Amblyopic perception of biological motion

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Although a number of low-level visual deficits in amblyopia have been identified, it is still unclear to what extent these deficits extend throughout the visual processing hierarchy. Biological motion perception can be a useful measure of local and global visual processing since the point-light stimuli that are often used to study this ability carry both local motion and global form information. To investigate the integrity of the biological motion processing system in amblyopia, we employed both detection and discrimination tasks with coherent or scrambled point-light walkers either alone or embedded in different types of point-light masks. These manipulations allowed for control over the amount of form and/or motion information available to the observers that could be used for task performance. We found that amblyopic eyes could process both the global form and local motion components of point-light walkers, indicating intact processing for these stimuli. However, amblyopic eyes did show an increased susceptibility to the addition of masking dots suggesting that segregation of signal from noise is deficient in amblyopia.

Keywords: amblyopia, biological motion, inversion effect, global form, local motion, segregation

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General introduction

Amblyopia is a developmental disorder of the visual system caused by ocular abnormalities early in life. While surgery or optical correction of refractive errors can often address the initial cause of the amblyopia (e.g., strabismus), once amblyopia has developed, such interventions cannot restore visual function since amblyopia itself is a cortical deficit (Anderson, Holliday, & Harding, 1999; Barnes, Hess, Dumoulin, Achtman, & Pike, 2001; Barrett, Bradley, & McGraw, 2004; Hess, 1995, 2001; Kiorpes, 2006; Kiorpes, Kiper, O'Keefe, Cavanaugh, & Movshon, 1998; Kiorpes, Tang, & Movshon, 1999; Levi, 2006; Thiele, Bremmer, Ilg, & Hoffmann, 1997). Specifically, the amblyopic visual system has been shown to have neural deficits at both striate (Barnes et al., 2001; Kiorpes et al., 1998, 1999; Movshon et al., 1987) and extra-striate (Barnes et al., 2001; Kiorpes et al., 1998; Kiorpes, Tang, & Movshon, 2006; Simmers, Ledgeway, & Hess, 2005; Simmers, Ledgeway, Hess, & McGraw, 2003; Simmers, Ledgeway, Mansouri, Hutchinson, & Hess, 2006) processing stages. Here we used highly salient stimuli, biological motion displays depicting the walking patterns of human actors to assess the function of both global form and local motion processes in amblyopic and fellow fixing eyes. Biological motion stimuli are typically presented in a point-light format whereby landmarks on the body, generally the major joints, are represented with marker elements which move against a uniform background (Johansson, 1973). We used point-light walker stimuli that were manipulated to allow the amount of information available to the form processing system and the motion processing system to be independently controlled.

Point-light displays carry a number of different sources of information that could potentially be used by the visual system to extract task relevant information. The two major visual cues are motion information carried by the individual motion trajectories of each dot or small group of dots (Casile & Giese, 2005; Mather & Murdoch, 1994; Mather, Radford, & West, 1992; Troje, Sadr, Geyer, & Nakayama, 2006; Troje & Westhoff, 2006) and the form information carried by the global configuration of all of the dots on a frame to frame basis (Beintema, Georg, & Lappe, 2006; Beintema & Lappe, 2002; Bertenthal & Pinto, 1994; Chatterjee, Freyd, & Shiffrar, 1996; Hiris, 2007; Lange, Georg, & Lappe, 2006). These cues are thought to rely on two different visual processing streams, the dorsal pathway for motion and the ventral pathway for form (Giese & Poggio, 2003). The neural area often

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considered to be at least partially specialized for biological motion perception, the posterior portion of the superior temporal sulcus (Bonda, Petrides, Ostry, & Evans, 1996; Grèzes et al., 2001; Grossman, Battelli, & Pascual-Leone, 2005; Grossman & Blake, 2001, 2002; Hirai, Fukushima, & Hiraki, 2003; Pelphrey et al., 2003; Peuskens, Vanrie, Verfaillie, & Orban, 2005; Puce & Perrett, 2003; Thompson, Clarke, Stewart, & Puce, 2005; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001), is well positioned to receive and to integrate information from both of these neural pathways as it receives input from dorsal and ventral streams (Giese & Poggio, 2003).

Although motion perception in amblyopia has been shown to be deficient for a number of different tasks (Constantinescu, Schmidt, Watson, & Hess, 2005; Hess & Anderson, 1993; Hess, Demanins, & Bex, 1997; Kiorpes et al., 2006; Levi, Klein, & Aitsebaomo, 1984; Simmers et al., 2003, 2005, 2006), this does not necessarily mean that biological motion processing itself is impaired. Studies have shown that in patients where lesions have disrupted lower-level motion perception, biological motion perception can remain intact (Jokisch, Troje, Koch, Schwarz, & Daum, 2005; Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990), suggesting that multiple sources of information are open to the biological motion processing system.

A recent study has used biological motion displays to probe global form from motion perception in amblyopia and found that one measure of biological motion perception, the reduction in task performance associated with inverting the stimulus (i.e., "the inversion effect"), was unaffected by amblyopia (Neri, Luu, & Levi, 2007). In order to isolate global form-based processing of biological motion, Neri et al., 2007 used limited lifetime dots and a masking technique whereby dots were added to the display which had the same local motion characteristics as the dots making up the point-light actors, thereby removing local motion trajectories as a source of information. The task itself also minimized the information carried by local motion trajectories as the participants had to discriminate coherent point-light actors from a spatially scrambled version of the actors. This ensured that the only distinguishing feature between the target and distracter displays was the configural information present in the target display as both displays contained identical local motion information. Neri et al. (2007) found that while amblyopic eye performance was substantially impaired, the inversion effect remained intact suggesting that form from motion processing was unaffected by amblyopia.

While the ability of the amblyopic visual system to process the global information present in point-light displays is certainly of interest, this is not the only source of information that is important for biological motion perception. Another recent study has shown that inversion effects can still be obtained by inverting spatially scrambled stimuli which lack any global form information, thereby demonstrating an alternative, orientation specific, stream of information to the biological motion perception system relying solely on local motion trajectory information (Troje & Westhoff, 2006). Current evidence would suggest therefore that there are two separate inversion effects that can affect performance in a biological motion task. The first is an inversion effect acting on the configural form of the point-light walker, which requires a global configuration to be present in the stimulus (Reed, Stone, Bozova, & Tanaka, 2003). The second is an inversion effect acting on the local motion trajectory information that requires only local motion. Here we will refer to these two distinct types of inversion effect as the form-based inversion effect and the local motion-based inversion effect. Importantly, it is possible to measure each of these separate inversion effects by strictly controlling the information that is available to the visual system when performing the specific biological motion task in question. Embedding the point-light stimulus in a mask constructed from dots that have identical local motion trajectories to the stimulus renders local motion information uninformative, isolates global/configural information and therefore allows measurement of the associated form-based inversion effect (Bertenthal & Pinto, 1994). Conversely, spatially scrambling the stimulus, by definition, removes all form/configural information from the display and renders only the local motion trajectory information informative allowing the local motion-based inversion effect to be measured (Troje & Westhoff, 2006). Given these considerations, biological motion stimuli provide a useful tool with which to investigate not only configural processes, but also the function of biologically relevant local motion processing. In addition, the type of cues that observers can use when viewing point-light displays relies on the type of stimuli and the exact task (Beintema et al., 2006). Accordingly, it is often desirable to employ different tasks and different types of stimuli to obtain a more complete picture of biological motion perception.

