

Deficient motion perception in the fellow eye of amblyopic children

Cindy S. Ho^{a,*}, Deborah E. Giaschi^{a,b,*}, Catherine Boden^c, Robert Dougherty^d,
Roy Cline^b, Christopher Lyons^b

^a Department of Psychology, University of British Columbia, Vancouver, Canada V6T 1Z4

^b Department of Ophthalmology and Visual Sciences, University of British Columbia, Children's and Women's Health Centre of British Columbia, BC's Children's Hospital, 4480 Oak Street, Vancouver, BC, Canada V6H 3V4

^c Department of Ophthalmology, University of California, San Diego, La Jolla, 92093-0946, USA

^d Department of Psychology, Stanford University, Stanford, 94305-2130, USA

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Abstract

The extent of motion processing deficits and M/dorsal pathway involvement in amblyopia is unclear. Fellow eye performance was assessed in amblyopic children for motion-defined (MD) form, global motion, and maximum displacement (D_{\max}) tasks. Group performance on MD form was significantly worse in amblyopic children than in control children. Global motion deficits were significantly related to residual binocular function. Abnormally elevated D_{\max} thresholds were most prevalent in children with anisometropia. Our findings from these three uncorrelated tasks implicate involvement of binocular motion-sensitive mechanisms in the neural deficits of amblyopic children with strabismic, anisometropic, and aniso-strabismic etiologies.

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1. Introduction

Amblyopia is a developmental condition that may affect a healthy eye during childhood if it is deprived of normal visual stimulation due to ocular misalignment (strabismus), unequal refractive errors (anisometropia), or both. M/dorsal and P/ventral pathways, the parallel neural pathways governing, respectively, temporal and spatial aspects of visual perception (Merigan & Maunsell, 1993; Ungerleider & Mishkin, 1982; Zeki, 1978), have different periods of development (Atkinson, 1992) and likely have different critical periods or windows of neural plasticity when they are vulnerable to changes

such as those induced by abnormal visual stimulation or by amblyopic treatment (Daw, 1998). Therefore, abnormal visual experience early in development could cause deficits to any of the subcortical pathways before the primary visual cortex (V1) and/or the cortical streams at V1 and beyond.

Clinically, reduced visual acuity (VA) on standard tests involving letter or shape recognition, is the diagnostic indicator of amblyopia. Unilateral amblyopia is characterized by reduced VA in the amblyopic eye with normal VA in the fellow eye when tested through an optimal refractive correction. Motion perception is rarely tested clinically but emerging research evidence suggests that it is not spared in amblyopic eyes (Buckingham, Watkins, Bansal, & Bamford, 1991; Elleberg, Lewis, Maurer, Brar, & Brent, 2002; Giaschi, Regan, Kraft, & Hong, 1992; Hess, Demanins, & Bex, 1997; Kelly & Buckingham, 1998; Paul, Giaschi, Cavanagh, & Cline, 2001; Schor & Levi, 1980a, 1980b; Steinman,

* Corresponding authors. Address: Department of Ophthalmology, University of British Columbia, Room A146, BC's Children's Hospital, 4480 Oak Street, Vancouver, BC, Canada V6H 3V4.

E-mail addresses: cindyh@interchange.ubc.ca (C.S. Ho), giaschi@interchange.ubc.ca (D.E. Giaschi).

Levi, & McKee, 1988). It has been suggested that motion perception deficits may provide a measure of neural change and visual loss more sensitive than form perception deficits (Kelly & Buckingham, 1998).

The fellow eye is often assumed to have normal visual function because it demonstrates normal VA. This assumption is likely not valid as numerous reports have claimed abnormal form (Davis et al., 2003; Kandel, Grattan, & Bedell, 1980; Kovacs, Polat, Pennefather, Chandna, & Norcia, 2000; Leguire, Rogers, & Bremer, 1990; Lewis, Maurer, Tytla, Bowering, & Brent, 1992) and motion (Elleberg et al., 2002; Giaschi et al., 1992; Kelly & Buckingham, 1998; Paul et al., 2001) perception in the clinically unaffected fellow eye.

Fellow eye deficits likely reflect abnormalities associated with binocular mechanisms. Binocular neurons are not dependent on specific input from only one eye but instead can be stimulated through input from either eye. One might speculate that deficits in the fellow eye could result from (a) transfer between the amblyopic and fellow eye through remaining binocular neurons (Leguire et al., 1990); and/or (b) abnormal or modified development of neurons responding to fellow eye stimulation due to abnormal binocular interactions and/or competition (Crewther & Crewther, 1993; Kiorpes & McKee, 1999 (review), McKee, Levi, & Movshon, 2003). Furthermore, perceptual deficits in the fellow eye could be induced, at least in part, by visual deprivation of that eye during occlusion therapy.

As one progresses through the visual pathway beyond area V1, a higher proportion of neurons are binocular (Zeki, 1978). It is widely accepted that amblyopia occurs because of reduced numbers of binocular neurons in V1 (reviewed in Hess, 2001), but the extent to and manner in which binocular neurons in higher visual processing areas are affected by abnormal binocular experience during development is not yet clear. Thus, perceptual deficits in the fellow eye could suggest involvement of extra-striate cortex. It has been suggested, however, that binocular neurons higher in the visual pathway, such as area V5/MT, are less vulnerable to unequal monocular visual input than binocular neurons in area V1 (McColl & Mitchell, 1998). If this were true, one might expect motion perception in the fellow eye to show only subtle deficits in cases of unilateral amblyopia.

Giaschi et al. (1992) previously reported very robust deficits in the fellow eyes of amblyopic children (aged 4–14 years) on a motion-defined (MD) letter identification task that measured minimum speed thresholds. Whether the highly prevalent MD form deficits observed represent a general deficit in motion perception or a specific deficit in form processing that exists despite normal VA in the non-amblyopic fellow eye is still unclear. To investigate the possibility of general motion processing deficits, we looked at performance in the fellow eyes of amblyopic children on three specific psychophysical

tasks chosen to represent different aspects of motion processing: coherence thresholds for direction discrimination of global motion, minimum speed thresholds for identification of motion-defined (MD) form, and maximum displacement thresholds for direction discrimination of coherent motion (D_{\max}). Performance between amblyopic and control groups on the three motion tasks was compared. D_{\max} and global motion stimuli shared the same display parameters. The D_{\max} task varied dot displacement and held coherence constant and the global motion task varied coherence but held dot displacement constant. Thus, these two tasks represented orthogonal 1-D slices through the 2-D coherence/displacement motion space. The MD form task used in this study was similar to that used previously by Giaschi and colleagues with the exception that our task involved identification of shapes that preschool children could identify rather than letters, and involved vertical instead of horizontal relative motion cues to minimize the influence of nasal-temporal oculomotor asymmetries.

