhan, et al. (2007) and are summarized here. One or more bright dots moved across a screen with a dark background, in a left-to-right direction, along trajectories that were either linear or bilinear (i.e., linear trajectories with one deviation exactly half-way through the trajectory), as illustrated schematically in the upper two panels of Figures 1 and 2. The dots had dimensions of $5 \times 5$ arcmin, luminance of 44.1 cd/m$^2$, speed of $4^\circ$/s, and were presented on a background of luminance 5.0 cd/m$^2$. The trajectories on a trial were presented for 51 frames (850 ms). Any trajectory deviations could only occur between the vertical lines demarking the screen midline (see stimuli in Figures 1 and 2), i.e., on frame 27. In the first experiment, on each trial, only one deviating trajectory (the target) was presented, along with zero or more non-deviating trajectories (the distractors); the magnitude of deviation and the total number of trajectories remained fixed within an experimental block and were varied across experimental blocks. In the second experiment, on each trial, one or more target trajectories were presented, with the total number of trajectories held constant across blocks; the magnitude of deviation and the number of deviating trajectories remained fixed within an experimental block and varied across experimental blocks. In trials with more than one target trajectory, all target trajectories deviated by the same angle and in the same direction (i.e., clockwise (CW) or counterclockwise (CCW)). On half the trials, the deviation of the targets was CW, and on the remaining trials the deviation was CCW. Following each stimulus presentation the observer, using appropriate keys on the keyboard, reported the perceived direction (CW or CCW) of deviation of the target. Performance was measured as the proportion of correct responses in each experimental condition, i.e., for each tested combination of total number of trajectories, number of deviating trajectories, and magnitude of deviation. Random jitter of the orientations of the trajectories over the range $\pm 80^\circ$ ensured that parallelism cues could not be used for identifying the direction of deviation of the target.

Experiment 1: 1-of-T trajectories deviating

Figure 1 shows schematically one instance each of 4-trajectory (top panel) and 6-trajectory (middle panel) stimuli, with the target trajectory deviating by $-38^\circ$ and $+38^\circ$, respectively. (We adopt the convention that CCW...
deviations are considered positive. All deviations are measured in the plane of the monitor.) Within each block of 100 trials, the magnitude of deviation of the target trajectory was fixed, as was the total number of trajectories ($T$) presented on each trial. For each combination of deviation angle and $T$, each amblyopic observer completed two blocks with the amblyopic eye (AE) and two blocks with the non-amblyopic eye (NAE); for each condition, the order in which the two eyes of an observer were tested was randomized. Percentages of correct responses were determined separately for the AE and the NAE for each observer for each condition tested. For each of the three magnitudes of deviations employed ($\pm 19^\circ$, $\pm 38^\circ$, and $\pm 76^\circ$), data were collected for the AE and the NAE, for values of $T = 1, 2, 3, 4, 6, 8, \text{ and } 10$ trajectories.

Tripathy, Narasimhan, et al. (2007) described the predicted performance of a limited capacity hypothetical observer (LCHO) that perfectly tracked $A$ of the $T$ trajectories present in the stimulus and completely ignored the remaining $(T - A)$ trajectories. The percentage of correct responses $P$ for this LCHO is given by the equations:

$$P = 100 \quad \text{for} \quad (A \geq T),$$  \hspace{1cm} (1)

$$P = 100 \times \frac{A}{T} + \frac{1-A}{T}/2 \quad \text{for} \quad (A < T).$$  \hspace{1cm} (2)

Figure 1 (bottom panel, reproduced from Figure 3 of Tripathy, Narasimhan, et al., 2007) plots the predicted performance of the LCHO, as a function of the number of trajectories in the stimulus ($T$), for different values of $A$. The experimentally measured percentage of correct responses for any particular value of $T$ can be converted into an effective number of tracked trajectories (E) by interpolating between these curves for the corresponding value of $T$.

**Experiment 2: D-of-T trajectories deviating**

In this experiment, the total number of trajectories presented on each trial ($T$) was held constant, and the number of deviating trajectories in each stimulus ($D$) varied between experimental blocks. Figure 2 schematically shows two instances of 6-trajectory stimuli ($T = 6$) with two trajectories deviating (top panel; $D = 2$) and four trajectories deviating (middle panel; $D = 4$); with all the target trajectories deviating by $+38^\circ$ in each panel. Within each block of 100 trials, the magnitude of deviation of each target trajectory was fixed, as were the total number

![Figure 2](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932856/)
of trajectories \( (T) \) and the number of deviating trajectories \( (D) \) presented on each trial. Observers knew in advance how many trajectories would be present and how many of these would deviate in each trial within a block. For each combination of deviation angle, \( T \) and \( D \) that was tested, each amblyopic observer completed two blocks with the AE and two blocks with the NAE; for each condition, the order in which the two eyes of an observer were tested was randomized. Percentages of correct responses were determined separately for the AE and the NAE of each observer for each condition tested. For each of the three magnitudes of deviations employed (\( \pm 19^\circ \), \( \pm 38^\circ \), and \( \pm 76^\circ \)), data were collected for each eye, for values of \( T = 6 \) trajectories, and \( D = 1, 2, 3, 4, \) and \( 6 \). The experiment was repeated with \( T = 8 \); \( D = 1, 2, 3, 5, 6, \) and \( 8 \) and with \( T = 10 \); \( D = 1, 2, 3, 5, 7, \) and \( 10 \).

Tripathy, Narasimhan, et al. (2007) described the predicted performance of an LCHO that perfectly tracked \( A \) of the \( T \) trajectories presented, when \( D \) of these \( T \) trajectories deviated. The percentage of correct responses \( P \) for this LCHO is given by the equations:

\[
P = 100 \quad \text{for } (D > (T - A)), \tag{3}
\]

\[
P = 100 \times \left[ \left( 1 - \left( \frac{T-D}{A} \right) / \left( \frac{T}{A} \right) \right) + \left( \frac{T-D}{A} / \left( \frac{T}{A} \right) \right) / 2 \right] \quad \text{for } (D \leq (T - A)), \tag{4}
\]

where \( \binom{x}{y} \) represent the number of different ways of selecting \( y \) items from a pool of \( x \) items.