In the current study, we assessed the ability of the amblyopic visual system to use either the configural or the local motion information present in point-light displays. In order to isolate configural information, we used a detection task and embedded a point-light walker in a scrambled walker mask (SWM) to render the local motion trajectories of individual dots uninformative (Bertenthal & Pinto, 1994). To assess how much of the deficit measured in the amblyopic eyes was due to the segregation of signal from noise component inherent in this detection task, we repeated the same experiment using a mask consisting of linearly moving dots. This linear masking technique allowed the observer access to both the local and global information present in the point-light display and therefore provided a measure of noise susceptibility without forcing a reliance on a specific set of cues within the stimulus. To clarify the difference between these two types of mask, in the SWM each dot had a local motion trajectory that was an exact duplicate of one of the local

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motion trajectories present in the target walker itself. Therefore, not only did each dot in the SWM move nonlinearly, its movement was identical to one of the movements present in the target walker. The only difference therefore between the target and the SWM was the spatial and temporal phase relationships between the dots since the masking dots in the SWM were spatially scrambled and the phase relationships between dots representing different joints were randomized. The linear mask on the other hand was constructed of dots that moved along a single linear trajectory with a randomly assigned direction and speed. These masking dots therefore can be thought of as a completely separate population from the dots of the target walker. The linear masking dots did not directly mask the local motion trajectories or the spatial relationships present in the target walker. Rather they were used to assess the effect of the presence of a noise population of dots on task performance. Finally, in order to assess the ability of amblyopic eyes to utilize the local motion trajectories present in point-light displays, we used a walking direction discrimination task whereby walkers could either be coherent or spatially scrambled. In the spatially scrambled case, no configural information was present, and therefore only local motion trajectories could be used to perform the task. To summarize, Experiment 1 employed a detection task with SWMs to address form processing, Experiment 2 employed a detection task using linear masks to address segregation of signal from noise deficits, and Experiment 3 employed a walking direction discrimination task using both coherent and spatially scrambled walkers to address local motion trajectory processing. We found that amblyopic eyes were largely normal at biological motion perception but seemed to rely more on local trajectory information than configural information. In addition, for detection tasks, amblyopic eyes showed a greater susceptibility to the presence of masking dots.

General methods

Apparatus

Stimuli were presented on a 22-in. Iiyama Vision Master pro 513 monitor, at a screen resolution of 1024 ×

Obs	Age/Sex	Type	Refraction	Dev	LA	Squint	Additional
ADS	21/F	RE	Ø		20/160	ET 15°	Detected age 4 y, patching at 4 y for
		LE strab	−0.5	DS	20/20		6 m, surgery at 7 y, no stereopsis
AR	47/M	RE	Ø		20/20		Detected age 6 y, no patching,
		LE strab	Ø		20/50	ET 1°	no surgery, no stereopsis
BH	27/M	RE	Ø		20/20		Detected age 2 y, patching and
		LE strab	Ø		20/50	XT 2°	glasses for 2 y, no surgery,
							stereo-acuity 400 SOA
EW	27/F	RE strab	+3.5–3.00	127°	20/40	ET 10°	Detected age 6 y, glasses and
		LE	+2.5–1.00	78°	20/25		patching for 10 m, no surgery,
							no stereopsis
GAC	20/F	RE	Ø		20/20		Detected age 7 y, patching for 1–2 y,
		LE strab	Ø		20/50	ET 1°	no surgery, no stereopsis
JD	21/M	RE strab	+4.00	DS	20/63	ET 5°	Detected age 5 y, patching for 3 y,
		LE	+1.50	DS	20/16		no surgery, stereo-acutiy 200 SOA
JL	29/M	RE	Ø		20/20		Detected age 4 y, no patching,
		LE mixed	+2.50	DS	20/40	XT 20°	no surgery, no stereopsis
KD	18/M	RE strab	+1.00	DS	20/50	XT 4.5°	Detected age 5 y, patching for 6 m and
		LE	Ø		20/25		glasses until 14 y, no surgery,
							no stereopsis
SA	29/F	RE mixed*	Ø		20/560	ET 23°	RE cataract at birth, surgery 2 m,
		LE	−3.25 + 0.5	90°	20/20		patched for 8 y, 2nd surgery at 12 y,
							no stereopsis
WM	20/M	RE	Ø		20/20		Detected age 12 y, no patching,
		LE strab	+1.75–0.5	180°	20/63	ET 1°	no surgery, no stereopsis
XL	31/F	RE	−2.50	DS	20/20		Detected age 13 y, no treatment,
		LE strab	−2.75 + 0.75	110°	20/400	ET 15°	no stereopsis

Table 1. Clinical details of the amblyopic observers. The following abbreviations have been used; Obs for observer, LA for letter acuity, M for male, F for female, strab for strabismus, aniso for anisometrope, RE for right eye, LE for left eye, ET for esotropia, XT for exotropia, SOA seconds of arc. *Note*: *Mixed refers to strabismic and aniometropic for participant JL and deprived and strabismic for participant SA. Local stereopsis was measured using the Randot® Test.

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768 pixels, with an 85-Hz refresh rate. One pixel subtended 2.88 arcmin of visual angle. Stimuli were presented using the psychophysics toolbox for Matlab (Brainard, 1997; Pelli, 1997) running on a PC equipped with an Intel 945 G integrated graphics Controller.

Participants

Eleven amblyopic observers took part in Experiments 1 and 2A, and a subset of 6 took part in Experiment 2B. Ten of these observers also took part in Experiment 3. Of the eleven amblyopic observers, nine had strabismic amblyopia, one had strabismic–anisometropic amblyopia, and one had strabismic–deprivation amblyopia. Details of the observers can be found in Table 1. Ten control observers took part in all three experiments. All control observers had normal or corrected to normal vision, and all but two (one author, BT, and one experienced psychophysical observer) had no previous psychophysical experience.

