

# Interocular Transfer: The Dichoptic Flash-Lag Effect in Controls and Amblyopes

Xi Wang,<sup>1,2</sup> Yutong Song,<sup>1,2</sup> Meng Liao,<sup>1,2</sup> Robert F. Hess,<sup>3</sup> Longqian Liu,<sup>1,2</sup> and Alexandre Reynaud<sup>3</sup>

<sup>1</sup>Department of Ophthalmology, West China Hospital, Sichuan University, Chengdu, Sichuan, China

<sup>2</sup>Laboratory of Optometry and Vision Sciences, West China Hospital, Sichuan University, Chengdu, Sichuan, China

<sup>3</sup>McGill Vision Research Unit, Department of Ophthalmology & Visual Sciences, McGill University, Montreal, Quebec, Canada

Correspondence: Alexandre Reynaud, McGill Vision Research Unit, Department of Ophthalmology and Visual Sciences, Montreal General Hospital, Montreal, Quebec H3G 1A4, Canada;

[alexandre.reynaud@mcgill.ca](mailto:alexandre.reynaud@mcgill.ca)

Longqian Liu, Department of Ophthalmology, West China Hospital, Sichuan University, 37 Guoxue Xiang, Chengdu, Sichuan 610041, China;

[b.q15651@hotmail.com](mailto:b.q15651@hotmail.com)

**Received:** April 12, 2022

**Accepted:** July 7, 2022

**Published:** August 2, 2022

Citation: Wang X, Song Y, Liao M, Hess RF, Liu L, Reynaud A. Interocular transfer: The dichoptic flash-lag effect in controls and amblyopes. *Invest Ophthalmol Vis Sci.* 2022;63(9):2. <https://doi.org/10.1167/iovs.63.9.2>

**PURPOSE.** The mammalian brain can take into account the neural delays in visual information transmission from the retina to the cortex when accurately localizing the instantaneous position of moving objects by motion extrapolation. In this study, we wanted to investigate whether such extrapolation mechanism operates in a comparable fashion between the eyes in normally sighted and amblyopic observers.

**METHODS.** To measure interocular extrapolation, we adapted a dichoptic version of the flash-lag effect (FLE) paradigm, in which a flashed bar is perceived to lag behind a moving bar when their two positions are physically aligned. Twelve adult subjects with amblyopia and 12 healthy controls participated in the experiment. We measured the FLE magnitude of the subjects under binocular, monocular, and dichoptic conditions.

**RESULTS.** In controls, the FLE magnitude of binocular condition was significantly smaller than that of monocular conditions ( $P \leq 0.023$ ), but there was no difference between monocular and dichoptic conditions. Subject with amblyopia exhibited a smaller FLE magnitude in the dichoptic condition when the moving bar was presented to the amblyopic eye and the flash to the fellow eye (DA condition) compared to the opposite way around (DF condition), consistent with a delay in the processing of the amblyopic eye ( $P = 0.041$ ).

**CONCLUSIONS.** Our observations confirm that trajectory extrapolation mechanisms transfer between the eyes of normal observers. However, such transfer may be impaired in amblyopia. The smaller FLE magnitude in DA compared to DF in patients with amblyopia could be due to an interocular delay in the amblyopic visual system. The observation that normal controls present a smaller FLE in binocular conditions raises the question whether a larger FLE is or is not an indicator of better motion processing and extrapolation.

Keywords: amblyopia, flash-lag effect, motion extrapolation

Amblyopia is a neurodevelopmental disorder of the visual cortex that is initiated by disruptions of visual information processing (e.g. strabismus or anisometropia) during the early critical period of maturation. Although amblyopia is primarily thought of as a disorder of spatial vision,<sup>1-6</sup> patients with amblyopia also exhibit deficits in temporal visual processing. It has been suggested that the amblyopic eye (AE) is associated with poorer temporal resolution,<sup>7</sup> lower critical flicker frequency,<sup>8</sup> and higher temporal synchrony thresholds.<sup>9</sup> As consequences of these monocular temporal deficits, accumulating evidence<sup>9,10</sup> indicates that patients with amblyopia show abnormal binocular functions in temporal processing as well. Typically, patients with amblyopia may observe a spontaneous Pulfrich phenomenon<sup>11-13</sup> – the illusory percept of an object moving in depth whereas it is moving in plane – which could be caused by an innate interocular delay.<sup>14</sup> But more surprisingly, the temporal vision in the fellow eye (FE), which is meant to have normal visual acuity when optically corrected,

may also be affected. St. John reported that the FE in strabismic amblyopia showed impaired perception of temporal order.<sup>15</sup> Huang et al. found that the FE presents a deficit in synchrony processing, although it was still slightly better than the AE.<sup>16</sup>