**Figure 2** (bottom panel) plots, for \( T = 6 \), the predicted performance of the LCHO as a function of the number of deviating trajectories in the stimulus \( (D) \) for different values of \( A \). The experimentally measured percentage of correct responses for any particular value of \( D \) can be converted into an effective number of tracked trajectories \( (E) \) by interpolating between these curves for the corresponding value of \( D \). The interpolation procedure has been elaborately discussed in Tripathy, Narasimhan, et al. (2007). Similar predictions can be plotted for \( T = 8 \), and for \( T = 10 \) (see Figure 4 in Tripathy, Narasimhan, et al., 2007), and the effective number of tracked trajectories \( (E) \) can be determined for any combination of \( T \) and \( D \), for any magnitude of angle of deviation.

**Observers**

Six amblyopic observers (JD, JS, SC, AP, JT, and SP) participated in **Experiment 1**, and the first three of these also participated in **Experiment 2**. One of the amblyopic observers was anisometropic, three were strabismic and two were both strabismic and anisometropic. Other details of the six observers are provided in **Table 1**. Observer SP was tested in Bradford, and the remaining observers were tested in Berkeley. All observers were tested monocularly, with their AE and their NAE separately.

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### Results and discussion

**Experiment 1: 1-of-\( T \) trajectories deviating**

**Figure 3** shows, for the AEs (filled symbols) and NAEs (open symbols) of the six amblyopic observers, the changes in the percentages of correct responses with changes in the total number of trajectories \( (T) \), when there was only one trajectory deviating. The figure shows the AE and the NAE data separately, for deviations of \( \pm 19^\circ \), \( \pm 38^\circ \), and \( \pm 76^\circ \) (triangles, squares, and circles, respectively).

<table>
<thead>
<tr>
<th>Observer</th>
<th>Age (years)</th>
<th>Gender</th>
<th>Type</th>
<th>Strabismus (at 6 months)</th>
<th>Eye</th>
<th>Refractive error</th>
<th>Line letter acuity (single-letter acuity)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>JS</td>
<td>22</td>
<td>F</td>
<td>Strabismic</td>
<td>L EsoT 6–8 &amp; L Hyper 4–6&lt;sup&gt;(\Lambda)</td>
<td>R</td>
<td>+1.25</td>
<td>20/16</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>L EsoT 4&lt;sup&gt;(\Lambda)</td>
<td>L</td>
<td>+1.00</td>
<td>20/40 (20/32&lt;sup&gt;+&lt;/sup&gt;)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>L Hyper 2&lt;sup&gt;(\Lambda)</td>
<td>R</td>
<td>−1.50/−0.50 × 180</td>
<td>20/12.5&lt;sup&gt;−2&lt;/sup&gt;</td>
</tr>
<tr>
<td>AP</td>
<td>19</td>
<td>F</td>
<td>Strabismic</td>
<td>L EsoT 4&lt;sup&gt;(\Lambda)</td>
<td>L</td>
<td>−0.75/−0.25 × 5</td>
<td>20/60 (20/32&lt;sup&gt;+&lt;/sup&gt;)</td>
</tr>
<tr>
<td>JT</td>
<td>52</td>
<td>F</td>
<td>Strabismic</td>
<td>L EsoT 5&lt;sup&gt;(\Lambda)</td>
<td>R</td>
<td>−1.00/−0.50 × 10</td>
<td>20/16&lt;sup&gt;−2&lt;/sup&gt;</td>
</tr>
<tr>
<td>SC</td>
<td>27</td>
<td>M</td>
<td>Anisometropic</td>
<td>None</td>
<td>L</td>
<td>−0.75/−0.50 × 80</td>
<td>20/63&lt;sup&gt;−1&lt;/sup&gt; (20/25&lt;sup&gt;−2&lt;/sup&gt;)</td>
</tr>
<tr>
<td>JD</td>
<td>19</td>
<td>M</td>
<td>Strabismic and anisometropic</td>
<td>L EsoT 3&lt;sup&gt;(\Lambda)</td>
<td>R</td>
<td>+2.50</td>
<td>20/16</td>
</tr>
<tr>
<td>SP</td>
<td>36</td>
<td>F</td>
<td>Strabismic and anisometropic</td>
<td>R EsoT 14&lt;sup&gt;(\Lambda)</td>
<td>R</td>
<td>+1.25/−0.50 × 147</td>
<td>20/52&lt;sup&gt;−2&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Table 1. Observer characteristics.  
**Note:** *The acuities listed in **Table 1** were determined using a Bailey–Lovett chart. We specify both the full line letter acuity and, when available, the single letter acuity is shown in parenthesis.*
with each observer plotted in a separate panel. Also superimposed on each panel is the predicted performance of the LCHO (dotted lines) as illustrated in the bottom panel of Figure 1. Figure 4 shows the same data averaged across the six observers, with each panel showing the data for one of the three magnitudes of deviation tested. Again the predicted performance of the LCHO has been presented in the background. Also shown in Figure 4 is the average performance of the three normal observers (green lines and symbols) in Experiment 1 of Tripathy, Narasimhan, et al. (2007).

The first question of interest is whether the performance in the AE was noticeably worse than in the NAE. From the individual performances in Figure 3, it is evident that observers varied in their ability to perform this task. For observers JD, JS, and SC, performance with the AE was slightly worse than that with the NAE for many of the conditions tested. For observers AP, JT, and SP, the performance with the AE was comparable to that with the NAE in almost all of the conditions. Since not all observers show better performance with their NAE compared to their AE, and since those observers who showed better performance did not show this under all conditions tested, it is appropriate to average the performance across the six observers (Figure 4). Averaged across the six observers, the performance of the AE was consistently worse than that of the NAE across almost all conditions, but the difference between the AEs and NAEs...
in terms of the absolute percentage of correct responses was never greater than 4.6% in any of the conditions tested; even when the difference was normalized by the percentage of correct responses for the NAE, the relative difference between the two sets of eyes was never greater than 6.0% in any of the conditions tested. The largest absolute difference between AEs and NAEs resulted when the magnitude of deviation was $\pm 76^\circ$ and there were six trajectories in the stimulus ($T = 6$), and the largest relative difference resulted when the magnitude of deviation was $\pm 38^\circ$ and there were four trajectories in the stimulus ($T = 4$).