Stimuli

Stimuli were viewed from a distance of 65 cm in a darkened room. In all four experiments, point-light walkers were used as stimuli. Point-light walkers were dynamic representations of the human form walking in side profile consisting of eleven bright white dots (102.6 cd/m^2, 0.1° visual angle) representing the feet, the knees, the elbows, the wrists, the hip, the shoulder, and the head. The dots were presented on a dark (0.2 cd/m^2) background. Coherent (non-scrambled) walkers were 7° tall. This large size was chosen to minimize the influence of any crowding (Hariharan, Levi, & Klein, 2005; Levi & Klein, 1985) or positional uncertainty effects (Hess, McIlhagga, & Field, 1997; Levi, Klein, & Yap, 1987; Simmers & Bex, 2004) that may have been present for amblyopic eyes on the ability of amblyopic participants to perceive the point-light walkers. This size of walker has also been shown to be well perceived in both central and peripheral vision in normal observers (Thompson, Hansen, Hess, & Troje, 2007). The motion of the walker was based on averaged motion capture data from 50 male and 50 female walkers. For a full explanation of the generation and representation of the stimuli, see Troje (2002).

Experiment 1—Form information

Introduction

In Experiment 1, we used a point-light walker detection task to assess global form-based processing in our amblyopic sample. We embedded the target walker in masks constructed from spatially and temporally scrambled point-light walkers to render local motion trajectories uninformative (Bertenthal & Pinto, 1994). In the distracter interval, we added a scrambled walker, which was constrained to the same area within which the target would have been presented, to further ensure that no lower-level cues such as dot density in a fairly central region of the display would aid performance.

Stimuli

Point-light walkers were embedded within a dot mask that covered 9.6 × 9.6° centered on the monitor screen. Walkers were randomly jittered within this display area from trial to trial by 1.4° left or right and 0.72° above or below central presentation. Walkers were presented facing left and could be either upright or inverted. In the inverted condition, walkers were mirror flipped about a horizontal axis. Masks were constructed from spatially and temporal-phase-scrambled point-light walkers. This technique resulted in a scrambled walker mask that contained all of the local motion trajectories present in the walkers themselves, but without any of the spatial relations between individual dots that provided the configural information present in the walkers. This masking technique effectively removes individual dot trajectory information from the display and therefore requires the observers to rely on configural information to perceive the walker (Bertenthal & Pinto, 1994).

Design and procedure

We used a 2AFC detection paradigm to test biological motion perception. Two stimuli, each lasting 2000 ms, were presented consecutively separated by a 500-ms ISI. The observer had to indicate, using a keyboard button press, which of the two stimuli contained a coherent point-light walker. Both stimuli contained a mask. The stimulus without a walker also contained eleven additional masking dots to equate dot density between the two stimuli. The additional dots were constrained to the area of the display that would have contained the walker to avoid any local dot density differences. Trials were presented in blocks of 180. Each block of trials included 6 different mask densities that were randomly sequenced within the block, 30 trials per density. Mask densities were 30, 43, 61, 88, 126, and 180 dots (0.33, 0.47, 0.66, 0.95, 1.37, and 1.95 dots per square degree of visual angle respectively). Subjects ran a block of trials for upright and inverted walkers for each eye (amblyopic and fellow fixing eye for amblyopes and dominant and non-dominant eye for controls). An eye patch was worn over the eye that was not viewing the display. Within a block, inversion and viewing eye were kept constant, and the sequence of

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blocks was randomized over participants. Prior to beginning the experiment, participants were familiarized with the stimuli and the task. For the amblyopic observers, it was confirmed that they could see the stimulus with their amblyopic eye by ensuring that they could correctly describe what they saw in a series of unmasked point-light displays. As can be seen from the data below, all amblyopic participants were able to see the stimuli.

Results

The results from Experiment 1 and all subsequent experiments were analyzed using repeated measures ANOVAs. For all ANOVA analyses reported here, degrees of freedom were adjusted to account for sphericity using the conservative Greenhouse–Geisser correction. Primary analyses were conducted on the amblyopic and control participant data sets individually to assess the effects of the independent variables on each group independently. Effects within each group were then further explored post hoc using additional repeated measures ANOVAs on the relevant subsections of the data sets. To avoid repetitious statements of statistical results, only significant meaningful interactions are discussed. For all experiments, the initial control group analysis revealed no differences between the dominant and the non-dominant eyes; therefore, subsequent comparisons between amblyopic and control groups were made by separately comparing the amblyopic and fellow fixing eye data from the amblyopic group with the pooled dominant and non-dominant eye data from the control group. This planned analysis was initially conducted with the inclusion of all independent variables and was then further broken down into more specific ANOVAs as required by the pertinent post hoc analyses. Accordingly, the results from Experiment 1 were analyzed using 4 ANOVAs. The first was conducted on the amblyopic participant data with the following factors; Eye (amblyopic eye vs. fellow fixing eye), Inversion (upright vs. inverted), and Mask Density (6 levels, measured in number of masking dots). The same ANOVA was also applied to the control data with the factor Eye changed to dominant vs. non-dominant. Finally, to directly compare the amblyopic observers to control observers, the data from control eyes were pooled (as there was no difference between eyes), and two ANOVAs were conducted with the within-subject factors of Inversion (upright vs. inverted) and Mask Density (6 levels, measured in number of masking dots) and the between-subject factor of Group, which for the first ANOVA was control eye vs. amblyopic eye and for the second was control eye vs. fellow fixing eye.

Figure 1 shows the mean data from Experiment 1 for both the amblyopic (Figure 1A) and control (Figure 1B) observers. A clear difference between the ability of amblyopic and fellow fixing eyes to perform the detection task ($F(1,10) = 5.807$, $p < .05$) can be seen in Figure 1A. In addition, it is clear from Figure 1A that inversion ($F(1,10)$, $= 30.9$, $p < .001$) and increasing mask density ($F(3,33) = 74.931$, $p < .001$) reliably reduced detection performance. Although there was a deficit for the amblyopic eye, when this deficit was accounted for, the effects of inversion and mask density did not have a reliably different effect on one eye than the other ($p > .5$ for both interactions). For controls, there was no performance difference between the dominant and non-dominant eyes ($p > .5$; Figure 2B) although, as for the amblyopic observers, inversion ($F(1,9) = 24.348$, $p < .001$) and increasing mask density ($F(4,34) = 78.624$, $p < .001$) had a detrimental impact on performance.