2. Methods

2.1. Subject selection

2.1.1. Amblyopic group

The amblyopic group consisted of 21 children ranging in age from 4.4 to 11.0 years ($M = 6.9$ years, $SD = 1.7$ years). The subjects were referred from the Department of Ophthalmology at the Children's and Women's Health Centre of British Columbia. Patients were assessed (by author RC or CL) and classified, based on clinical evaluation and history, into three amblyopic subgroups: strabismic (S) [$M = 7.0$ years, $SD = 2.0$ years], anisometric (A) [$M = 6.8$ years, $SD = 1.7$ years], or aniso-strabismic (A + S) [$M = 7.4$ years, $SD = 1.3$ years]. None of the subjects included had eccentric fixation, latent or manifest nystagmus, anomalous retinal correspondence, or oculomotor dysfunction with the exception of strabismus. Only the fellow eye was tested. The ages and clinical diagnoses of the amblyopic group are summarized in Table 1. The age range of subjects was kept similar to that used by Giaschi et al. (1992) because their results suggest that children and adults may perform differently on the MD form task.

The Regan 96% contrast letter chart was used to measure VA because it has letter spacing designed to minimize crowding effects and has a logarithmic progression of letter size (Regan, 1988). Line VA was measured monocularly and recorded as a decimal VA measure. For example, a VA measure of 6/7.5 would be expressed as a decimal VA of 0.80. VA in children aged 3–5 years who were unfamiliar with letters was

Table 1
Clinical data at time of testing for 21 pediatric amblyopic patients

Age (years)	Diagnosis	Refractive error	Ocular deviation	Decimal VA (fellow or tested eye)	Decimal VA (amblyopic or non-tested eye)	Stereoacuity
4.4	A	R: +5.00 + 1.00 × 090 L: +5.00 + 3.50 × 100	orthophoria	1.00	0.48	70
5.7	A	n/a	n/a	1.00	0.20	>500
5.8	A	R: +0.50 L: +4.00	orthophoria	1.05	0.50	30
6	A	R: +1.50 L: +2.50	4Δ esophoria	1.08	0.65	>500
6.1	A	R: +2.25 L: +6.50	orthophoria	1.20	0.10	200
6.3	A	R: +0.50 L: +6.25	3Δ exophoria	1.28	0.88	50
6.3	A	R: +0.75 + 4.00 × 100 L: +1.00 + 1.50 × 080	orthophoria	0.98	0.80	30
6.7	A	R: +4.50 L: +1.50	orthophoria	1.00	0.40	>500
7	A	R: +0.25 + 0.75 × 090 L: -2.00 + 0.75 × 090	orthophoria	1.25	0.80	50
7.5	A	n/a	n/a	1.23	0.05	>500
8.7	A	n/a	n/a	1.00	0.23	70
11	A	n/a	n/a	1.20	0.80	50
5.9	A + S	R: +6.00 L: +4.75	R microtropia	1.00	0.50	70
7.8	A + S	R: +4.50 + 1.00 × 25 L: +5.00 + 1.50 × 160	15Δ esotropia (accommodative)	1.25	0.44	70
8.4	A + S	R: +4.00 + 1.00 × 170 L: +2.00 + 1.00 × 170	R microtropia	1.00	0.10	100
4.6	S	n/a	n/a	1.00	0.50	>500
6	S	R: +0.75 + 2.00 × 090 L: +1.00 + 2.25 × 090	L microtropia	1.00	0.20	>500
6.3	S	n/a	n/a	1.10	0.80	>500
6.5	S	R: +2.50 + 3.50 × 105 L: +2.50 + 3.50 × 075	10Δ L esotropia	1.00	0.67	>500
8.3	S	R: +6.50 L: +6.75	L microtropia	1.00	0.10	>500
10.2	S	n/a	n/a	1.33	1.00	70

A: anisometropic amblyopia; S: strabismic amblyopia; A+S: aniso-strabismic amblyopia.
n/a: clinical history unavailable.

No subjects with clinical data available had surgery for strabismus.

All subjects with clinical data available were treated for a period with full time occlusion therapy.

determined with a picture chart (Lighthouse Low Vision Products). To avoid the possibility of testing subjects with bilateral amblyopia, the inclusion criteria for the fellow eye was the same as that for the control subjects, described below. For 3–4 year old subjects, best corrected decimal VA was required to be at least 0.67. For subjects aged 5 years and older, best corrected decimal VA was required to be at least 1.00. Seven additional amblyopic subjects were excluded from the study for having VA in the fellow eye that did not meet the inclusion criteria. Stereoacuity was assessed using the Randot Stereotest (Stereo Optical Co., Inc.). VA and stereoacuity data are summarized in Table 1.

2.1.2. Control group

The control group consisted of 75 children ranging in age from 3 to 11 years. Inclusion criteria for control subjects were age dependent to account for the improve-

ment expected during visual development. For 3–4 year old subjects, best corrected decimal VA and stereoacuity were required to be, respectively, at least 0.67 and better than 100 seconds of arc (sec). For subjects aged 5 years and older, best corrected decimal VA and stereoacuity measures were required to be, respectively, at least 1.00 and better than 70 s. No subject had a history of ocular pathology, strabismus, or amblyopia. The eye with the higher decimal VA measure was chosen for testing. In cases where both eyes had equal VAs, the subjects were allowed to choose the eye to be tested.