Performance differences between the AEs and NAEs were very small in this experiment. Could it be that performance in both eyes was compromised by amblyopia (e.g., Ho et al., 2006)? A comparison of the data from the AEs and the NAEs in this study with the data from normal observers in the Tripathy, Narasimhan, et al. (2007) study suggests that this may indeed be the case (illustrated in Figure 4). When the target trajectory deviated by $\pm 19^\circ$, normal observers (tested binocularly) in the earlier study performed consistently better than the amblyopic observers did with either eye in the current study. When the target trajectory deviated by $\pm 38^\circ$, again the normal observers performed better for all conditions, but the better performance was more evident when there were fewer trajectories in the stimulus, i.e., for $T = 2$, 3, or 4. When the target trajectory deviated by $\pm 76^\circ$, better performance was evident in the normal observers only when there were few trajectories in the stimulus, i.e., for $T = 2$, 3, or 4. Interestingly, one might have anticipated that for deviations of $\pm 76^\circ$ differences in performance would have been more evident for larger values of $T$, on account of saturation effects (i.e., percentages of correct responses being close to 100%) for small values of $T$; however, the data obtained did not follow this anticipated pattern. The normal observers consistently performed better than the amblyopic observers did with either eye when there were few trajectories in the stimulus. The largest absolute difference between the performance of the normal observers and that of the amblyopic eyes was 13.9% for a target deviation of $\pm 19^\circ$ with $T = 2$, and the largest relative difference was 15.8%, which also occurred for the same values of deviation and $T$. In summary, only small differences were found between AEs and NAEs, but the differences between the performance of the normal observers and that of either eye of amblyopic observers were substantially larger.

**Experiment 2: D-of-T trajectories deviating**

Figure 5 shows, for the AEs (filled symbols) and NAEs (open symbols) of the three amblyopic observers, the
changes in the percentages of correct responses with changes in the number of deviating trajectories (D), when there were 6 trajectories in the stimulus. The figure shows the AE and NAE data separately for deviations of ±19°, ±38°, and ±76° (triangles, squares, and circles, respectively), with each observer plotted in a separate panel.

Also superimposed on each panel is the predicted performance of the LCHO (dotted lines) as illustrated in the bottom panel of Figure 2. Figures 6 and 7 show, using an identical format, the data for the same three observers for 8- and 10-trajectory stimuli, respectively (i.e., T = 8, and T = 10); the performance of the LCHO has also been recalculated using the appropriate values of T and plotted for A = 1, 2, ..., 5.

A comparison of the percentages of correct responses obtained for the AEs with those for the NAEs for the 6-trajectory stimuli again yields an inconsistent pattern of results (see Figure 5). In the majority of conditions, observers showed little or no differences in performance.
between their AE and NAE, and when differences were seen, the conditions that yielded the biggest differences in one observer were not the same as those yielding the biggest differences in the other observers. For example, observer JD showed the biggest difference between the two eyes when the deviation was ±38°, but observer JS showed almost no difference between the two eyes for this deviation; the difference in performance for SC was midway between that of the other two observers. A comparison of the difference in performance of the two eyes across the three conditions (T = 6, 8, and 10) yields a different pattern of results for the three observers. Observer JD’s performance was better in the NAE compared to the AE in almost all of the conditions tested. Observer JS showed little or no difference between the two eyes on almost all of the conditions tested, while observer SC showed a consistent difference for many of the ±38° deviation conditions and to a lesser extent for some of the ±19° deviation conditions. The largest absolute difference in performance between the two eyes for JD, JS and SC was 17.50, 11.50, and 9.50%, respectively; the largest relative difference in performance between the two eyes was 24.65%, 16.65%, and 13.38%, respectively, with reference to the NAE. However, these large differences were the outliers—in most conditions we tested, the inter-eye differences in performance were just a few percent, with the AE occasionally performing better than the NAE.

We converted much of the percent correct data seen in Figures 5, 6, and 7 into effective numbers of tracked trajectories. We did not compute effective number of tracked trajectories for conditions in which one or more of the observers had a percentage of correct responses that was 96% or greater (because we wanted to avoid effects from saturation) or for conditions in which one or more of the observers had a percentage of correct responses that was 54% or lower (i.e., for conditions in which performance was close to chance). This resulted in effective numbers of trajectories not being evaluated for larger values of D, particularly when the deviation was ±76°. Likewise, data were not evaluated in some conditions with D of 1 because the performance of one or more observers was close to chance.

Figure 8 plots the effective number of tracked trajectories as a function of the number of deviating trajectories for 6-, 8-, and 10-trajectory stimuli (upper, middle, and lower panel, respectively). In each panel, the effective numbers of tracked trajectories for the AEs and the NAEs have been plotted separately for each of the three angles of deviation tested. In conditions in which enough data were available, straight lines were fit to the data for each combination of eye and magnitude of target deviation. As in Tripathy, Narasimhan, et al. (2007), the current study too shows that the effective numbers of tracked trajectories are primarily determined by the angle of deviation of the target trajectories and are affected to a lesser extent by the number of deviating targets (D) and the total number of trajectories (T); this is also true for the AEs and the NAEs. Since D only had a small influence on the effective number of tracked trajectories, for each of the three magnitudes of deviation tested, for the AEs and NAEs, we averaged the effective number of tracked trajectories over the different values of D. Table 2 shows the mean number of trajectories tracked in the different experimental conditions. The effective number of tracked trajectories changed only slightly for the different values of T tested, and hence Table 2 also shows the effective number of trajectories tracked, averaged over the three values of T. Our observers showed idiosyncratic differences in the
Figure 8. The effective number of trajectories tracked in Experiment 2. Most of the data in Figures 5, 6, and 7 have been converted into effective numbers of trajectories tracked, and these have been plotted as a function of the number of deviating trajectories (D), for T = 6 (top), T = 8 (middle), and T = 10 (bottom). The different symbol shapes (triangles, squares, and circles) represent the different magnitudes of target deviation (±19°, ±38°, and ±76°, respectively). Open symbols represent data for the non-amblyopic eye, and the dashed lines are the fits to these data. Closed symbols represent data for the amblyopic eye, and the continuous lines are the fits to these data. The closed symbols have been shifted slightly along the abscissa to enhance readability of the data; this does not affect the fitted lines.