A direct comparison between the amblyopic eye of amblyopes and the pooled dominant and non-dominant

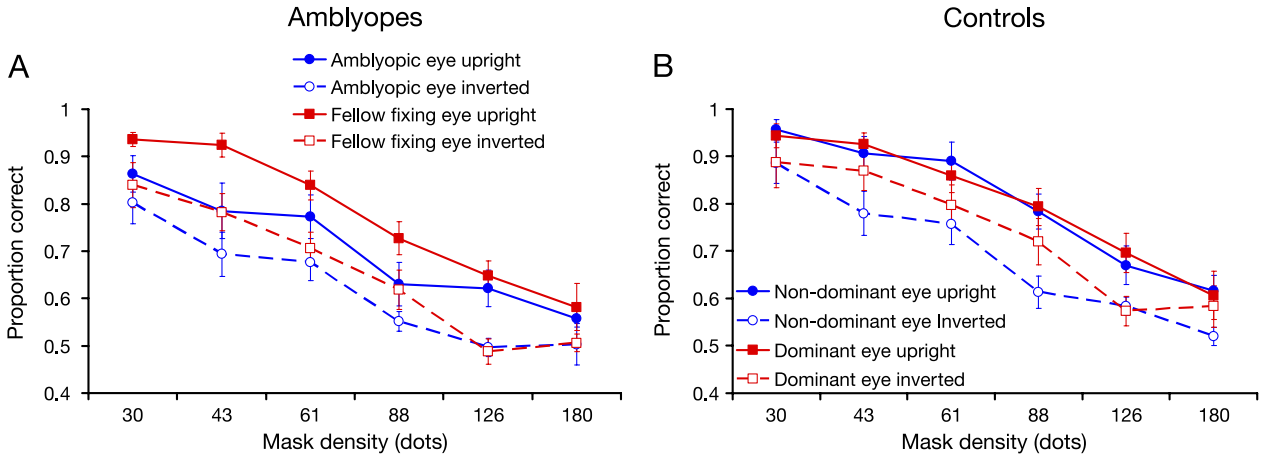

Figure 1. Average proportion correct for amblyopic (A) and control (B) observers as a function of mask dot density for Experiment 1. Closed symbols with solid lines depict upright walker performance, open symbols and dashed lines depict inverted walker performance. Circular symbols denote amblyopic eye (A) and non-dominant eye (B). Square symbols denote fellow fixing eye (A) and dominant eye (B). Error bars show ±1 *SEM*.

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eye data of controls revealed that amblyopic eyes were significantly impaired at biological motion detection relative to controls ($F(1,19) = 7.548$, $p < .05$). However, when this impairment was accounted for, other variables (inversion and mask density) did not affect amblyopic eye performance any differently from the control eyes ($p > .5$). The same analysis comparing the fellow fixing eyes of amblyopic observers with the pooled control data revealed that fellow fixing eyes did not differ from control eyes in any respect for this experiment.

Discussion

Amblyopic eyes showed a clear deficit for biological motion detection; however, the size of the form-inversion effect did not differ between amblyopic eyes and fellow fixing or control eyes, suggesting that the global form-based processing of biological motion information was intact. As argued by Neri et al. (2007), if global form-based visual processes were not functioning correctly for amblyopic eyes, we would not expect the presence of a form-inversion effect for the amblyopic eye data as the inversion effect is typically considered to be the signature of a neural system specialized for the specific stimulus attribute being processed (Blake & Shiffrar, 2007; Neri et al., 2007; Pavlova & Sokolov, 2000; Sumi, 1984). The results of Experiment 1 support the findings of Neri et al. (2007); however, there was still a pronounced deficit in the ability of amblyopic eyes to perform this task. Experiment 2 was designed to address this issue.

Experiment 2—Segregation of signal from noise

Although amblyopic eyes showed a normal form-inversion effect, there was still a pronounced deficit in task performance in Experiment 1. We were interested in whether this deficit could be explained by the presence of masking dots in the display, as it has been shown that amblyopic eyes have difficulties with segregation of signal from noise (Mansouri & Hess, 2006). In addition, it has recently been shown that signal from noise segregation abilities in the periphery may be separate from the ability to process biological motion information (Thompson et al., 2007). To test whether amblyopic eyes were deficient at the segregation of signal from noise required for accurate performance in the task used in Experiment 1, we repeated Experiment 1 but this time using linearly drifting masking dots that masked neither the global form of the walker nor the local motion trajectories. This technique of masking therefore tested the ability of the visual system to segregate two separate populations of moving dots, one signal population containing both salient global organization and informative local motion trajectories and one noise population with a common motion pattern unrelated to that of the signal population. In Experiment 2A, we used the same range of mask dot densities used in Experiment 1, however, as biological motion detection is highly resilient to the presence of linearly drifting masking dots as one might expect since both form and motion information is available to the system; in Experiment 2B, we re-ran a subset of observers using a range of higher mask densities to assess whether amblyopic eyes would show a deficit in detection performance when more dense linear masks (i.e., masks with a greater number of dots) were employed.

Design and procedure

All experimental procedures were the same as those used in Experiment 1 with the exception of the type of masking dots used and in Experiment 2B the number of masking dots used. In Experiments 2A and 2B, each masking dot moved along a linear trajectory. The direction of each dot was random and did not change until the dot reached the edge of the display and was deleted. The speed of each dot was chosen randomly from those present in the walker itself and remained constant throughout the dot's lifetime. When a dot reached the edge of the stimulus region, it was deleted and replaced by a new dot that was allocated a random starting position within the stimulus display area. In the distracter stimuli, additional dots were added randomly to the mask area to keep the global dot densities constant between distracter and target stimuli. The same range of mask dot densities as used in Experiment 1 was used in Experiment 2A in order to facilitate a direct comparison between the two experiments. In Experiment 2B, the mask dot densities used were 200, 257, 330, 424, 545, and 700 dots (2.17, 2.79, 3.58, 4.60, 5.91, and 7.60 dots per square degree of visual angle, respectively). Only a subset of observers took part in Experiment 2B, six amblyopic observers (ADS, AR, GAC, KD, SA, and WM) and six control observers.

Results

As in Experiment 1, detection performance was analyzed with respect to which eye was viewing the stimulus, whether the stimulus was inverted or not and the number of masking dots present (mask dot density). As can be seen in Figures 2A and 2B which show the results for Experiment 2A, when the same mask density levels as used in Experiment 1 were used for linear masks, performance was at ceiling for controls and close to ceiling for amblyopic observers. The statistical analyses presented below must therefore be interpreted in the context of this ceiling effect. For Experiment 2A, there was no difference