2.2. Apparatus

The psychophysical tasks were programmed in Custom C Code and run on a Macintosh Power PC 8500. The stimuli were displayed on a 17" Sony Trinitron

monitor with a resolution of 1024×768 (horizontal \times vertical) pixels and a refresh rate of 75Hz. For the global motion and D_{\max} tasks, responses were collected with a modified MacGravis gamepad that was placed in a child-friendly case with cartoon character buttons. Verbal responses for the MD form task were entered by the experimenter.

2.3. Procedure

The study was approved by the University of British Columbia's Behavioural Research Ethics Board. All testing was completed in one session that lasted approximately 1 h. Prescribed optical correction was worn throughout testing. Testing was performed under diffuse illumination with lights directed away from the display screen to prevent glare. The non-tested eye was occluded with an opaque black patch. Vertically moving dots were used in all the visual stimuli. Test distances were monitored throughout all the experimental trials to ensure that they remained constant. Stimulus presentation for all three tasks was based on a forced choice modified descending method of limits (Regan & Hong, 1990). Subject responses were self-paced and subjects were asked to guess the correct response if they were unsure. Feedback was provided for the subjects to motivate and encourage them throughout the trials. Rest was provided between tasks. Parents were allowed to remain present but were asked not to face the monitor. The order in which the tasks were performed was constant across all subjects. The visual stimuli for all three tasks consisted of randomly generated patterns of white 1 pixel dots (100 cd/m^2) on a black background (5 cd/m^2).

2.3.1. Global motion

The viewing distance was 1.4 m. Dot density was 5%. The entire random-dot display subtended a visual angle of 12.8×9.6 deg (horizontal \times vertical). Each dot subtended 0.014 deg^2 . Each trial consisted of eight frames of animation lasting 106.7 ms each. The resulting total trial duration was 853.6 ms. Speed of the moving dots remained constant at 1.26 deg/s and this was achieved by maintaining a constant dot displacement of 0.142 deg from frame to frame. This speed was chosen because it was found previously to reveal deficits in global motion perception in children with dyslexia (Edwards et al., 2004) and was the same as the fastest speed used in the MD form task described below. In each trial, a percentage of dots moved coherently upwards or downwards (signal dots). The rest of the dots moved randomly in all directions (noise dots). The coherence level corresponded to the percentage of dots that were signal dots. The task was to identify the direction in which the pattern of dots appeared to be moving by pressing the appropriate button on the response pad (inset to Fig. 1a). The task used a two-alternative forced-

choice (2AFC) paradigm where the probability of accurately guessing the correct response was 50%.

The test trials were presented in blocks each consisting of 10 trials at a given coherence level. The first test block of trials had a coherence level of 100%; all of

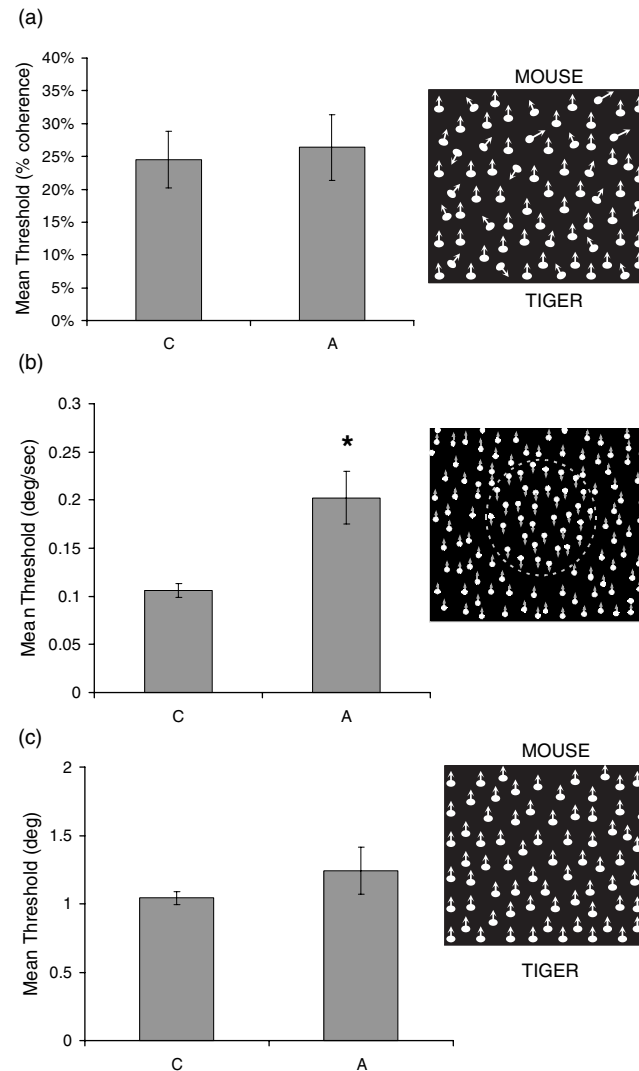


Fig. 1. (a)–(c): Mean threshold values on the 3 motion tasks for the control group (C), and the amblyopic group (A). The amblyopic group includes subjects with anisometric, strabismic and aniso-strabismic amblyopia. Error bars represent standard errors. A significant difference from the control group mean is indicated by *. (a) Global motion thresholds. A lower threshold value represents better performance. Inset: Global motion stimulus. The task was to identify if MOST of the dots on the display were moving towards the picture of the tiger or the mouse. A given percentage of dots moved coherently in one direction and the remaining dots moved in random directions. (b) Motion-defined (MD) form thresholds. A lower threshold value represents better performance. Inset: MD form stimulus. The task was to identify the shape seen on the display. The shape was created by dots that moved in relative motion. (c) Maximum displacement (D_{\max}) thresholds. Inset: D_{\max} stimulus. The task was to identify if the dots on the display were moving towards the picture of the tiger or the mouse. The perception of smooth motion was achieved by successively shifting the entire display of dots upwards or downwards by a given displacement.

the dots in the display moved in the same direction. Children were required to achieve 80% accuracy on this block before continuing on with the task. Coherence levels for the remaining blocks were 50%, 25%, 12.5%, 6.25%, 3.125% and 1.6%. Testing continued with successive blocks until the accuracy rate for correctly responding at a given coherence level reached or dropped below the guess rate of 50% correct.