different conditions in which an amblyopic deficit was observed. However, when performance is averaged across observers for different values of T, the amblyopic deficit, estimated from the last two columns of Table 2, corresponds to a reduction in the effective number of tracked trajectories by 14.7%, 14.3%, and 15.1% for deviations of ±19°, ±38°, and ±76°, respectively. On average, for a given angle of deviation, the effective numbers of trajectories tracked by the amblyopic eyes were approximately 15% lower than those tracked by the fellow eyes. Paired 2-tailed t-tests comparing the mean of the effective numbers of trajectories tracked by the NAEs to that for the AE found the amblyopic deficit to be significant for ±19° deviations (t = −2.675, df = 35, p = 0.011) and for ±38° deviations (t = −2.680, df = 26, p = 0.013) but not for ±76° deviations (t = −1.694, df = 8, p = 0.123). The data for (T = 6, D = 3, deviation of ±38°, AE) and (T = 10, D = 1, deviation of ±76°, NAE) conditions were dropped when performing the paired t-test because the effective number of tracked trajectories was not calculated for the other eye (the percentage of correct responses being close to 100% and 50%, respectively). The non-significant difference between the two sets of eyes for the ±76° deviation is probably because the number of data points for which the effective number of trajectories could be estimated was small on account of saturation effects.

Figure 9 plots the effective number of tracked trajectories as a function of the number of deviating trajectories for the AEs (upper panel) and the NAEs (lower panel). The different symbol shapes represent the three angles of deviation tested and the three colors represent the different numbers of trajectories present in the stimuli. When enough data were available (i.e., for deviations of ±19° and ±38° for either set of eyes for each value of T, and for deviations of ±76° for the NAEs for T = 10), straight lines were fit to the data for the different values of D for each combination of angle of deviation and T. Visual inspection of the figures indicates that the ranges of the effective numbers of trajectories tracked when T = 6, 8, and 10 are largely overlapped, suggesting that the effective numbers of trajectories tracked are largely independent of T, for either set of eyes, particularly in comparison to the influence that the angle of deviation has on the effective number of trajectories tracked. For this reason, the effective numbers of trajectories tracked for the different values of T were combined when performing the t-test described above and in the analysis that follows.

The upper panel of Figure 10 summarizes all of the data on the effective number of tracked trajectories presented so far. Straight lines were fitted to all of the effective number tracked data for the AEs (green) and for the NAEs (red) separately, for deviations of ±19°, ±38°, and ±76°. Also shown are the straight-line fits to the effective number of tracked trajectories data from the Tripathy, Narasimhan, et al. (2007; adapted from their Figure 8) study. The blue triangles are the average (±1 standard deviation) of the effective number of tracked trajectories for ten normal observers who are matched in age to the three observers in Experiment 2; these data are taken from Kennedy, Tripathy, and Barrett (2008) and are discussed further in the Tracking and aging section. For all three
deviations, the NAEs of the amblyopic observers, on average, performed better than their AEs. For deviations of $19^\circ$, the normal observers from the Tripathy, Narasimhan, et al. (2007) study performed slightly better, on average, than the amblyopic observers did in the current study with either their AEs or their NAEs. However, for deviations of $38^\circ$ and $76^\circ$, the normal observers’ performance, on average, was comparable to the performance of the amblyopic observers with their AEs and was worse than the performance of the amblyopic observers with their NAEs. The largest differences between normal eyes, AEs, and NAEs were observed in the data obtained in the $76^\circ$ deviation condition, but this deviation also yielded greater variability in the data as well as the smallest quantity of data. To illustrate better the relative performance of the three sets of eyes, the lower panel of Figure 10 plots the

<table>
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<td>4.00 ± 2.00</td>
<td>4.91 ± 0.99</td>
<td>4.17 ± 1.57</td>
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Table 2. The mean numbers of trajectories effectively tracked.

Figure 9. Summary of the effective number of trajectories tracked in Experiment 2. The data in Figure 8 have been replotted, separating the data for the amblyopic eye (top) from that for the non-amblyopic eye (bottom). The different symbol shapes (triangles, squares, and circles) represent the different magnitudes of target deviation ($19^\circ$, $38^\circ$, and $76^\circ$, respectively). The different colored symbols (green, blue, red) represent the data for different numbers of trajectories in the stimuli ($T = 6$, $8$, and $10$, respectively), and the different colored lines are fits to the symbols of the corresponding color. The red and blue symbols have been shifted slightly along the abscissa to enhance readability of the data; this does not affect the fitted lines.

Figure 10. Comparing the effective number of tracked trajectories by amblyopic, non-amblyopic, and normal eyes in Experiment 2. The upper panel shows straight-line fits to the effective number of tracked trajectories in Figure 9 for $T = 6$, $8$, and $10$, fitted separately for each magnitude of target deviations ($19^\circ$, $38^\circ$, and $76^\circ$) for amblyopic (green) and non-amblyopic (red) eyes. Similar fits to the effective number of trajectories tracked by normal observers in the Tripathy, Narasimhan, et al. (2007) study have also been superimposed (blue lines). The blue triangles are the means ($±1$ standard deviation) of the effective number of trajectories tracked by 10 age-matched control observers (see text) from Kennedy et al. (2008). The lower panel shows, using a similar color code, a slice through the data in the upper panel at an abscissa value of 2, i.e., when there are two trajectories deviating.
effective number of trajectories tracked by normal eyes [from Tripathy, Narasimhan, et al., 2007 (blue line), and from Kennedy et al., 2008 (blue triangles)], NAEs, and AEs as a function of the magnitude of deviation when the stimulus contained two deviating trajectories (i.e., this figure is a slice through the figure in the upper panel at an abscissa value of 2). It is evident that for two deviating trajectories the performance of the normal observers was comparable to that of the AEs and worse than that of the NAEs of the amblyopic observers.