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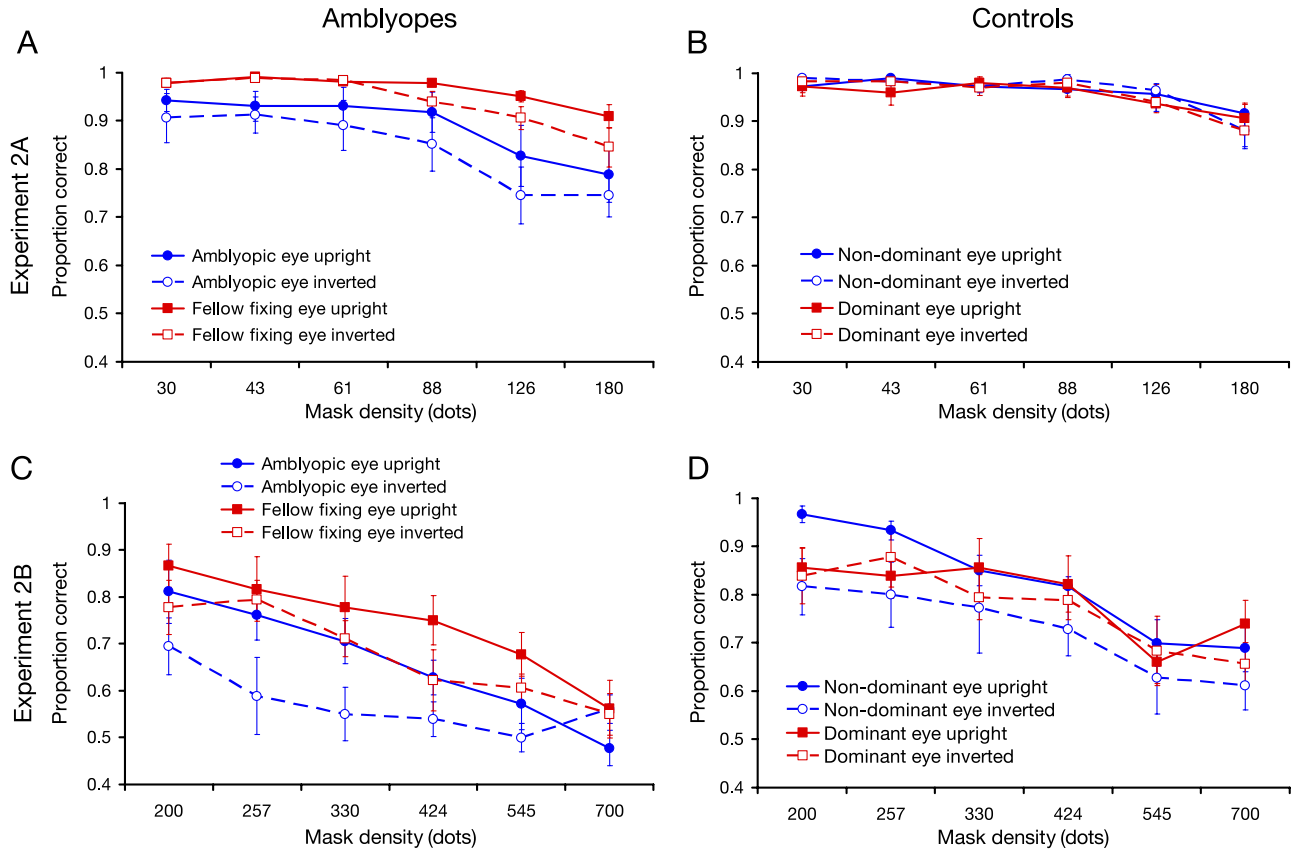

Figure 2. Mean proportion correct for Experiment 2A (A and B) and 2B (C and D) for amblyopic (A and C) and control (B and D) observers. Closed symbols with solid lines depict upright walker performance, open symbols and dashed lines depict inverted walker performance. Circular symbols denote amblyopic eye (A) and non-dominant eye (B). Square symbols denote fellow fixing eye (A and C) and dominant eye (B and D). Error bars show ±1 *SEM*.

in performance between amblyopic and fellow fixing eyes ($p > .5$); however, as can be seen in Figure 2A, increasing mask density tended to reduce amblyopic eye performance at a faster rate than fellow fixing eye performance ($F(3,32) = 4.260$, $p < .05$). As in Experiment 1, inversion effects were present for this experiment ($F(1,10) = 7.112$, $p < .05$) and did not differ between eyes for the amblyopic participants ($p > .5$).

Control participants showed a pronounced ceiling effect demonstrating the resilience of biological motion detection to these types of masking dots. A comparison between amblyopic eyes and the control data (pooled across eye) showed that although amblyopic eyes were only marginally impaired relative to controls ($F(1,19) = 4.102$, $p = .06$) there was a faster drop off with increasing mask density for the amblyopic eye data than the control data (which was essentially at ceiling, $F(2,44) = 5.280$, $p < .01$). Fellow fixing eye and pooled control data did not differ.

The results for Experiment 2B are shown in Figures 2C and 2D. Increasing the noise densities did indeed reduce performance; however, even at the highest noise density, control performance was still impressive for both dominant and non-dominant eyes, with upright walker performance close to 70% correct. At these higher mask densities, amblyopic eye detection performance was reliably worse than both fellow eye performance ($F(1,5) = 15.646$, $p < .05$) and controls ($F(1,10) = 11.805$, $p < .01$). An inversion effect was also apparent ($F(1,5) = 10.596$, $p < .05$) for the amblyopic participants. Once again, fellow fixing eyes did not differ from control subject's detection performance.

Discussion

To assess whether the cause of the reduced overall performance for amblyopic eyes shown in Experiment 1 was due to mid-level impairments such as the ability to segregate signal from noise (Mansouri & Hess, 2006), a different type of mask constructed from linearly drifting dots was used in Experiment 2. When considering the differences between the efficacy of the linear masks used in Experiment 2 and the scrambled walker masks used in Experiment 1, it is important to bear in mind that while scrambled walker masks render local motion trajectory information uninformative for detection of a biological

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motion walker and therefore force a reliance on form information, linear masks have no specific effect on either the form or the local motion trajectory information, and therefore both sources of information are available to the observer for detection purposes. Therefore, it follows that detection in a linear mask could be successfully accomplished by detecting a global configuration of dots that provide form from motion cues, detecting the presence of a single non-linear motion trajectory or both. When the range of dot densities used for linear masking matched those used in Experiment 1 which had been shown to greatly impair detection performance, linear masks, as can be seen from the control observer data in Figure 2B, were completely ineffective at impeding the task performance of normal eyes. This stark difference between the effectiveness of SWM and the linear masks for normal eyes (compare Figure 1B with Figure 2B) also highlights how important local motion trajectory information, which is preserved in the linear mask case and not in the SWM case, can be for detecting biological motion. Within Experiment 2A, increasing mask dot density had a greater impact on amblyopic eye performance than non-amblyopic eyes, although amblyopic eye performance was still well above chance. This effect cannot be due to the preferential removal of form or motion information from the stimulus since neither of these visual cues were removed by the linear masks; therefore, it may be accounted for by a more general deficit in the segregation of signal from noise within the amblyopic visual system. Experiment 2B, which employed linear masks with a greater density (increased dot number), showed that at higher densities of linear masking dots, amblyopic eyes showed significantly poorer performance than both fellow fixing and control eyes. In combination with the results of Experiment 2A, these findings suggest that the presence of masking dots, even if they are a completely distinct population from the target dots and do not directly interact with the target, impacts on amblyopic eye performance more than that of fellow fixing or control eyes. This effect is characterized both by the presence of masking dots reducing performance at low densities that have no measurable effect on detection performance for non-amblyopic eyes (Experiment 2A) and by a sustained level of poorer performance for higher mask dot densities as seen in Experiments 1 and 2B. An alternative interpretation that cannot be ruled out by our experiments is that the biological motion signal itself is attenuated in the amblyopic visual system thereby resulting in a greater susceptibility to the addition of masking dots. However, indirect evidence that the biological motion signal may be intact in the amblyopic visual system is that although performance for amblyopic eyes was poorer as compared with non-amblyopic eyes, there was still an inversion effect, an indication that processing of biological motion is intact (Neri et al., 2007). This particular inversion effect cannot be attributed fully to either the form- or motion-based inversion effects as both form and local motion information were preserved in this task. This result supported the findings of Experiment 1 and those of Neri et al. (2007).