In visual perception, intrinsic neural delays are incurred by the neural transmission and sensory integration time from the retina to the cortex. This creates a potential challenge for the visual system to accurately localize a time-varying moving object because its position signal arriving at the cortical processing stage would be already outdated. One way the brain might overcome this is through motion extrapolation: using the past trajectory of a moving object to predict its future position.<sup>17-19</sup> One potential neural mechanism subserving motion extrapolation could be that the moving object would be processed faster due to facilitatory neural activity on its motion trajectory path within the primary visual cortex,<sup>20-22</sup> which could provide an explanation for a range of motion-induced illusions. For example,

the flash-lag effect (FLE), in which a flashed bar is perceived to lag behind a moving bar when their two positions are physically aligned. Or the flash-grab effect (FGE), the illusory mislocalization of a briefly flashed object in the direction of a reversing moving background. Actually, by using the FLE and the FGE, we previously investigated how the amblyopic visual system implements motion extrapolation within the monocular visual processing stage.<sup>23,24</sup> In addition, we also found that patients with amblyopia exhibit a smaller FLE and a larger FGE both in their AE and FE. Such reduced FLE would characterize less anticipation of the position of the moving object along its trajectory.<sup>23</sup> Hence, these findings suggest that the amblyopic visual system suffers from impairments in motion extrapolation computations that could be done in V1.<sup>20,21</sup>

In most studies, it has been usual to study motion extrapolation in the monocular or binocular pathways of the human visual system. Few studies have investigated whether motion processing can transfer between the eyes.<sup>25</sup> In particular, whether the extrapolation mechanisms could operate between the two eyes of normal observers remains unknown. Moreover, whether patients with amblyopia, for whom there is evidence of an interocular delay,<sup>12,13</sup> would have specific deficits in such interocular transfer has not been addressed. In the present study, we developed a dichoptic FLE paradigm to assess the motion extrapolation in controls and patients with unilateral amblyopia under monocular, binocular, and dichoptic viewing conditions. We set out to address two issues: (1) whether the extrapolation mechanism can transfer between the eyes in normal sighted observers; and (2) whether the interocular delay in amblyopia could lead to a longer or shorter FLE in dichoptic conditions, therefore disrupting extrapolation processes. We analyzed the amplitude of the FLE and the slope of the

psychometric function as it would be indicative of the position uncertainty in space and time.

## METHODS

### Participants

Twelve adults with amblyopia (average age = 25.33 years old, range = 18–38 years old) and 12 controls (average age = 25.25 years old, range = 22–30 years old) with normal or corrected-to-normal vision participated in this study. Amblyopia was defined as a minimum of a two logMAR line difference in best-corrected visual acuity between the eyes. The clinical characteristics of amblyopic subjects are listed in the Table. The dominant eyes of the control subjects were determined by the Porta test. Participants, except the first author, were all naïve to the purpose of the study. Written informed consent was obtained from each participant. The study followed the tenets of the Declaration of Helsinki and was approved by the Ethics Committee of West China Hospital of Sichuan University.

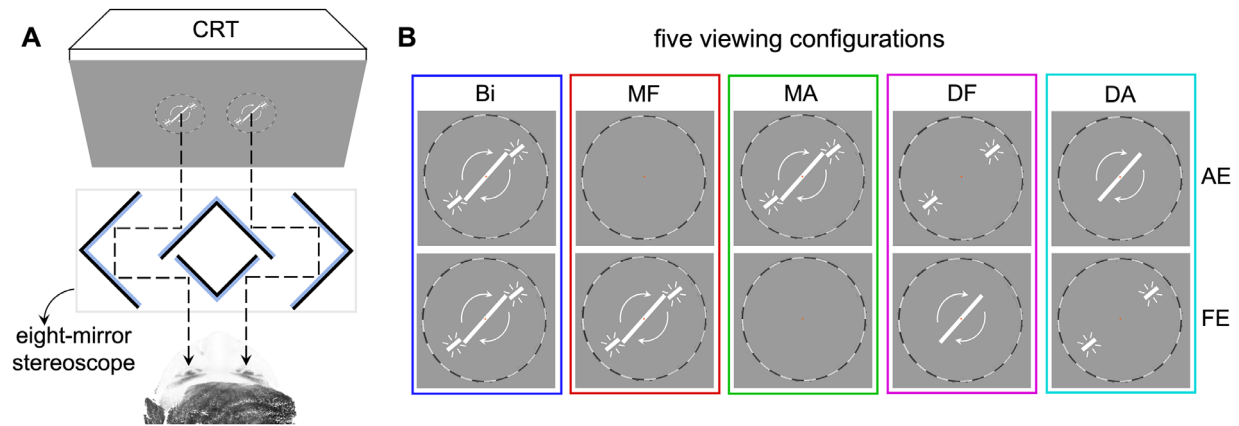
### Apparatus

Stimuli were programmed with Matlab R2018b (the MathWorks) with the PsychToolBox extensions 3.0.9 on a MacBook Pro. All stimuli were displayed on a gamma-corrected CRT monitor (SONY SUN GDM-5510, 21 inches) with a mean luminance of 36 cd/m<sup>2</sup>. The resolution of the monitor was set at 1280 × 1024 pixels @ 100 HZ refresh rate. Participants fixed their head on a chinrest and viewed the display through an eight-mirror custom Wheatstone stereoscope in order to present the images dichoptically to the left and right eyes (Fig. 1A). The effective viewing distance along