2.3.2. Motion-defined form

The viewing distance was 5.6m. Dot density was 25%. The entire random-dot display subtended a visual angle of 2.5×2.5 deg and the motion-defined shapes within the display subtended a visual angle of 2.1×2.1 deg. Each dot subtended 0.004 deg^2 . The shapes were defined only by relative motion of the moving dots (inset to Fig. 1b). The shapes had no luminance-defined contours. If the dots ceased to move or moved in the same direction, no shape could be perceived. The dots within the shape moved coherently upwards or downwards and simultaneously, the dots outside the shape moved coherently in the opposite direction. Speed of the moving dots remained constant inside and outside the shape and the perceived shape remained stationary in the display. Each trial consisted of eight animation frames lasting 80.0 ms each. The resulting total trial duration was 640 ms. The task was to identify verbally the shape on the display as circle, duck, fish, heart, or gingerbread man. A pilot study conducted on 3 year old children using a sample of 10 shapes, showed that these 5 shapes were equally identifiable. The shapes were presented in random order throughout the trials.

To ensure that subjects understood the task and could identify the shapes, five practice trials were given prior to the test trials with moving dots of higher luminance inside the shape than in the background. During the test trials, the moving dots were of equal luminance both inside and outside the shapes. The test trials were presented in blocks each consisting of 10 trials at a given speed. The first test block of trials had dots moving at a speed of 1.26 deg/s. Children were required to achieve 80% accuracy on this block before continuing on with the task. With each subsequent block of trials, the speed was reduced by reducing the dot displacement between frames and keeping the frame duration constant. Dot speeds for the remaining blocks were 0.628, 0.314, 0.158, 0.079, and 0.039 deg/s. As the speed of the moving dots became slower, the task became harder. Testing continued with successive blocks until the accuracy rate for correctly responding at a given velocity level approached the 5AFC guess rate of 20%.

2.3.3. Maximum displacement

The visual stimulus was identical to that used for the global motion task. In each trial, the entire dot display was displaced (100% coherence) successively upwards

or downwards by a constant dot displacement. The task was to identify the direction in which the dots on the display were moving by pressing the appropriate button on the response pad (inset to Fig. 1c). The maximum displacement (D_{\max}) level corresponds to the largest dot displacement that can still produce the perception of smooth apparent motion in a single direction.

The test trials were presented in blocks each consisting of 10 trials at a given displacement level. The first test block of trials had a dot displacement of 0.31 deg. Children were required to achieve 80% accuracy on this block before continuing on with the task. Dot displacements for the remaining blocks were 0.57, 1.14, 1.42, 1.70, 1.99, 2.27, 2.56, 2.84, 3.12, 3.41, and 3.69 deg. As the displacement level became higher, the perception of smooth apparent motion became faster and direction discrimination became more difficult. Testing continued with successive blocks until the accuracy rate for correctly responding at a given displacement level approached the 2AFC guess rate of 50%.

2.4. Threshold calculations

Thresholds were determined by fitting a Weibull function to the data for each participant on each of the three tasks using a maximum-likelihood minimization procedure (Watson, 1979). Threshold was defined as the point of maximum slope on the fitted curve, which occurs at 71% correct in a 5AFC procedure (MD form) and at 82% correct in a 2AFC procedure (global motion and D_{\max}) (Strasburger, 2001). A χ^2 test was performed to ensure that threshold estimates were valid by confirming that the Weibull function adequately fit the data for each child.

3. Results

The individual and mean thresholds obtained by the amblyopic subjects for all three tasks are shown in Table 2. Analyses of individual subject scores, multivariate, and correlational analyses were performed on the data.

3.1. Individual subject analysis

For the individual subject analysis, the 75 control subjects were divided into three age categories ($n = 25$): 3–5 years, 6–8 years, 9–11 years. The mean ages for the three age dependent control groups are summarized in Table 3. Prevalence of abnormal performance across all control subjects on each task was compared to that which would be expected based on 95% confidence limits and our observed findings did not differ significantly from that expected ($\chi^2 = 1.12, p > 0.77$). This confirmed that comparisons were being made to control subjects that indeed showed normal performance.

Table 2
Test data for 21 pediatric amblyopic patients

Age (years)	Diagnosis	MD form (deg/s)	Global motion (% coherence)	D_{\max} (deg)
4.4	A	0.21	81 ^a	0.98
5.7	A	0.07	14	1.19
5.8	A	0.27	47	1.31
6	A	0.31 ^a	8	1.14
6.1	A	0.15	11	1.82 ^a
6.3	A	0.09	3	1.02
6.3	A	0.20	66 ^a	0.50 ^b
6.7	A	0.31 ^a	4	1.05
7	A	0.07	9	0.67
7.5	A	0.08	13	2.97 ^a
8.7	A	0.61 ^a	10	0.75
11	A	0.17	27	1.19
5.9	A + S	0.19	42	3.70 ^a
7.8	A + S	0.07	66 ^a	0.76
8.4	A + S	0.11	38	1.80 ^a
4.6	S	0.34	14	1.04
6	S	0.15	26	0.75
6.3	S	0.13	10	0.55
6.5	S	0.19	42	1.03
8.3	S	0.27 ^a	11	0.49 ^b
10.2	S	0.24 ^a	13	1.37
	Mean	0.16	19	0.99
	SD	0.08	14	0.24

A: anisometropic amblyopia; S: strabismic amblyopia; A+S: aniso-strabismic amblyopia.

One-tailed normal limits for MD form and global motion are set at 1.64 standard deviation (SD) limit for a 95% confidence level.

Two-tailed normal limits for D_{\max} are set at 1.97 SD limit for a 95% confidence level.

Abnormal performance is based on comparison of the individual threshold score to the normal limit calculated for the control group ($n = 25$) that includes the participant's age.

^a Result is greater than the normal upper limit shown in Table 3 for appropriate age group.

^b Result is less than the normal lower limit shown in Table 3 for appropriate age group.

For global motion and MD form, we expected abnormal performance to occur only at the tail of the normal distribution corresponding to higher coherence levels and faster speed respectively. A one-tailed 95% confidence interval suggests that 5 out of 100 people performing the task would obtain scores that differ by at least 1.64 standard deviations from the population mean. The cut off for abnormal performance on global motion and MD form was defined as a threshold value greater than 1.64 standard deviations compared to the mean threshold obtained by each age-dependent control group.