**General discussion**

When detecting suprathreshold deviations in target trajectories among linear distractor trajectories, Tripathy, Narasimhan, et al. (2007) found that the effective number of tracked trajectories was primarily determined by the angle of the deviations and was largely independent of the number of deviating trajectories and the total number of trajectories in the stimulus. We find a similar pattern of results for the amblyopic and fellow eyes of amblyopic observers. In both cases, the effective number of trajectories tracked is primarily determined by the angle of deviation of the target trajectories, with larger angles of deviation resulting in greater number of trajectories effectively tracked. The following sections discuss, in terms of the effective numbers of tracked trajectories, whether amblyopic eyes are different from the fellow eyes, and whether normal eyes are different from amblyopic eyes or their fellow eyes.

**Amblyopic deficit for tracking**

Amblyopic abnormalities have been reported in attentional selection (Sharma et al., 2000), in high-level tracking tasks (Ho et al., 2006), and in pursuit eye-movements (Bedell et al., 1990; Schor & Levi, 1980a, 1980b). On the other hand, with a paradigm similar to that used here, Levi and Tripathy (2006) found amblyopic tracking performance to be essentially identical to that in the fellow eye and in normal eyes. Is an amblyopic deficit present in the current study?

We estimated the effective number of tracked trajectories for a range of deviations, a range of total number of trajectories, and a range of number of deviating trajectories. Interestingly, there were no combinations of these variables for which amblyopic performance was consistently bad across all observers. In conditions for which large differences were observed between the two eyes in one observer, differences for the other observers were smaller or non-existent. Most differences in performance between the two eyes were idiosyncratic, and no systematic patterns were evident. When performance in each eye was averaged across the three observers in Experiment 2, there was a consistent difference between the two eyes, with the effective number of tracked trajectories being about 15% lower in the amblyopic eyes compared to the fellow eyes (Figure 10, upper panel; Table 2). This was true whether the deviation was ±19° or ±38°; for ±76° deviations, the variability of the data and the sparseness of data do not permit a reliable quantification of the amblyopic deficit, although a deficit is clearly evident. A point to note is that the three observers who were very systematically tested in Experiment 2 had amblyopic eye visual acuities that were almost 800%, 400%, and 250% worse than their fellow eyes. Yet, this substantial visual acuity difference was reflected in a loss of only 15% in the effective number of tracked trajectories. This is remarkable, considering that the stimuli used were not scaled in any way, either in size or luminance, to compensate for the large difference in acuity in the two eyes. This is all the more surprising taking into account the physiological/anatomical extrastriate abnormalities and the behavioral high-level deficits that have been reported in amblyopic vision (see Introduction section).

Ho et al. (2006) reported finding deficits in multiple object tracking in the amblyopic eye compared to fellow eyes in amblyopic children aged 12–17 years. They found that, on average, their observers could track 3.7 trajectories with their amblyopic eye and 4.0 trajectories with their fellow eyes. This represents an amblyopic loss of less than 10%, which is slightly smaller than the loss we find in the current study. The very small magnitude of the amblyopic deficit may be one reason why Levi and Tripathy (2006) did not find substantial differences between amblyopic and fellow eyes.

**Non-amblyopic eye deficit for tracking?**

The question of whether the non-amblyopic eye is “normal” is of some interest, because previous reports have considered non-amblyopic eye deficits to reflect a “central” deficit in visual processing (e.g., Kandel, Grattan, & Bedell, 1980; Levi & Klein, 1985) and non-amblyopic eye enhancements (i.e., a supernormal NAE performance) to reflect neural alterations in the relative proportions of monocular and binocular neurons (McKee, Levi, & Movshon, 2003). Deficits have been reported in the non-amblyopic eyes of amblyopic human observers with regard to the processing of motion-defined form (Giaschi et al., 1992), oscillatory motion (Kelly & Buckingham, 1998), global motion (Ho et al., 2005), and multiple-object tracking (Ho et al., 2006). How does the performance of the non-amblyopic eyes of amblyopic observers compare with that of normal eyes in our current task? The upper panel of Figure 10 compares, using the effective number of tracked trajectories, the average performance of the non-amblyopic eyes (red lines) of amblyopic observers with the average performance of
normal observers (blue lines) from the earlier study (Tripathy, Narasimhan, et al., 2007). Compared to normal eyes, the performance of the non-amblyopic eyes of amblyopic observers was very slightly worse than that of normal eyes for a $\pm 19^\circ$ deviation and noticeably better for deviations of $\pm 38^\circ$ and $\pm 76^\circ$. In general, the non-amblyopic eyes of amblyopic observers were comparable to, or better than, normal eyes, in terms of the effective number of trajectories that they could track. This is a surprising result and is discussed below in the context of the ages of the observers.

**Tracking and aging**

Is it possible that the performance of the non-amblyopic eyes was better than that of the normal eyes simply because the observers in the current study were younger than those in the study of Tripathy, Narasimhan, et al. (2007)? Trick, Perl, and Sethi (2005) compared the tracking performance of young adults, with a mean age of 19 years, with that of older adults, with a mean age of 73 years; the younger group’s performance suggested that they were tracking 4 objects at a time, whereas the older group’s performance indicated that they were tracking 3 objects at a time. We have measured tracking performance in 22 observers with ages ranging from 18 to 62 years for a subset of the conditions described in Experiment 2 and found, for deviations of $\pm 19^\circ$, $\pm 38^\circ$, and $\pm 76^\circ$ ($\pm 76^\circ$ deviation was not tested in that study), the effective number of tracked trajectories decreased with increasing age at the rate of approximately 15%/decade for each of the three deviations tested (Tripathy, Barrett, & Kennedy, 2007; Kennedy et al., 2008). In the current study, the average age of the three observers tested in Experiment 2 was almost 23 years, whereas the average age of the three observers in the Tripathy, Narasimhan, et al. (2007) study was about 1.5 decades greater. Therefore, based on the age difference between the two groups of observers, we would expect that the effective number of tracked trajectories in the non-amblyopic eyes of amblyopic observers in the current study to be about 23% greater than that of the normal eyes of the observers in Tripathy, Narasimhan, et al. (2007). This is roughly consistent with the enhancement in performance of the non-amblyopic eye for deviations of $\pm 38^\circ$ and $\pm 76^\circ$, but this enhancement was not seen for deviations of $\pm 19^\circ$. The enhancement in performance of the non-amblyopic eye of the amblyopic observers is probably a consequence of the mean age of these observers being less than that of the normal observers in Tripathy, Narasimhan, et al. (2007) by one-and-half decades. There was no evidence in the current study to suggest that tracking performance was significantly compromised in the non-amblyopic eye of amblyopic observers.