Experiment 3—Local motion trajectory information

Introduction

Experiment 1 targeted the use of form cues in biological motion displays by isolating the configural form information using a SWM and a detection task. Amblyopic eyes showed a deficit at a detection task in terms of absolute performance, but not in terms of the form-inversion effect that under the specific conditions used in Experiment 1 can be regarded as a measure of the global form component of biological motion processing. The deficit in absolute performance was traced to a deficit in segregating signal from noise for amblyopic eyes in Experiment 2. The aim of Experiment 3 was to assess the local motion trajectory component of biological motion processing. This required a change of task and stimulus.

It has recently been shown that inversion effects do not only reflect the use of configural information within point-light displays but are also dependent on individual dot trajectories (Troje & Westhoff, 2006). Troje and Westhoff (2006) showed that an inversion effect could still be measured for point-light displays that had been spatially scrambled, phase scrambled, and within which each dot had been temporally offset, demonstrating that the trajectories of individual dots were processed by motion mechanisms tuned to biologically plausible motion patterns that are orientation sensitive. Here we used the same technique to assess local motion trajectory processing in our amblyopic observers. Observers were required to discriminate the walking direction of both coherent and spatially scrambled point-light walkers both in the absence of noise and in varying levels of linear noise.

Design and procedure

Following Troje and Westhoff (2006), the discrimination task used in Experiment 3 required participants to report the walking direction of a point-light walker presented in a single epoch. The stimulus remained on the screen until the participant responded with a key press indicating the perceived walking direction. The point-light walker could be facing left or right, could be spatially scrambled or coherent, and could be upright or inverted. In the spatially scrambled configuration, the only sources of information available to the observers were the local motion trajectories of each individual dot. The coherent

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stimuli provided both form and motion information. As in the previous experiments, inversion (upright or inverted) was kept constant within a block of 360 trials, but walking direction and scrambling (coherent or scrambled) were randomized within a block (180 trials for scrambled and 180 trials for coherent). When walkers were scrambled, the phase relations between the dots were left intact, but the dots were randomly positioned (spatially scrambled) within an area 7.7° × 2.9°. Stimuli could either be unmasked (mask density of 0) or presented within masks with dot densities of 25, 47, 87, 161, or 300. Linear masking was used for this experiment since in the scrambled walker condition, SWMs, which remove local motion trajectory information from the display would have rendered the task impossible as local motion trajectories were the only source of information. Each mask density was sampled 30 times within a block for both the coherent and the spatially scrambled stimuli. Stimulus presentation order was randomized within a block and block order (upright or inverted and amblyopic vs. fellow fixing eye or dominant vs. non-dominant eye) was randomized over participants.

Results[1]

Figure 3 shows the data for the coherent (Figures 3A and 3B) and scrambled conditions (Figures 3C and 3D) for both amblyopic observers (Figures 3A and 3C) and controls (Figures 3B and 3D). It is clear from Figures 3A and 3C that the amblyopic eyes showed very similar performance to fellow fixing eyes for this task, although the amblyopic eyes were more susceptible to the effect of masking dots at the medium-high densities (marginal difference between the eyes, $F(1,9) = 4.980$, $p = .053$). As anticipated, both inversion ($F(1,9) = 8.402$, $p < .05$) and spatial scrambling ($F(1,9) = 22.292$, $p < .001$) decreased discrimination performance for the amblyopic observers. Importantly, neither inversion nor spatial scrambling affected the amblyopic eye differently than the fellow fixing eye ($p > .05$).

An analysis of only the data for the spatially scrambled walker revealed a significant difference between the amblyopic eye and the fellow fixing eye ($F(1,9) = 6.181$, $p < .05$). An inspection of Figure 3C suggests that this effect was not due to absolute differences in discrimination