Abnormal scores would be expected to occur at either tail of the distribution for D_{\max} . D_{\max} increases with age (Parrish, Giaschi, Boden, & Dougherty, 2005; Wattam-Bell, 1996) and with reduced VA (Zwicker, Hoag, Edwards, Boden, & Giaschi, 2004). Amblyopic children, therefore, could show a developmental delay in D_{\max} performance (small D_{\max}) or could perform as though

Table 3
Mean control group data in individual analyses ($n = 75$)

	Age (years)	MD form (deg/s)	Global motion (% coherence)	D_{\max} (deg)
<i>3–5 years ($n = 25$)</i>				
Mean	4.63	0.24	30	0.90
SD	0.65	0.16	25	0.28
Normal upper limit		0.50	71	1.45
Normal lower limit				0.35
<i>6–8 years ($n = 25$)</i>				
Mean	7.46	0.13	22	1.03
SD	0.88	0.08	16	0.27
Normal upper limit		0.26	48	1.56
Normal lower limit				0.50
<i>9–11 years ($n = 25$)</i>				
Mean	10.65	0.12	19	1.00
SD	0.93	0.07	10	0.22
Normal upper limit		0.23	35	1.43
Normal lower limit				0.57

One-tailed normal limits for MD form and global motion are set at 1.64 standard deviation (SD) limit for a 95% confidence level.

Two-tailed normal limits for D_{\max} are set at 1.97 SD limit for a 95% confidence level.

they have reduced acuity (large D_{\max}). A two-tailed 95% confidence interval suggests that 2.5 out of 100 people performing D_{\max} would obtain scores that are better than and 2.5 out of 100 people would score worse than 1.97 standard deviations from the population mean. This would give a total of five abnormal results out of 100 people performing the task. The cut off for abnormal performance on D_{\max} was defined as a threshold value greater than 1.97 on either side of the mean threshold obtained by each age-dependent control group.

The mean threshold values and normal cut off limits for each task were calculated for the three control groups to account for developmental differences in performance and are summarized in Table 3. Each individual score was compared to performance on the same task by the control group that included his/her age. Table 2 identifies scores that are abnormal for each amblyopic subject based on these age-dependent control group comparisons.

Overall, 12 out of 21 amblyopic subjects (57%) had significant deficits on at least 1 motion task in the fellow eye. The prevalence rate for deficits on at least 1 motion task for anisometropic, strabismic, and aniso-strabismic amblyopia were respectively: 58%, 33%, and 100%. Only two subjects had deficits on more than 1 task. Relative to mean performance in the control subjects of the relevant age category, the prevalence rates for abnormal performance on global motion, MD form, and D_{\max} in the 12 amblyopic children with motion deficits, respectively, were: 25%, 42%, and 50%. Of those with deficits in D_{\max} , 33% had depressed D_{\max} , and 67% had elevated D_{\max} .

We subdivided the amblyopic subjects into categories of non-binocular (worse than 500 s of arc stereoacuity), and binocular (better than or equal to 500 s of arc stereoacuity) (McKee et al., 2003). Of the 9 non-binocular amblyopic subjects, 5 (56%) had abnormal performance on at least 1 task. When we looked at the 10 amblyopic subjects with moderate-to-severe depth of amblyopia (decimal VA in the amblyopic eye $< .50$), 8 (80%) had abnormal performance on at least 1 task. Of the 5 amblyopic subjects with no binocularity and moderate-to-severe depth of amblyopia, 3 (60%) had abnormal performance on at least 1 task.

3.2. Multivariate analysis of variance

Before analyzing the data with multivariate analysis of variance (MANOVA), the distributions of scores were normalized with log transformation of MD form scores and D_{\max} scores, and square root transformation of global motion scores. Different transformations were applied because the distributions for untransformed data differed in skewness and kurtosis. The transformations effectively reduced the influence of outliers and ensured that the assumption of normality for the MANOVA was not violated (Tabachnick & Fidell, 1989). Also, we tested that the MANOVA assumption of multicollinearity and singularity was met which assumes correlations among dependent variables to be low and ensures that the three dependent variables we are testing represent non-redundant aspects of motion perception (Tabachnick & Fidell, 1989). In theory, as R^2 determined with regression analysis approaches the value 0.99 for any dependent variable then that variable represents almost completely redundant information to that provided by other dependent variables. R^2 values were determined using transformed thresholds for MD form ($R^2 = -0.035$), global motion ($R^2 = -0.039$), and D_{\max} ($R^2 = -0.389$) confirming that our variables statistically represent non-redundant or independent aspects of motion perception.

A MANOVA was performed to determine whether amblyopic fellow eyes overall performed differently from normal control eyes on the three different motion tasks. For this group analysis, an age-matched control group consisting of 21 children ranging in age from 4.3 to 11.2 years ($M = 7.0$ years, $SD = 1.9$ years) was randomly selected from the total sample of 75 control subjects to compare to the group of 21 amblyopic children. Of the 21 control children selected, only one 6.5 year-old child showed abnormal performance on global motion. No deficits were noted on MD form, or D_{\max} . Mean decimal VAs in the tested eye and the non-tested eye in this age-matched group of 21 subjects were, respectively, 1.25 ($SD = 0.18$) and 1.17 ($SD = 0.17$).

The Wilks' lambda indicated that performance on the 3 motion tasks differed significantly between control and

fellow eyes ($F(3, 38) = 4.71$, $p < 0.01$). However, when post-hoc univariate F s were calculated with a Bonferroni adjustment (to maintain an overall α level of 0.05) only performance on the MD form task differed significantly between control eyes and amblyopic fellow eyes ($F(1, 40) = 13.55$, $p < 0.01$). The effect size of the group difference in MD form threshold was large ($f = 0.58$) (Cohen, 1992). Univariate F s calculated for transformed D_{\max} ($F(1, 40) = 0.23$, $p = 0.63$) and global motion ($F(1, 40) = 0.01$, $p = 0.91$) indicated insignificant mean differences. Effect sizes for D_{\max} ($f = 0.08$) and global motion ($f = 0.00$) were both small.