TABLE. Clinical Details of Amblyopic Subjects

Subject	Age/Sex	Type	Eye	Refraction	VA (LogMAR)	Squint (PD)	Stereoacuity arc Seconds	History
A1	32/M	Aniso	FE (OD)	+2.50	0	∅	200	Detected at 10 y old, no treatment
			AE (OS)	+4.25/−0.50 × 70 degrees	0.4			
A2	21/F	Mixed	FE (OD)	Pl	−0.2	ET 8	NA	Detected at 2 y old, patched for 6 y
			AE (OS)	+1.25/+0.25 × 85 degrees	0.1			
A3	22/F	Strab	FE (OS)	−3.00/−0.50 × 110 degrees	0	ET 30	NA	Detected at 10 y old, patched for 2 mo
			AE (OD)	−5.00	1.0			
A4	28/F	Aniso	FE (OD)	−2.25	0	∅	NA	Detected at 11 y old, patched for 1 mo
			AE (OS)	+3.75/−1.00 × 150 degrees	0.4			
A5	23/M	Aniso	FE (OS)	−2.50/−0.75 × 170 degrees	−0.1	∅	200	Detected at 8 y old, patched for 4 y
			AE (OD)	−1.75	0.1			
A6	19/M	Aniso	FE (OS)	−1.50	0	∅	NA	Detected at 15 y old, patched for 2 mo
			AE (OD)	+2.75	0.2			
A7	35/F	Mixed	FE (OS)	+0.25 × 100 degrees	0	ET 20	NA	Detected at 5 y old, patched for 2 y
			AE (OD)	+3.50/−1.75 × 135 degrees	0.2			
A8	19/M	Aniso	FE (OS)	−0.50 × 180 degrees	0	∅	NA	Detected at 5 y old, patched for 1 y
			AE (OD)	+3.50/+1.75 × 85 degrees	1.0			
A9	23/F	Mixed	FE (OD)	−0.50	0	XT 20, R/L 10	NA	Detected at 12 y old, no treatment
			AE (OS)	+5.75/−2.50 × 15 degrees	0.2			
A10	18/M	Aniso	FE (OD)	−5.25/−0.50 × 165 degrees	0	∅	400	Detected at 15 y old, no treatment
			AE (OS)	+3.00/+0.75 × 105 degrees	0.7			
A11	26/F	Aniso	FE (OD)	−1.75/−0.50 × 50 degrees	−0.1	∅	NA	Detected at 10 y old, patched for 2 y
			AE (OS)	+6.50/−2.50 × 10 degrees	0.7			
A12	38/M	Aniso	FE (OD)	+4.00	0	∅	NA	Detected at 7 y old, no treatment
			AE (OS)	+6.00/+1.75 × 115 degrees	0.4			

VA, visual acuity; FE, fellow eye; AE, amblyopic eye; Strab, strabismus; Aniso, anisometropia; EX, exotropia; ET, esotropia; PD, prism diopters; pl, plano; y, years; mo, months.



**FIGURE 1.** (A) Apparatus arrangement. (B) Illustration of the experimental stimuli. There were five viewing configurations: binocular viewing condition, where the rotating bar and flashed bars were presented to both eyes (Bi); monocular viewing conditions, where the rotating bar and flashed bars were presented to the fellow eye (MF) or the amblyopic eye (MA); dichoptic viewing conditions, where the rotating bar was presented to the fellow eye and the flashed bars were presented to the amblyopic eye (DF) or the opposite way (DA). FE, fellow eye; AE, amblyopic eye.

the light path was 51 cm. To achieve eye alignment, subjects were asked to align two vertical line segments through the stereoscope, a green one seen by the left eye and a red one seen by the right eye. The coordinates of the two segments were then used to present the stimuli to the right and left eyes. All the experiments were run in a dark room.

### Stimuli and Procedure

The rotating FLE stimuli consisted of a rotating bar (4 degrees  $\times$  0.2 degrees) and two flashed bars (1 degree  $\times$  0.2 degrees). Bars were white, and were presented on a mean grey background. The rotating bar, starting at a random position (0, 30, 60, or 90 degrees), moved with a speed of 180 degrees/s for 1000 ms. About half-way through the motion rotation, 2 flashed bars were presented for 10 ms at symmetrically opposite points with an eccentricity of 2 degrees. The flashed bars were presented at varied angular distance from the rotating bar (–20, –10, 0, 5, 10, 15, 20, 25, 30, and 40 degrees). In a run, each angle was tested with 20 repetitions. All stimuli were presented within a binocular circle frame to help binocular fusion (radius = 3.4 degrees). A binocular orange fixation point was presented at the center of the frame throughout the experiment. In each trial, the subject was asked to stare at the fixation point, and judge whether the flash was presented ahead or behind of the rotating bar when the flash occurred by using a keyboard.