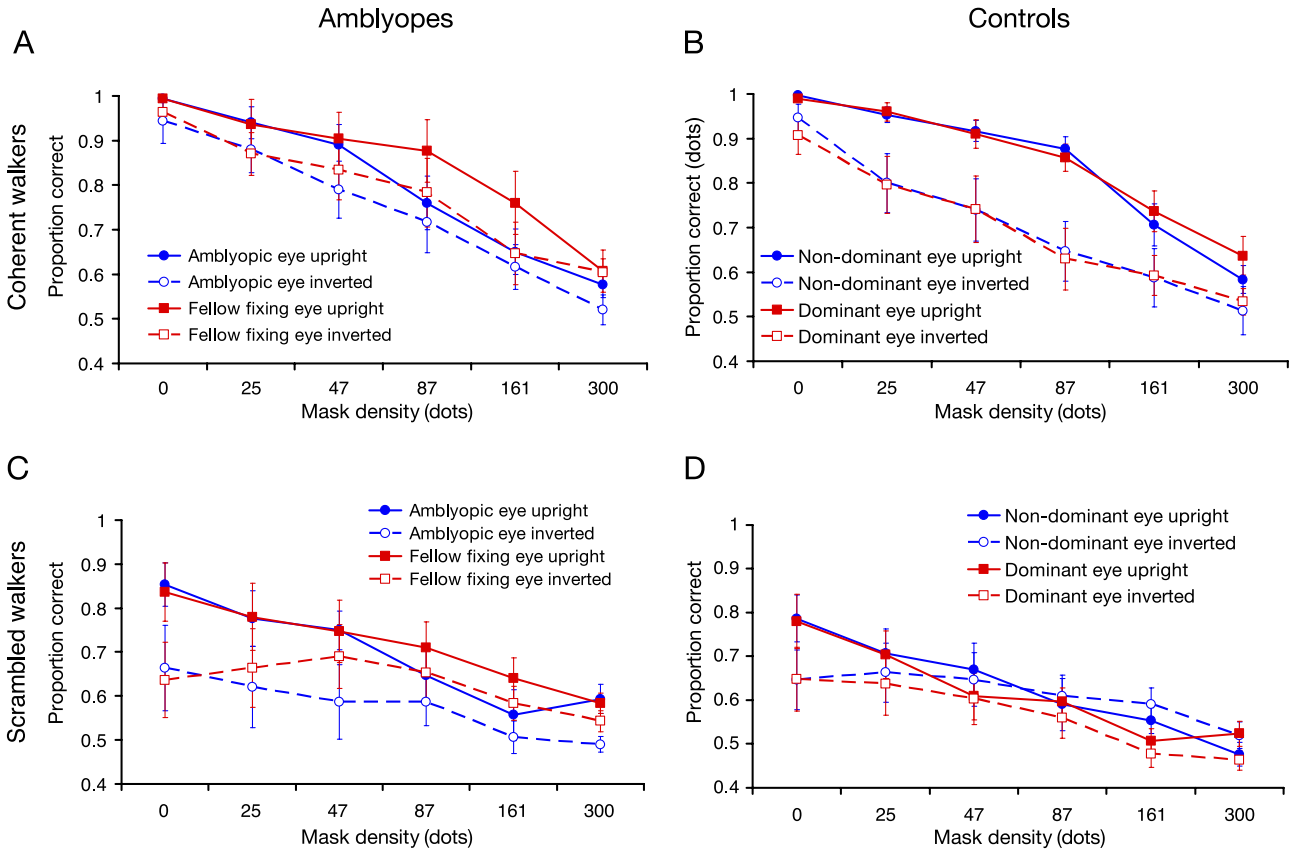

Figure 3. Mean proportion correct for Experiment 3. Data for coherent (A and B) and spatially scrambled stimuli (C and D) are shown separately for both amblyopic (A and C) and control (B and D) observers. Closed symbols with solid lines depict upright walker performance, open symbols and dashed lines depict inverted walker performance. Circular symbols denote amblyopic eye (A and C) and non-dominant eye (B and D). Square symbols denote fellow fixing eye (A and C) and dominant eye (B and D). Error bars show ±1 *SEM*.

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for upright scrambled walkers (compare the solid blue line with the solid red line) but rather a result of a difference in the effect that inversion had on each eye.[2] An additional analysis was conducted to test for the presence of an inversion effect for spatially scrambled stimuli using only the data from the 0 mask dot density condition, i.e., the condition in which no masking dots were added to the display. The rational for looking only at the no masking dots condition was two-fold. Firstly, masking dots had a pronounced impact on discrimination performance for the spatially scrambled stimulus particularly when compared with the impact that masking dots had on the coherent walkers. Secondly and more importantly, performance for spatially scrambled stimuli was not at ceiling in the absence of masking dots (Figure 3C). Figures 4A and 4B show the individual amblyope data for the spatially scrambled stimulus in the absence of noise. Although there is some variability in individual performance as one would expect, is it clear that as a group, there is no reliable bias toward better performance for the fellow fixing eye for this task. One-tailed paired *t* tests were conducted for each eye using only the no masking dots data (mask density = 0) to test for the anticipated local motion-inversion effects. As can be seen in Figure 4C, both the amblyopic, $t(9) = 2.032$, $p < .05$, and the fellow fixing, $t(9) = 2.530$, $p < .05$, eyes showed significant local motion-inversion effects.

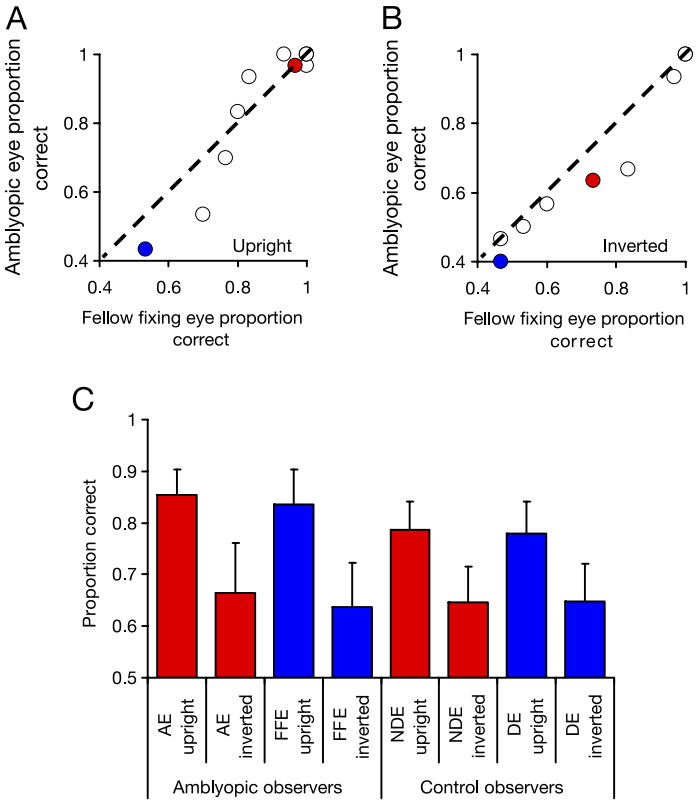

Figure 4. Individual amblyope data and inversion effect sizes for Experiment 4, spatially scrambled stimuli with no mask only. Panels A and B show individual data for amblyopic observers for upright and inverted stimuli, respectively. The red symbol represents the strabismic–anisometropic participant. The blue symbol represents the strabismic–deprivation participant. Data points lying below the dashed line indicate superior performance for the fellow fixing eye. Panel C shows group data for upright and inverted spatially scrambled stimuli for each eye of amblyopes and controls. Error bars show ±1 *SEM*. The following abbreviations are used in panel C; AE, amblyopic eye; FFE, fellow fixing eye; NDE, non-dominant eye; DE, dominant eye.

When considering only the coherent stimuli, there was no difference in the discrimination performance of the amblyopic and fellow fixing eyes ($p > .05$). Coherent stimuli were subject to a reliable inversion effect ($F(1,9) = 6.836$, $p < .05$).

For the control participants, no differences were observed between the dominant and the non-dominant eyes ($p > .05$). As was the case for the amblyopic participants, an inversion effect was present ($F(1,8) = 23.814$, $p < .001$) as was a deterioration in discrimination performance associated with spatial scrambling of the stimuli ($F(1,8) = 51.929$, $p < .001$). To test for the presence of a local motion-inversion effect in the absence of masking dots (mask dot density = 0), one-tailed paired *t* tests were conducted between the upright and the inverted data for both the dominant and the non-dominant eye for the spatially scrambled stimuli only. Both eyes showed significant local motion-inversion effects (dominant eye $t(9) = 3.06$, $p < .001$, non-dominant eye $t(9) = 2.462$, $p < .05$). Similarly to the amblyopic observers, an analysis of only the coherent stimulus data for the control group revealed a reliable inversion effect ($F(1,8) = 22.648$, $p < .01$). See Appendix A for additional findings.

Amblyopic eye performance did not differ from controls (data pooled across eyes) for this experiment with the exception of a significant 3-way interaction between inversion, spatial scrambling, and group ($F(1,18) = 5.97$, $p < .05$), suggesting that the difference in the size of the inversion effects for the coherent and the scrambled stimuli was different between the two groups. As can be seen from a comparison of Figures 3A and 3B and also Figures 3C and 3D, it seems that amblyopic eyes showed a larger inversion effect for the scrambled stimuli than the control participants whereas the opposite was true for the coherent stimuli. Evidence for this interpretation of the interaction was found by comparing amblyopic eye performance with control performance for the spatially scrambled and coherent stimulus data separately. For the spatially scrambled stimuli, there was no reliable difference between the amblyopic eyes and the control eyes in the size of the inversion effect ($p > .05$); however, this was not the case for the coherent stimuli where the magnitude of the inversion effect did indeed differ between the amblyopic eyes and the control eyes ($F(1,18) = 5.570$, $p < .05$). Fellow fixing eyes did not differ from control eyes ($p > .05$).