The sample size in each of our 3 amblyopic subtypes was too small to allow for means analysis comparing performance between subtypes of amblyopia. Given the high prevalence of deficits in the non-binocular amblyopic subjects and those with moderate-to-severe depth of amblyopia, however, group analyses were performed to determine if significant differences in performance overall existed between binocular ($N = 12$) and non-binocular ($N = 9$) subjects and those with mild ($N = 11$) vs moderate-to-severe ($N = 10$) depth of amblyopia. Hotelling's T^2 statistics were calculated to determine if there were overall group differences in performance on the 3 motion tasks. Performance in the non-binocular vs binocular amblyopic subjects did not significantly differ ($T^2 = 5.450$, $F(3,14) = 1.590$, $p > 0.05$). Similarly, overall performance between the subjects with mild vs moderate-to-severe depth of amblyopia did not significantly differ ($T^2 = 0.61$, $F(3, 17) = 0.18$, $p > 0.05$). Post-hoc comparisons revealed that the binocular subgroup ($M = 34\%$, $SD = 12\%$) tended to perform worse overall in their fellow eyes than the non-binocular subgroup ($M = 16\%$, $SD = 29\%$) on global motion, although this finding was not significant at the Bonferroni adjusted alpha level of 0.017 ($p = 0.04$). The effect size for the global motion threshold difference between the binocular and non-binocular groups was large ($f = 0.86$). All other comparisons were not significant.

3.3. Correlational analysis

LogMAR VA was used instead of decimal VA in all the correlational analyses. It was calculated by taking the log of the reciprocal of decimal VA (which is equal to the minimum angle of resolution or MAR). LogMAR VA is more appropriate to use than decimal VA in statistical analyses (Holladay, 1997). A LogMAR VA difference was calculated for each subject by subtracting the logMAR VA in the fellow/tested eye from the logMAR VA in the amblyopic/non-tested eye.

The only significant correlations related to task performance, across all 42 subjects, were small correlations between D_{\max} thresholds and both LogMAR VA in the amblyopic/non-tested eye ($r = 0.35$, $p = 0.02$) and

LogMAR VA difference ($r = 0.36$, $p = 0.02$). No other significant correlations existed between threshold scores on any of the three tasks and age, logMAR VA in the tested eye, logMAR VA in the non-tested eye, logMAR VA difference between the two eyes, and stereoacuity. Since disparate subgroups within a given population, or groups obtained from two different populations (e.g. amblyopic children and children with normal vision) can tend to have low or high scores overall, combining data from the two has potential to falsely result in a significant correlation. It is important to confirm that the significant relationship found to exist amongst all the subjects is not driven by one group more than the other, and that the relationship can be generalized appropriately to both groups. When analysis was performed across the 21 control subjects and the 21 amblyopic subjects separately, we found that D_{\max} did not significantly correlate to any other variables in either group. In the control group, no significant correlations to task performance were found. In the amblyopic group, a significant correlation was found between global motion thresholds and stereoacuity ($r = -0.44$, $p = 0.05$). This was consistent with the results of Hotelling's T^2 test reported above that found a tendency for amblyopic children in the non-binocular subgroup to perform better in their fellow eye than those in the binocular subgroup on global motion.

There were no significant correlations between the three motion tasks in the amblyopic or the control groups. Correlations between MD form and global motion in the amblyopic and control group were $r = -0.158$ ($p = 0.494$) and $r = -0.195$ ($p = 0.396$) respectively. Corresponding correlations in the two groups for: global motion and D_{\max} were $r = 0.006$ ($p = 0.98$) and $r = 0.164$ ($p = 0.477$); MD form and D_{\max} were $r = -0.189$ ($p = 0.412$) and $r = -0.274$ ($p = 0.23$).

History regarding angle of ocular deviation at diagnosis (in strabismic subjects), extent of occlusion therapy prior to testing, and age at which therapy was initiated were unattainable for a few subjects making correlational analyses difficult for these variables. From the clinical history that was available and ocular deviation at the time of testing, no clear relationship between these factors and motion task performance appeared evident.

4. Discussion

Our findings suggest deficits in motion processing can exist in fellow eyes of children with unilateral amblyopia despite measures of normal visual acuity. A deficit on at least one of the three motion tasks was evident in the fellow eye of 57% of the 21 amblyopic children we tested.

4.1. Motion-defined form

We determined that mean minimum speed thresholds for MD form recognition were significantly higher in the fellow eyes of amblyopic children than in the normal eyes of control children. All children were able to perform the task with 100% accuracy when the stimuli were luminance-defined and when the speed of motion was at the fastest speed of 1.26 deg/s. This ruled out the possibility that deficits arose from an inability to understand the task.

Identification of MD form is based on relative motion and thus, should be possible only if directionally selective neurons in V1 and/or beyond are functional. Steinman et al. (1988) reported a deficit in low velocity discrimination in amblyopic individuals and concluded that the existence of high spatial frequency receptive fields is important for motion perception at slow speeds. Because increased difficulty on this task is directly related to slower speeds (smaller dot displacements while keeping frame duration constant), a general difficulty perceiving slow motion due to spatial limitations in the amblyopic children might have affected performance on this task. Subsequent upstream projections to V5/MT, where local motion signals are integrated, might then receive a degraded motion signal from V1 as a result. However, it is not certain whether the M/dorsal and/or P/ventral pathway projections to V5/MT dominate at threshold for this task since there is evidence to suggest that P-pathway projections to V5/MT exist also (Maunsell, Nealy, & DePriest, 1990) and that motion processing requires normal function of both the M- and the P- pathways (De Valois, Cottaris, Mahon, Elfar, & Wilson, 2000).

Several lines of evidence suggest that although MD form involves motion, it appears to have parallels to the P/ventral pathway (Giaschi, Lang, & Regan, 1997; Parrish et al., 2005; Zwicker et al., 2004). Performance of this MD form task likely relies also on P-pathway projections from V1 to extra-striate form processing areas. Parietotemporal regions are implicated in MD form because white matter lesions in these areas can result in MD form deficits in the absence of VA deficits (Regan, Giaschi, Sharpe, & Hong, 1992). The parallels to the P/ventral pathway are not surprising if both the motion AND form processing aspects of this task are P-pathway mediated.