We tested the FLE of the participants in five configurations (Fig. 1B): (1) Bi: binocular viewing, where the rotating and flashed bars were presented to both eyes; (2) MF: monocular fellow eye viewing (controls: monocular dominant eye [DE] viewing), where the rotating and flashed bars were presented to the FE or DE; (3) MA: monocular amblyopic eye viewing (controls: monocular nondominant eye [NDE] viewing), where the rotating and flashed bars were presented to the AE or NDE; (4) DF: dichoptic fellow eye, where the rotating bar was presented to the FE and the flashed bars were presented to the AE; and (5) DA: dichoptic amblyopic eye, where the rotating bar was presented to the AE and the flashed bars were presented to the FE. One direction of rotation was tested in each block: clockwise or coun-

terclockwise resulting in a total of 10 conditions (5 viewings  $\times$  2 directions). The order of the conditions was randomized.

### Data Analysis

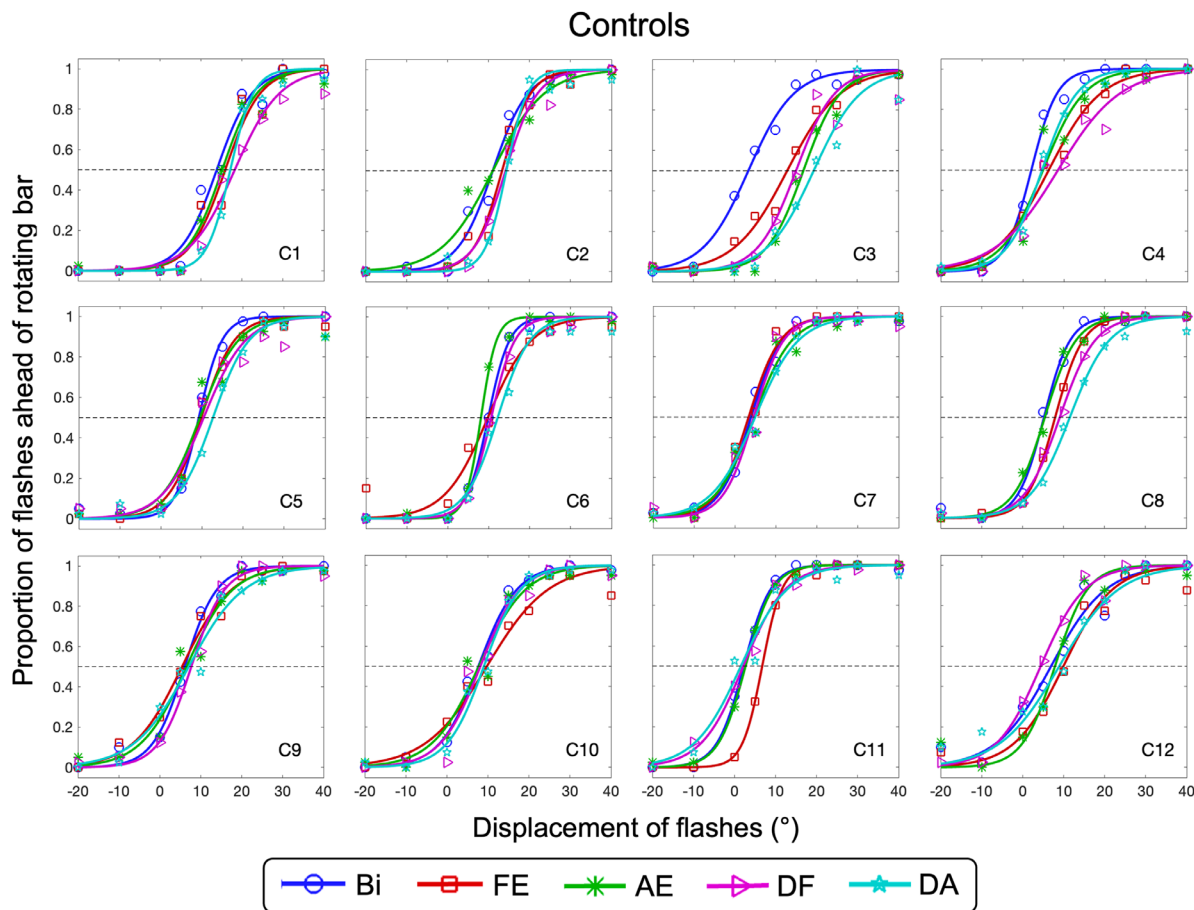
The data was analyzed with Matlab R2018b (the MathWorks). Participant's psychometric function describing the proportion of “ahead” response at each spatial point was fitted with a logistic function constrained between zero and one. The estimated midpoint of the logistic function characterized the point of subjective equality (PSE), at which the subject would give 50% “ahead” response and 50% “behind” response, indicating the perceived alignment between the rotating and flashed bars. Significant PSE shift from zero would then characterize the FLE magnitude.