The three observers in Experiment 2 were aged 19 (JD), 22 (JS), and 27 (SC). Kennedy et al. tested 22 normal observers between the ages of 18 and 62 years, with ten of them between the ages of 18 and 30 years. Since these normal observers were close in age to the three amblyopic observers tested in the current experiment, we estimated, for the five stimulus conditions that overlapped with the current study, the effective number tracked by each of these observers and averaged these estimates for each of the five conditions. These estimates and their standard deviations have been superimposed on the data in Figure 10 (blue triangles). The normal observers were age-matched to the amblyopic observers; however, their performance was substantially poorer than that seen in either the AESs or the NAEs of the amblyopic observers. An important difference between the current study and that of Kennedy et al. (2008) was that in the current study the amblyopic observers were experienced observers having undergone tens of hours of testing with the multiple object tracking paradigm, whereas in the latter study each observer was tested for less than 4 hours, typically spread over 3 sessions. Our trained amblyopic observers easily outperformed, with either eye, normal age-matched observers who had approximately an hour’s practice prior to data collection and were tested binocularly. Again, we can find no evidence that suggests that the NAEs of the amblyopic observers are deficient in tracking multiple objects when compared with normal age-matched observers. In Experiment 2, the NAEs of our highly trained amblyopic observers performed better than our older practiced normal observers (Tripathy, Narasimhan, et al., 2007) and substantially out-performed our age-matched, unpracticed normal observers (Kennedy et al., 2008). However, it remains an open question whether, with adequate practice, our normal age-matched observers might have equaled or bettered the performance of our amblyopic observers using their NAEs. Answering this question is beyond the scope of the present study, and for now we only claim that the performance of non-amblyopic eye is somewhat better than that of older, but equally practiced normal observers, and also of age-matched, but less practiced observers.

The aging study of Kennedy et al. (2008) can help to put into context the tracking deficits seen in the amblyopic eye. As discussed previously the amblyopic deficits seen in the current study, with regard to the effective number of tracked trajectories, are of the order of 15%, with regard to the fellow eye. A deficit of this magnitude would correspond to aging by a decade in the normal population. Thus, the performance of adult amblyopic observers with their amblyopic eye would be comparable to the performance of observers in the normal population who are ten years older. When seen in this context, it is indeed surprising that, given all the deficits that have been reported in amblyopic vision (see Introduction section), the ability of amblyopic eyes to track multiple objects is comparable to the tracking ability that one expects to find frequently in the non-amblyopic normal adult population. The amblyopic deficit in the ability to track in our observers is comparable to the loss normal observers experience every decade of their adult lives.
Effects of practice

All observers who participated in both experiments were first tested in Experiment 1 and then Experiment 2. The upper and middle panels of Figure 4 show that for deviations of $\pm 19^\circ$ and $\pm 38^\circ$, the performance of the amblyopic observers with either eye is worse than that for normal observers. However, in Experiment 2 the performance of the fellow eye of amblyopic observers was generally better than that of the normal observers. It should be noted that Experiment 1 is a special case of Experiment 2 with $D = 1$. So the change in the pattern of results, in particular the improvement in performance of the fellow eye, is unlikely to be a consequence of the stimulus used and is more likely to reflect practice effects. This might be a fundamental difference between our study and some of the earlier studies. For example, Ho et al. (2006) tested each of their observers with 16 practice trials followed by 64 test trials, whereas each observer in our study performed several thousands of trials. It is likely that the performance of the fellow eyes of the amblyopic observers improved substantially on account of prolonged testing in Experiment 1, so that by the time they were tested in Experiment 2 their ability to track with their non-amblyopic eye was comparable to that of normal observers. It is possible that amblyopic observers find monocular viewing with their non-amblyopic eye to be substantially different to how things appear when they view things with both eyes, and many thousands of trials are needed to shake off the effects of habituation. In short, some of the fellow eye deficits in amblyopic observers may result from the novelty of the monocular percept compared to the percept when viewing with both eyes.

In Experiment 1, observer SP’s performance was noticeably poorer than the remaining observers (Figure 3). Under the best of conditions, with either eye, she barely tracked two trajectories, whereas all other amblyopic observers tracked 3 or more trajectories with either eye when conditions were ideal. SP was a volunteer who was tested over several months with the typical separation between experimental sessions being a week or more, whereas the remaining observers were paid for their participation and experimental sessions were typically separated by a few days. Since SP was not more amblyopic than all the other observers, it appears likely that long durations separating testing sessions are detrimental to performance.

Some clarifications regarding the effective number of tracked trajectories

In the current paper, we have estimated the effective numbers of trajectories tracked by amblyopic observers for a range of stimulus conditions and compared these to estimates obtained in normal observers. There are several issues to be taken into account when interpreting these estimates, some of which have been outlined previously (Tripathy, Narasimhan, et al., 2007). Below we elaborate on some of these issues.

The effective number of tracked trajectories is not intended to be an explanation for tracking performance; it is a description of tracking performance. The percentage of correct responses is an inappropriate measure of tracking performance since this would change when the number of targets or the number of distractors in the stimulus is changed. On the other hand, the effective number of trajectories tracked is a performance measure that takes into consideration the greater probability of detecting one or more targets when there are more targets in the stimulus and also takes into account the necessary correction for guessing. This measure permits comparison of performance across different stimulus conditions in our experiments. The procedure of converting the percentage of correct responses into the effective number of tracked trajectories does not involve any claim regarding the actual strategy used by human observers and the actual number of trajectories tracked by human observers. However, if the effective number of tracked trajectories (i.e., the performance once target/distractor probabilities in the stimulus have been accounted for) is found to be the same in a variety of stimulus conditions, i.e., the human observer repeatedly behaves as if he/she were tracking a fixed number of trajectories and ignoring the rest, then a parsimonious inference from these results is that this similarity is not entirely coincidental. This inference however is not part of the LCHO; the LCHO merely converts the percentage of correct responses obtained into a stimulus independent measure of human performance.