Interestingly, early unilateral enucleation in humans has been reported to cause deficits in minimum speed thresholds for MD form identification without impairing VA (Steeves, Gonzalez, Gallie, & Steinbach, 2002) suggesting, as our findings do, that normal binocular interaction and competition appear to be required for development of normal MD form processing mechanisms.

4.2. Global motion

Newsome and Pare (1988) showed that lesions to V5/MT in monkeys raised coherence thresholds for global motion. Similar studies in humans with lesions to the hypothesized homologue of V5/MT also show global motion deficits (Baker, Hess, & Zihl, 1991; Zihl, Von Cramon, & Mai, 1983). The role of V5/MT in global motion perception has recently been supported with evidence from functional MRI and monkey single-cell recordings (Rees, Friston, & Koch, 2000). Deficits in global motion in amblyopia suggest V5/MT involvement.

In our study, global motion deficits were present but not highly prevalent in the amblyopic group. Of the 21 amblyopic children tested, only three showed abnormal performance. Because the slow speed of 1.26 deg/s used in our stimulus does not fall within the optimal speed range of neurons in MT/V5 (Britten, Shadlen, Newsome, & Movshon, 1993), one could argue that our stimulus does not involve V5/MT to the same extent that a faster speed would. Recent research by Chapman, Hoag, and Giaschi (2004) showed that flicker adaptation or a red background, techniques designed to disrupt the sub-cortical M pathway, elevate coherence thresholds on a global motion task to a similar extent for both fast (8.0 deg/s) and slow (0.935 deg/s) speeds. Their study provides evidence that slow motion still relies on the M-pathway.

Because we did not test for global motion deficits at a faster speed, we can not rule out the possibility that deficits would be more prevalent with a faster stimulus. However, previous studies investigating global motion deficits in the fellow eye of children with amblyopia, have found differing results. A recent study by Simmers, Ledgeway, Hess, and McGraw (2003) identified a global motion deficit in the fellow eye of a few amblyopic adults using both luminance-defined and contrast-defined global motion stimuli. They used a dot speed of 5.7 deg/s. A study by Ellemberg et al. (2002) found that performance on a global motion task (using a fast speed of 18 deg/s) in amblyopic individuals with non-congenital bilateral deprivation or non-congenital unilateral deprivation was not significantly different in *either* eye compared to a control group of normal observers. In contrast, they found significant global motion deficits in both eyes of individuals with congenital bilateral and congenital unilateral deprivation compared to normal observers. The group with congenital bilateral deprivation had worse performance in both eyes than the group with congenital unilateral deprivation. The authors conclude that unequal visual deprivation may not affect binocular neurons mediating global motion perception to the extent that equal visual deprivation does. Although deficits in congenital deprivational

amblyopia are not typically compared to those in anisometropic amblyopia because of differences in etiology and severity (Kushner, 1991; Von Noorden, 1974), the functional deficits between the two groups have been found to be indistinguishable (McKee et al., 2003). From these reports, the extent and speed tuning of global motion deficits in unilateral amblyopia still seem unclear.

Other studies have also claimed that mechanisms involved in processing global motion may not be markedly affected by unequal visual input during development. These studies looked at global motion aftereffects that are also mediated by neurons in area MT. The partial interocular transfer (IOT) of conventional motion aftereffects and complete IOT of global motion aftereffects show that fewer binocular neurons process the former in normal observers (Raymond, 1993). Because stereodeficient adults maintain high IOT of a global motion aftereffect but extremely low or no IOT of a conventional motion aftereffect (McColl & Mitchell, 1998), it has been suggested that binocular neurons in area MT are less vulnerable to unequal monocular visual input than those in area V1 (which presumably mediate stereopsis).

An interesting finding was the significant correlation between global motion and stereoacuity. Amongst the nine stereodeficient children—six with strabismic amblyopia—in the amblyopic group, 100% had normal global motion performance. The mean coherence threshold obtained for the amblyopic subjects with any degree of stereoacuity ($M = 34\%$) was more than double the coherence threshold obtained for the stereodeficient amblyopic subjects ($M = 16\%$). A possible explanation might be related to a two-stage model for processing global motion. The first stage of processing is thought to be contrast and V1 dependent, and the second stage is thought to involve global motion integration at V5/MT. Contrast sensitivity has been found to be better in non-binocular individuals than in binocular individuals (McKee et al., 2003). If amblyopic individuals with residual binocularity have reduced contrast sensitivity in V1, then the input to V5/MT in these individuals will be degraded compared to that in non-binocular individuals. This could result in an elevated coherence threshold.

Our findings seem to suggest that the deficit in global motion perception at slow speeds in the fellow eye of amblyopic children is not robust despite previous studies that have shown abnormal motion perception at slow speeds in amblyopia (Schor & Levi, 1980a, 1980b; Steinman et al., 1988). Because our study did not focus on the amblyopic eye, we can not draw any conclusions regarding performance in the amblyopic eye for slow global motion. Although we can not directly compare performance on this task to the minimum speed threshold

deficits for MD form, our results seem to suggest that abnormal slow motion perception does not account fully for the MD form deficits observed in the fellow eye.

4.3. Maximum displacement

There have been no previous studies of D_{\max} in fellow eyes of amblyopic children. Our findings suggest that abnormally elevated D_{\max} is more prevalent in subjects with a history of anisometropia (i.e. anisometric or aniso-strabismic amblyopia). None of the children with strabismic amblyopia showed elevated thresholds. In fact, strabismic subjects showed a tendency towards smaller D_{\max} . In the strabismic group, one child had D_{\max} less than 1.97 standard deviations from the control group mean for his age (Table 2). Two additional strabismic children had abnormal performance on D_{\max} at a 90% ($z < 1.64$) significance level.

Multiple motion processing mechanisms have been proposed in the literature, however, not all are thought to be involved in determining D_{\max} . The D_{\max} stimulus used in this study is luminance-defined. Therefore, it is a first order stimulus (Cavanagh & Mather, 1989) and is likely processed by short-range (Braddick, 1974), passive (Cavanagh, 1991, 1992), and/or Fourier mechanisms (Chubb & Sperling, 1988).