All statistical analyses were conducted by using IBM SPSS Statistics, version 26.0 (Armonk, NY, USA). FLE magnitude was compared between and within groups by using analysis of variance (ANOVA). For the post hoc analysis, two-sided Mann–Whitney *U* tests were used for comparison of the FLE magnitude difference between the control and amblyopic groups, whereas two-sided Wilcoxon signed rank tests were used for within group comparisons. The level of significance was established at  $P < 0.05$ .

### RESULTS

The individuals' psychometric functions of controls and amblyopes for the 5 viewing conditions are plotted in Figures 2 and 3, respectively. Logistic function fits are accurate in all conditions in all subjects ( $R^2 = 0.963$ ). In addition, the FLE magnitude, characterized by the PSE difference from zero, was significant across all viewing conditions for both the control ( $F_{1,110} = 247.2$ ,  $P < 0.001$ ) and amblyopic ( $F_{1,110} = 36.4$ ,  $P < 0.001$ ) groups. This is an indicator that most participants experienced a flash-lag illusion in all testing conditions.

For controls (see Fig. 2) it looks like the psychometric functions of the binocular viewing condition are shifted to the left compared to the monocular and dichoptic viewing



**FIGURE 2.** The psychometric functions for each viewing configuration for control subject. Individuals' data are displayed in each separate panel. Distinct colored symbols represent the data for the five viewing configurations which are illustrated in Figure 1. Blue circle, red square, green asterisk, pink triangle, and turquoise pentastar represent Bi, FE, AE, DF, and DA configurations, respectively. Continuous lines represent logistic function fits.

conditions, particularly for subject C3. In addition, it appears that the slopes of the psychometric functions of the amblyopic group (see Fig. 3) are shallower than that of controls, particularly in the dichoptic conditions. To quantify better these observations, we then analyzed the estimated PSEs and slopes in each group.

### FLE Under Binocular and Monocular Viewings

In Figure 4A, we illustrate the mean FLE magnitude in binocular and monocular viewing conditions for the control and amblyopic groups. It clearly appears that the subjects with amblyopia present an overall FLE that is shorter by approximately 20 ms compared to controls ( $F_{1,66} = 9.89$ ,  $P = 0.002$ ), whereas the interaction of group and viewing conditions was not significant ( $F_{2,66} = 0.31$ ,  $P = 0.73$ ). The post hoc analysis showed that the mean FLE magnitude of amblyopes ( $5.06 \pm 1.53$  degrees, mean  $\pm$  standard error) is significantly smaller than that of controls ( $9.26 \pm 1.04$  degrees) under MF configuration ( $P = 0.038$ ).

To compare the mean FLE magnitudes among the different viewing conditions, we performed 1-way ANOVA with conditions (3 levels) for each group. In the control group, the effect of viewing condition was significant ( $F_{2,22} = 4.11$ ,  $P = 0.03$ ). The results of post hoc analyses show that the binocular viewing condition demonstrated the smallest FLE magni-

tude ( $6.79 \pm 1.07$  degrees) compared to the two monocular viewing conditions (MF:  $9.26 \pm 1.04$  degrees and MA:  $8.37 \pm 1.22$  degrees,  $P \leq 0.023$ ). These effects were still significant even when removing outlier subject C3. In the amblyopic group, however, the differences in FLE magnitude among the binocular and monocular viewings were not significant ( $F_{2,22} = 0.17$ ,  $P = 0.841$ ).

In Figure 4B, we plotted the slope of the fitted psychometric function under binocular and monocular viewing configurations. There was no significant difference in slope among the viewing conditions between groups ( $F_{1,66} = 2.29$ ,  $P = 0.135$ ). Compared to the controls, the slope was shallower in subjects with amblyopia only under the MA viewing condition ( $P = 0.0496$ ).