While the effective number of tracked trajectories cannot tell us exactly how many trajectories are actually tracked by the human observer, it has important implications for the tracking performance of human observers. The LCHO assumes that any trajectories tracked are tracked perfectly. If the effective number of tracked trajectories is 4 (say), then the human observer must be tracking 4 trajectories perfectly, or a greater number of trajectories imperfectly. Thus, the effective number of trajectories tracked places a lower bound on the number of trajectories that the human observer must track (i.e., direct attentional/memory resources towards) but cannot tell us exactly how many trajectories were actually tracked (i.e., allocated resources) by the human observer. A similar situation exists in the Pylyshyn and Storm (1988) paradigm. Consider a situation in which performance was found to be 100% correct when there were 4 targets to be tracked and 80% correct when there were 5 targets to be tracked. The errors may have been caused because only 4 of the 5 targets were being tracked, or because all 5 of the targets were being tracked, but each target was tracked imperfectly to give an overall percentage of correct responses of 80%. The “number tracked” in the Pylyshyn task gives us a lower bound on the number of targets that must have had attentional and memory resources directed towards them, but it does not tell us exactly how many targets had...
resources allocated to them. The available resources may have been distributed among 4 targets at the expense of the 5th, or they may have been distributed among all the 5 targets. The “number tracked” in the Pylyshyn paradigm and the effective number tracked in the current paradigm are similar measures—they are lower bounds on the number of targets (or potential targets) that must have been allocated computational resources.

The effective number of trajectories tracked as outlined in Tripathy, Narasimhan, et al. (2007) has other advantages as a measure of tracking ability, aside from being a stimulus independent measure of performance. The effective number of trajectories tracked can be estimated even when the number of targets far exceeds the capacity of the human visual system. For example, it is possible to estimate how many trajectories are effectively tracked, even when there are as many as 7 or 10 trajectories that are deviating. Additionally, the effective number is an absolute measure and is not based on an arbitrarily determined level of performance (say 75% correct performance).

An important point to be noted regarding the LCHO and the effective number of trajectories tracked is that the actual angle of deviation of the trajectories is not represented in any of Equations 1–4. When the angle of deviation is small, the human observer’s performance (i.e., the proportion of correct responses) drops; the LCHO correctly reflects (describes) this lower level of performance by assigning to it a smaller magnitude for the effective number of trajectories tracked.

A notable difference from the Pylyshyn paradigm is that the current task does not require the trajectories be tracked for their entire lengths. For our experiments, it is adequate that the visual system track the trajectories immediately before and immediately after the deviation, ignoring the extremities of the trajectories. Alternatively, since our trajectories were either linear, or bilinear, tracking each trajectory at 5 instances of time (at the time of deviation, two instances each, before and after the deviation) is adequate for determining the direction of deviation. The tracking requirements in our task are substantially different from those in the Pylyshyn paradigm. Our task does not require the continuous monitoring of the targets as is necessary for the Pylyshyn task. For our task, we consider a target, or a potential target, to have been successfully tracked if adequate resources have been allocated to that target to determine a deviation in its trajectory were it to occur. For a given magnitude of deviation, the effective number of trajectories tracked is the number of trajectories that would have to be allocated adequate resources (to be able to correctly detect any deviation every time) in order to match the human observer’s performance.

**Tracking versus orientation averaging**

So far, our approach has been to consider resources to be allocated to some trajectories, individually, in order to determine if a deviation has occurred in any of these trajectories. An alternative to this would be pool information from a set of trajectories in order to determine if a deviation occurred within this set of trajectories. For example, the visual system might average all the trajectory orientations before and after the deviation(s) and look for differences in the two averages. Alternatively, the visual system might average a subset of the trajectory orientations before and after the deviation(s) and difference them. These two situations are considered below.

**Averaging of all orientations**

The ability of the visual system to efficiently integrate motion signals in the context of global motion has been well documented (Barlow & Tripathy, 1997; Watamaniuk, Sekuler, & Williams, 1989; also see Dakin, Maeschal, & Bex, 2005; Mansouri & Hess, 2006). In these experiments, the observers’ task is to judge the global direction of motion and to integrate all of the motion signals helps to solve the correspondence problem (Barlow & Tripathy, 1997). In the current experiments, frequently, the observers’ task is to judge the direction of deviation of a single trajectory, or a few trajectories, from among 10 trajectories, most of which do not contain deviations. In these situations, averaging the orientations of the trajectories would only dilute the signal (the deviation). If individual trajectories can be monitored (as indicated by the studies of Pylyshyn and colleagues), averaging of orientations would make sense when a majority of the trajectories undergo a deviation but would serve no useful purpose if only a few trajectories undergo deviations. It must be recognized that the displacements between frames in the current experiments are small, and correspondence noise is not an issue, unlike the situation in global motion. The experimental evidence too does not support the hypothesis that all orientations are averaged.

Thresholds for detecting deviations in single trajectories are approximately 2°, while thresholds for detecting a target deviation when there are four trajectories (three distractors) are typically greater than 25° (Tripathy & Barrett, 2004; Figures 5, 6, and 8). A simple averaging of orientations would predict that performance would be the same if the average deviation is the same. If a 2° deviation (average deviation = 2°) is at threshold when there is one trajectory in the stimulus, then an 8° deviation (average deviation = 2°) should be at threshold when there are four trajectories in the stimulus. But an 8° deviation is well below threshold.

Tripathy, Narasimhan, et al. (2007; Figure 10) performed a control experiment in which half the distractors deviated clockwise by a fixed angle and the other half deviated counterclockwise by the same angle. This manipulation did not change the average orientation since the clockwise and counterclockwise deviations canceled each other. As the angle of deviation of the distractors increased, the performance dropped in spite of there...
having been no change to the average pre- and post-deviation orientations on account of these manipulations.