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Discussion

The use of local motion trajectories in amblyopic perception of biological motion was measured by using a walking direction discrimination task as the ability to perceive walking direction can tolerate the complete removal of any form information in the display through spatial scrambling of the stimuli (Troje & Westhoff, 2006). Amblyopic eyes showed a reliable local motion-inversion effect for the spatially scrambled stimuli in the absence of masking dots, demonstrating accurate local motion trajectory processing for biological motion information. Interestingly a comparison between amblyopic and control eyes suggested that control eyes showed a greater inversion effect for coherent than scrambled stimuli (although an inversion effect was present for both conditions) whereas the opposite was true for amblyopic eyes. This suggests that amblyopic eyes may not be able to access the form information present in the point-light displays for direction discrimination purposes as well as control eyes. This idea is consistent with the slightly better performance for amblyopic observers than control observers at lower mask dot densities with spatially scrambled stimuli that can be observed by comparing Figures 3C and 3D. This suggests that spatial scrambling had less effect on amblyopic observer performance than control performance.

General discussion

Biological motion perception can rely on global form from motion information, local motion trajectories or a combination of both (Giese & Poggio, 2003). By using different types of tasks and stimuli, it is possible to assess the ability of an observer to use these distinctly different sources of information for biological motion perception. In the current study, we used these techniques to assess the ability of amblyopic eyes to perceive the global form and local motion information present in point-light displays. We found that amblyopic eyes could process both the form and the motion components of point-light walkers accurately, as measured by the presence of either form-inversion effects (supporting the previous findings of Neri et al., 2007) or local motion-inversion effects.

Experiment 3 demonstrated local motion-inversion effects (an inversion effect for a spatially scrambled walker) for normal, fellow fixing, and amblyopic eyes. These findings support those of Troje and Westhoff (2006) who argued that the presence of such an inversion effect is evidence for filters tuned to the characteristic, gravity-defined, local motion trajectories of biological movements. We have shown that these filters remain intact in the amblyopic visual system and may in fact be more important to amblyopic perception of biological motion than in normal visual systems. Across experiments, we did not find a consistent pattern to the individual losses of each of the amblyopic observers.

The ability of the amblyopic visual system to utilize both form and local motion trajectory information for the perception of biological motion appears therefore to be largely intact. However, it is clear from the experiments presented here that amblyopic eyes do show a general deficit in task performance relative to fellow fixing and control eyes. This deficit was also reported by Neri et al. (2007) who attributed the reduced performance to lower-level deficits. It is not quite clear however how any of the low-level deficits that have been reported in amblyopia, such as reduced contrast sensitivity and acuity, could account for the clear reduction in performance exhibited by the amblyopic eyes. Biological motion perception appears to be largely resilient to lower-level manipulations such as blurring of the dots (Ahlström, Blake, & Ahlström, 1997). Our experimental design allowed us to test the hypothesis that it was in fact segregation of signal from noise that was causing the reduced performance of the amblyopic eye by testing the influence of two different types of dot masks. As has been shown to be the case for peripheral vision (Thompson et al., 2007), amblyopic eye performance showed a greater performance reduction in response to the addition of masking dots, even when the motion of these dots did not mask either the global form or the local motion trajectory information. In other words, this type of noise that was ineffective for normal controls, because it could be easily segregated from the point-light walker signal, was highly effective in reducing amblyopic performance. This suggests that while biological motion perception may remain intact, systems dealing with segregation of signal from noise may be deficient in amblyopia (Mansouri & Hess, 2006).

Appendix A

The analysis for Experiment 3 was different from the previous two experiments as there was an additional factor, namely, spatial scrambling, whereby walkers could either be presented spatially scrambled or coherent (not spatially scrambled). The ANOVA analysis was conducted as follows. For each group (amblyopic observers and controls), an omnibus ANOVA was conducted with factors of Eye (amblyopic vs. fellow fixing or non-dominant vs. dominant), Inversion (upright vs. inverted), Scrambling (scrambled vs. coherent), and Mask density (in units of number of masking dots, 6 levels). This analysis was then broken down by Scrambling as this was the factor of particular interest. Therefore, two further ANOVAs were conducted for each group, one on the scrambled data and one on the coherent data with factors of Eye, Inversion, and Mask density. Finally, paired t tests were conducted on the 0 mask density condition (i.e., no

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masking dots present) for each eye to test for the anticipated local motion-inversion effect for the scrambled walkers in the absence of masking dots. This test was conducted because linear masking quickly drives down performance for the scrambled walker stimulus and performance was not at ceiling for the scrambled walkers in the 0 mask density condition. To assess the differences between eyes, a further set of ANOVAs were conducted comparing the performance of both amblyopic and fellow fixing eyes with control data (pooled across eyes).

An additional finding for the amblyope ANOVA was that spatial scrambling interacted with mask dot density ($F(2,19 = 4.135$, $p < .05$). As can be seen from Figure 3, this interaction was characterized by masking dots having a greater impact on task performance for the spatially scrambled stimuli than the coherent stimuli, suggesting that the configural information present in the coherent displays made them more resistant to the addition of masking dots. This supports previous findings with normal participants (Thompson et al., 2007). This same effect was marginal for the control participants ($F(2.13) = 3.5$, $p = .068$).

For the controls, there was also a difference in the size of the inversion effect for the spatially scrambled and coherent stimuli ($F(1,8) = 11.974$, $p < .01$). As can be seen in Figures 3B and 3D, this interaction between inversion and spatial scrambling was characterized by a larger inversion effect for the coherent stimuli than the spatially scrambled stimuli, which may have partially been driven by the fact that performance dropped off toward chance more rapidly for the spatially scrambled stimuli with increasing mask dot density. When considering only the spatially scrambled stimuli across all mask dot densities, a marginal effect of inversion was apparent ($F(1,8) = 4.659$, $p = .06$).

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Footnotes

[1]The analysis for Experiment 3 was slightly different as compared with the previous two experiments, see Appendix A for further details.

[2]Partial support for this interpretation was that inversion was found to marginally differ in its effect on the amblyopic and the fellow fixing eyes ($F(1,9) = 5.0$, $p = 0.052$). To verify the direction of this effect, we assessed the effect of inversion on the amblyopic eye and fellow fixing eye separately. Considering all mask dot densities that were tested, for amblyopic eyes inversion had a marginal effect ($F(1,9) = 4.744$, $p = 0.052$), whereas for fellow fixing eyes inversion did not reliably influence discrimination performance ($F(1,9) = 2.144$, $p = .177$), suggesting that for the spatially scrambled stimulus there was a larger inversion effect for amblyopic eyes as compared with fellow fixing eyes.

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