### FLE Under Dichoptic Viewing

Additionally, we wanted to investigate whether the FLE can transfer between the eyes using a dichoptic protocol in which the rotating bar and the flashed bars were presented to different eyes (Fig. 5). In the DF condition, the rotating bar was presented to the fellow (or dominant) eye and the flashed bars to the amblyopic (or non-dominant) eye; and in the DA condition, the rotating bar was presented to the amblyopic (or non-dominant) eye and the flashed bars were presented to the fellow (or dominant) eye. Interest-

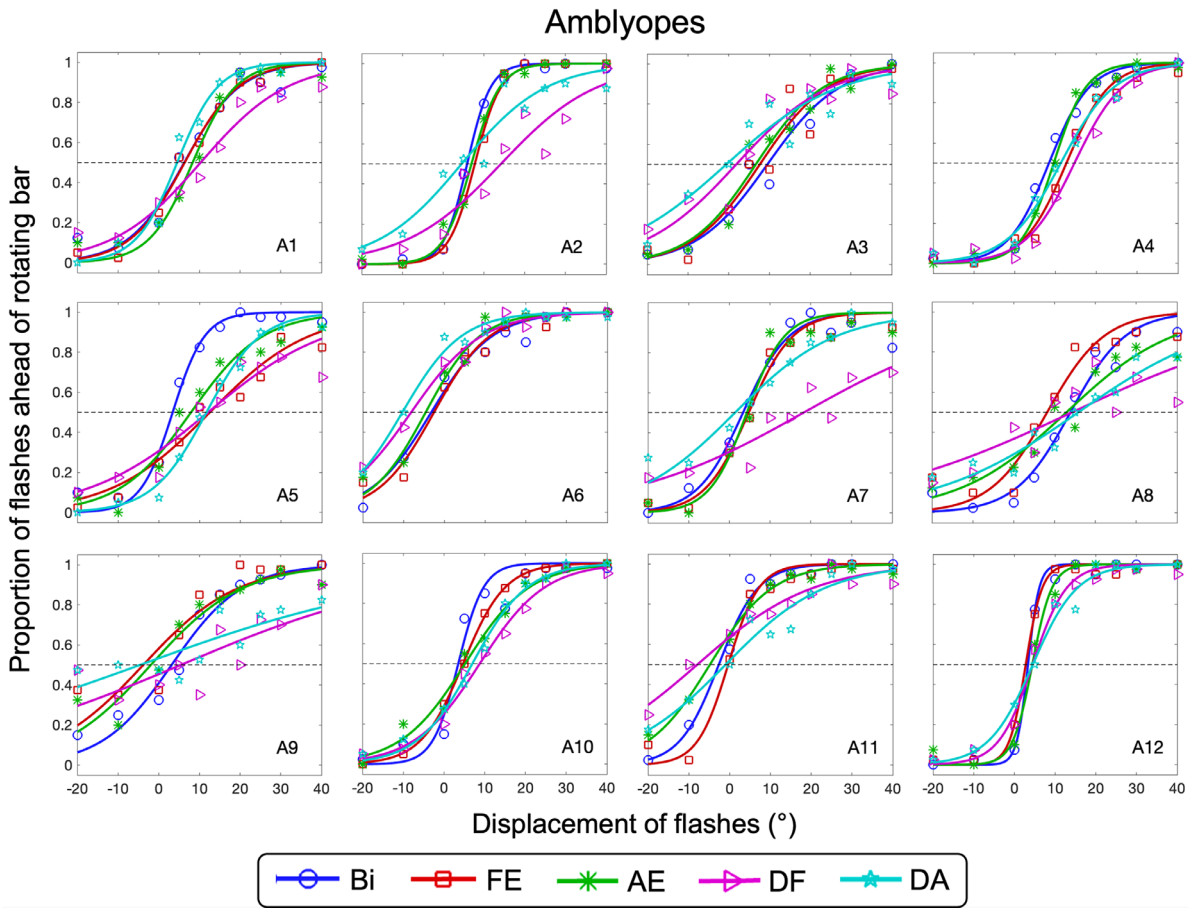


FIGURE 3. The psychometric functions for each viewing configuration for amblyopes. Individuals' data are illustrated in separate panels. Same presentation as in Figure 2.