**Averaging of some orientations**

If the visual system averages the pre- and post-deviation orientations of a subset of trajectories and differences them, then the effective number of trajectories tracked is still a useful measure of tracking performance—it tells us the minimum number of trajectories that must be averaged perfectly in order to explain the performance of human observers.

Does the experimental evidence support the hypothesis that a subset of the orientations is averaged, or that information from a subset of trajectories is pooled in order to increase efficiency? Tripathy and Barrett (2004; see Figures 4 and 9) measured thresholds for detecting deviations when there were $T$ ($1 \leq T \leq 10$) trajectories in the stimulus and all of them deviated in the same direction and by the same amount. If pooling of information was efficient over $A$ trajectories, thresholds should decrease by a factor of the square-root of $T$, until $T > A$, and then remain constant. But the data show no decrease in thresholds as $T$ is increased from 1 to 10. Thus, we find no evidence of efficient pooling of information across a subset of trajectories, even when there were as few as 2 trajectories ($T = 2$) in the stimulus. The absence of any integration of information from the two trajectories when $T = 2$, suggests that trajectories are monitored individually.

In short, the evidence from the earlier studies does not support the efficient pooling of information across all the trajectories or across a subset of the trajectories.

In our experiments, we did not ask the observers to specifically identify the deviating trajectories. So can we say with confidence that the observers were monitoring/tracking individual trajectories? A point to note is that our experimental conditions were blocked, i.e., within a block $T$, $A$ and the angle of deviation were fixed, and the angle of deviation was substantially suprathreshold. A few trials of our stimulus will convince observers that on some trials within a block they can confidently identify some of the deviating trajectories (presumably because these were individually monitored or tracked) and on other trials within the same block they cannot identify with confidence any of the deviating trajectories (presumably because these were monitored or tracked). It is obvious that observers do indeed have the ability to identify a subset of the deviating trajectories on a trial-by-trial basis. In fact, a couple of studies have investigated the shapes of the deviating trajectories in stimuli with more than one trajectory (Tripathy & Barrett, 2003, 2006).

**Enhancement of the amblyopic deficit?**

The amblyopic deficits in the current study seem small. Could varying some of the stimulus conditions increase this amblyopic deficit? In Figure 4, we have compared the averaged performance of the amblyopic and non-amblyopic eyes with the performance of normal observers from an earlier study (Tripathy, Narasimhan, et al., 2007). This comparison with the earlier study was not part of the design of the current study but was added as an afterthought at the time of writing up. Figure 4 shows that the deficit in the non-amblyopic and amblyopic eyes of the amblyopic observers is greater when there are few (between two and four) trajectories in the stimulus. In Experiment 2, we tested observers using stimuli with 6, 8, or 10 trajectories since we thought that greater numbers of trajectories would permit us to have a better understanding of attentional capacity. In hindsight, it is possible that using fewer trajectories might have resulted in greater amblyopic deficits than presented in Experiment 2 of this paper. On the other hand, the differences seen in Experiment 1 may have largely been practice effects as discussed above.

Another point of interest is that five of our observers were amblyopic in their left eye and one (SP) was amblyopic in her right eye. The stimuli in both experiments involved left-to-right moving trajectories, i.e., the observers that were amblyopic in their left eye saw motion that was nasally directed, while the other observer saw motion that was temporally directed. Fu and Boothe (2001) found that the worse eye of monkeys reared with binocular deprivation (alternating monocular occlusion) had normal motion thresholds for nasally directed motion and deficient thresholds for temporally directed motion. From our Figure 3, it is apparent that the five observers who were presented with nasally directed motion performed better than the single observer (SP) who was presented with temporally directed motion. While the poorer performance of SP in Experiment 1 most likely is a consequence of the longer delays between experimental sessions (see above), we cannot rule out that laterality of motion may have played a part with regard to the performance of the amblyopic eyes of the observers. However, it should be noted that Fu and Boothe (2001) did not find any difference between nasally directed and temporally directed motion in the better eyes of their monkeys. Moreover, while there are well-documented losses in temporally directed optokinetic nystagmus (OKN) in both eyes of humans with amblyopia, these deficits are not evident in psychophysical measures of sensitivity (Schor & Levi, 1980a, 1980b). Laterality of motion is thus not likely to be an explanation for our finding that fellow eyes of human amblyopic observers appear normal. A difference between the Fu and Boothe study and the current one is that their stimuli were random dot kinematograms; it is an open question whether differences in motion direction result in different levels of performance in the current task. In summary, it is possible that having fewer trajectories, or having trajectories that are temporally directed, would result in larger amblyopic deficits than those seen in this study.
Does the case of amblyopia provide insights into the factors limiting trajectory tracking in normal vision?

In the Introduction section, we pointed out that tracking performance might reflect limitations of attentional, memory, or indexing systems and that tracking performance in amblyopic observers might be compromised if mechanisms of spatial localization or mechanisms of form perception or mechanisms of motion perception are compromised. As noted in the Introduction section, despite the well-documented abnormalities in amblyopic eye-movement tracking, spatial localization, form perception, and motion perception, trajectory tracking is minimally impaired. Alvarez and Franconeri (2007) suggest that trajectory tracking (as measured in the present paper) and multiple object tracking (as measured in the standard Pylyshyn task) reflect different resource limitations: In their view, the resource in multiple object tracking is attention, while the resource in trajectory tracking is visual sensory memory (as suggested by Narasimhan, 2006; Narasimhan, Tripathy, & Barrett, 2005, 2006; Tripathy, Narasimhan, et al., 2007). In this view, it may not be altogether surprising that humans with amblyopia are only minimally impaired in tracking trajectories.

Summary

We found a small but consistent deficit when comparing the effective numbers of trajectories tracked by the amblyopic eyes with that for the fellow eyes. We found no deficit in tracking ability in the fellow eye when compared with that of normal eyes from a previous study (Tripathy, Narasimhan, et al., 2007). In fact, an enhancement in performance was seen in the fellow eyes, which we attribute to the observers in the current study being younger (Trick et al., 2005; Kennedy et al., 2008). We have suggested a few modifications to our stimuli that may increase the deficits seen in the amblyopic eye, but these need further investigation.

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