D_{\max} can be determined by two possible mechanisms. The first involves the spatial frequencies to which Fourier sensors of single motion detectors are tuned (Bischoff & Di Lollo, 1990). The second involves feature matching mechanisms using detectors that extract and track specific attributes of a moving object in space over time (Morgan, 1992). Snowden and Braddick (1990) suggest that both Fourier sensors and feature matching are involved in the short-range process and that D_{\max} is thought to define the upper displacement limit of the short-range process (Braddick, 1974; Snowden & Braddick, 1990). Furthermore, D_{\max} can be increased by filtering out high spatial frequencies from the stimuli (Chang & Julesz, 1983, 1985) because motion signals from high spatial frequency receptive fields may mask the motion signal carried by low spatial frequency filters.

Differences in D_{\max} for anisometric and strabismic amblyopia may be explained by looking at the neural deficits underlying the two subtypes of amblyopia (Kiorpes & McKee, 1999 (review)) in the context of the mechanisms determining D_{\max} . In anisometric amblyopia, the cortex comprises fewer high spatial frequency receptive fields and more medium and low spatial frequency receptive fields than normal. The number of cortical receptive fields remains normal but the spatial frequency to which they are tuned is shifted towards lower frequencies. If Fourier sensors are also tuned to lower spatial frequencies, this could result in a larger D_{\max} . Alternatively, there could be less of a masking effect in

anisometric amblyopia because of the relative loss of high spatial frequency receptive fields.

In strabismic amblyopia, two theories have been proposed to account for deficits in form vision: undersampling (Levi & Klein, 1985) and neural disarray (Hess, Field, & Watt, 1990). The undersampling theory suggests that there is a reduced quantity of high spatial frequency receptive fields compared to normal. The disarray theory suggests that there is no loss of high spatial frequency receptive fields but that inappropriate connections exist between cortical receptive fields. Our findings seem to support the disarray hypothesis more. If high spatial frequency receptive fields are present to mask the motion signal carried by low spatial frequency receptive fields, then D_{\max} is more likely to be similar to or smaller than that in control subjects. This receptive field arrangement might also provide some insight into our global motion results. Abnormal global motion was not identified in any subjects with strabismic amblyopia. It is possible that subjects that do not show a loss of high spatial frequency receptive fields in V1 are more capable of processing global motion at the slow 1.26 deg/s stimulus speed used.

4.4. The role of eye movements

Bedell and Flom (1985) reported oculomotor abnormalities in strabismic individuals with amblyopia. While it is possible that abnormal eye movements and fixation in fellow eyes could contribute to the observed motion perception deficits in this study, this seems unlikely to be the case. Firstly, none of our subjects had eccentric fixation. Secondly, horizontal eye movements (nasal drifts or asymmetric pursuits) interact with a vertically moving dot in such a manner that it appears to move with a slanted trajectory (Becklen, Wallach, & Nitzberg, 1984). Increasing stimulus speed or the speed of the horizontal pursuit eye movement increases the perceived slant, which is displaced in the direction of the pursuit (Souman, Wertheim, & Hooge, 2003). In this study, perceived slant would be influenced by stimulus speed more than pursuit eye movement speed and it would be most marked for vertically moving stimuli presented at fast speeds.

Abnormal eye movements likely do not explain the MD form deficit because the threshold measured was based on slow speeds (i.e. minimum speed threshold) and all children were able to perform the task at the fastest speed. In the MD form task, perceived slant of upward and downward relative motion cues would decrease the visibility of the form by reducing the overall relative motion signal. In other words, both the motion in the figure and background would appear to share similar horizontal velocity components making the task most difficult at the fastest speed when the slant is most

pronounced, which was not our finding. We found that the fastest speed was also the easiest speed.

It is also unlikely that eye movement asymmetries affect performance on global motion. The global motion task was presented at a constant speed which was equal to the fastest speed used in the MD form task. Perceived slant of the coherently moving dots would make vertical direction discrimination on a global motion task more difficult especially at low coherence levels. Contrary to this, we found that all six strabismic children tested performed normally on the global motion task.

As dot displacement increases in the D_{\max} task, stimulus speed also increases, and the task becomes more difficult. Theoretically, if children perceived more slant as dot displacement increased then vertical direction discrimination would be even more difficult and performance would be expected to be worse. This might have contributed to the trend of depressed D_{\max} scores observed in a few strabismic participants but this finding was neither consistent nor highly prevalent amongst these children.

4.5. Clinical implications

It can not be excluded that complete visual deprivation of the fellow eye induced by occlusion therapy may contribute to motion perception deficits. The extent of occlusion (i.e. time that the fellow eye is visually deprived) varies depending on the VA loss in the amblyopic eye at the time of diagnosis, compliance with and the efficacy of occlusion therapy. A mildly amblyopic eye measured at the time of the study could have been a child with severe amblyopia and successful results from occlusion therapy or could be a child with mild amblyopia that received minimal occlusion therapy. Contrary to this, it is feasible that motion deficits on tasks that are mediated by highly binocular cortical areas could improve with occlusion therapy. Leguire et al. (1990) found this to be the case for contrast sensitivity deficits in the fellow eye. Because of developmental differences between M/dorsal and P/ventral pathways (Atkinson, 1992; Parrish et al., 2005), the critical period during which improvement is possible for global motion, D_{\max} , MD form, and VA may not be simultaneous.

4.6. Conclusion

Motion perception deficits on three uncorrelated motion tasks in the fellow eyes of some amblyopic children imply that neural deficits underlying amblyopia may involve binocular mechanisms within the M/dorsal pathway that likely involve higher level processing in extrastriate cortical areas. Although we can not directly rule out abnormal low level input from V1 to higher cortical areas, our evidence suggests dysfunction of the extrastriate cortical area V5/MT to some extent in unilateral

amblyopia of strabismic, anisometric, and aniso-strabismic origins. The presence of motion processing deficits in the fellow eye may be dependent on factors that include etiology and degree of residual binocularity.

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