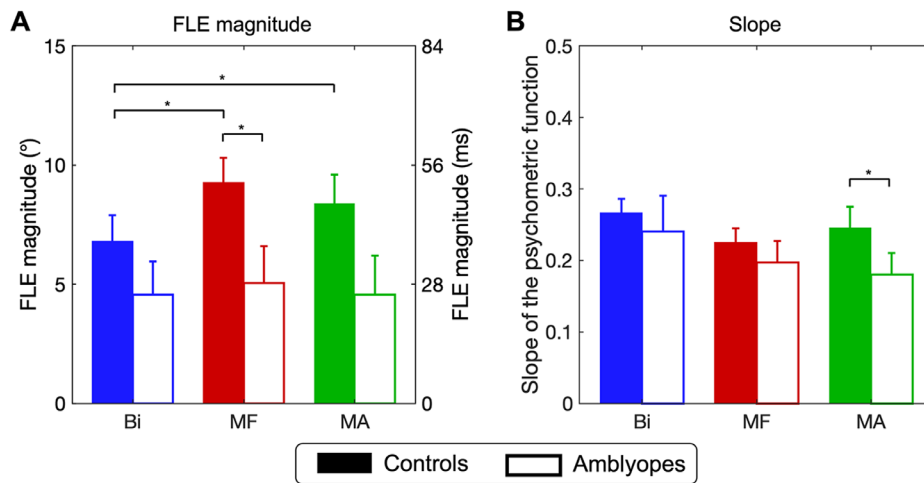
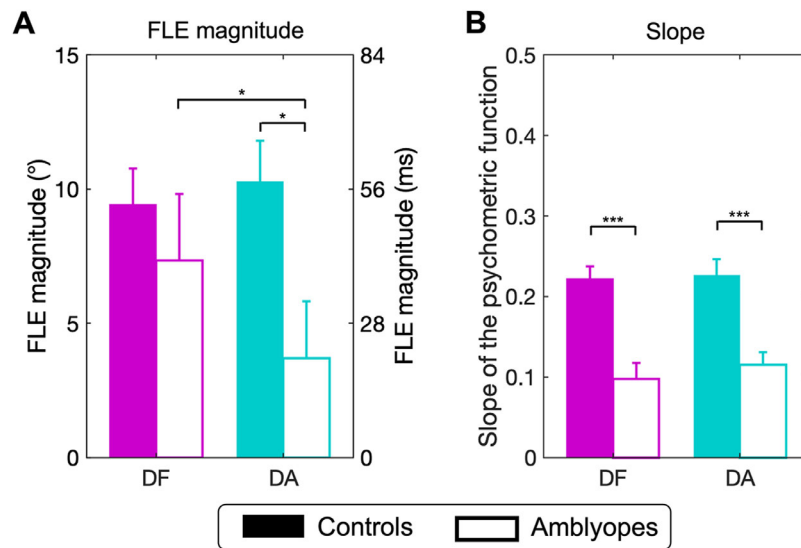


FIGURE 4. The mean flash-lag effect (FLE) magnitude (A) and slope of the fitted psychometric function (B) of control and amblyopic groups under binocular and monocular viewing. Filled and open bars represent the results of control and amblyopic groups. Error bars represent standard error. \* $P < 0.05$ . In the left panel, the left y-axis indicates the FLE magnitude in space units (degrees), and the right y-axis indicates the FLE magnitude in time units (ms).

ingly, there was no statistical difference between the monocular and dichoptic FLE in both the control ( $F_{1,11} = 3.42, P = 0.091$ ) and amblyopic groups ( $F_{1,11} = 0.44, P = 0.523$ ) which indicates that the FLE seamlessly transfers between the eyes.

To check the difference of FLE magnitude under the dichoptic viewings between the control and amblyopic eyes, we performed a 2-way ANOVA and we found a main effect of group ( $F_{1,44} = 5.07, P = 0.029$ ), but there was no significant



**FIGURE 5.** The mean flash-lag effect (FLE) magnitude (**A**) and the slope of the fitted psychometric function (**B**) of control and amblyopic groups under dichoptic viewing. *Filled* and *open bars* represent the results of control and amblyopic groups. Error bars represent standard error. \* $P < 0.05$ ; \*\*\* $P \leq 0.001$ . In the *left* panel, the left y-axis indicates the FLE magnitude in space units (degrees), and the right y-axis indicates the FLE magnitude in time units (ms).

interaction between group and dichoptic viewing conditions ( $F_{1,44} = 1.38$ ,  $P = 0.247$ ). Compared to controls ( $10.28 \pm 1.53$  degrees), amblyopes exhibited a much smaller mean FLE magnitude in DA configuration ( $3.69 \pm 2.12$  degrees,  $P = 0.013$ ). Moreover, we observed a significant FLE magnitude difference between the DF ( $7.34 \pm 2.48$  degrees) and DA ( $3.69 \pm 2.12$  degrees) configurations for amblyopia ( $P = 0.041$ ; see Fig. 5A). Converting the FLE magnitude into time units (milliseconds, the right hand of the graphs), this makes a difference of approximately 20 ms between the DF and DA configurations in subjects with amblyopia (see Fig. 5A). However, there was no difference in FLE magnitude between these two dichoptic viewing conditions for controls ( $P = 0.209$ ).

Figure 5B shows the slope of the fitted psychometric function. The slope of the amblyopes was significantly shallower than that of controls ( $F_{1,44} = 43.94$ ,  $P < 0.001$ ). This indicates that the performance of subjects with amblyopia was more inconsistent than that of controls under dichoptic viewing.

## DISCUSSION

The FLE is a classic motion-induced illusion which is assumed to derive from motion extrapolation computations in the visual system as a means of overcoming precortical neural delays.<sup>17,19</sup> In the present study, we wanted to investigate whether motion extrapolation can transfer between the eyes in control and amblyopic observers. For this purpose, we assessed the FLE under binocular, monocular, and dichoptic viewing conditions in both groups. We found that (1) amblyopes exhibit a smaller FLE compared to controls, of approximately 20 ms; (2) controls present a reduced FLE magnitude in binocular viewing compared to monocular viewing, which was not observed in amblyopes; and (3) in the amblyopic group, in dichoptic viewing conditions, the FLE magnitude is significantly larger of approximately 20 ms when the moving bar is presented to the FE

and the flashed bars to the AE (DF condition) compared to the opposite way around (DA condition).

First, we found that amblyopes had a smaller FLE magnitude of approximately 20 ms compared to controls under binocular and monocular viewing conditions (see Fig. 4A), suggesting impaired motion extrapolation in the amblyopic visual system, consistent with our previous studies using monocular viewing.<sup>25,24</sup> In addition, we found a shallower slope of the psychometric function in the AE compared with that in the NDE (see Fig. 4B). Such flatter slope could be due to positional uncertainty,<sup>26,27</sup> blurriness,<sup>28,29</sup> increased level of noise,<sup>30,31</sup> or any other deficit in spatial processing of the amblyopic eye. However, it should not impact our estimates of the PSE.<sup>24,32,33</sup>

In controls, we found a smaller FLE magnitude of the binocular compared to the monocular viewing condition (see Fig. 4A). This finding is quite surprising as we assumed that a larger FLE magnitude would indicate better anticipation consistent with binocular vision being usually superior to monocular vision. Indeed, two eyes are known to be better than one for performance on several detection visual tasks. In spatial vision, previous studies reported that binocular summation effects are seen on contrast sensitivity,<sup>34–36</sup> visual acuity,<sup>37</sup> and orientation discrimination threshold.<sup>38</sup> Apart from spatial vision, binocular summation could also benefit the temporal visual processing in the visual system. In animal models, neurons in the primary visual cortex can generate not only stronger but also faster response when they receive bilateral visual inputs, compared to monocular input.<sup>39</sup> Psychophysical studies in humans showed that binocular viewing can enhance reaction time,<sup>40,41</sup> critical flicker frequency threshold,<sup>8</sup> and even audiovisual temporal acuity.<sup>42</sup> Additional evidence from electrophysiological studies in humans reveals that response latency is shorter when using two eyes compared to one.<sup>43</sup> This body of evidence indicates that binocular visual processing is faster than monocular.

If binocular visual processing was just faster than monocular processing, this would just generally speed up the

processing but may not necessarily affect the magnitude of the FLE. Our hypothesis is that only the appearance of the flashes benefit from this binocular advantage because it is actually processed only when it is seen, whereas the moving bar position involves a prediction by brain mechanisms.<sup>17,19,20</sup> Such binocular enhancement, which would be specific to the flashing stimuli, would then lead to a smaller FLE magnitude in the binocular condition compared to the monocular condition in controls. The same mechanism could explain why such an effect was not observed in the amblyopic group as patients with amblyopia present a lack of binocular summation.<sup>8,44,45</sup>

In addition, there was no difference of FLE magnitude between the monocular and dichoptic viewing conditions for both controls and subjects with amblyopia, which suggests that FLE, like serial dependence in visual perception,<sup>46</sup> can transfer between the eyes. However, we observed an interocular difference of approximately 20 ms between the two dichoptic viewing conditions in subjects with amblyopia: the FLE magnitude is significantly larger by approximately 20 ms when the moving bar is presented to the FE and the flashed bars to the AE (DF condition) than the opposite (DA condition). Imaging and behavioral studies have reported the existence of an interocular processing delay between the eyes in amblyopia. Chadnova et al. demonstrated a delay of 20 ms between the FE and AE by using magnetoencephalography.<sup>14</sup> Behaviorally, Reynaud and Hess,<sup>12</sup> and Wu et al.<sup>13</sup> found that patients with amblyopia could experience a spontaneous Pulfrich effect due to their innate interocular delay. These results provided more evidence that the visual processing of FE is faster than the AE when both of the eyes of patients with amblyopia are open. Therefore, in our dichoptic FLE experiment, as the rotating bar and flashes were separately presented to the two eyes, this interocular delay would induce a larger FLE when the flashes are presented to the AE and the rotating bar to the FE (DF condition) than in the opposite condition (DA condition). This finding adds additional evidence that motion extrapolation mechanisms operate at a site that is common for monocular and binocular information.<sup>25</sup> As discussed above, at this binocular site, the FLE magnitude in binocular viewing could be reduced due to a relative faster processing of the flashes. However, in addition, the FLE magnitude difference observed in patients with amblyopia between dichoptic viewing conditions could be explained at this stage as well; because of the delay of the information from the amblyopic eye when it reaches this binocular site.

Notably, patients with amblyopia exhibited shallower slopes of psychometric functions in monocular and dichoptic viewings (see Fig. 4B, Fig. 5B). As we mentioned earlier, the increased spatial noise in the processing of amblyopic visual system could be explained the flatter slope of amblyopic eye monocular viewing condition. However, this may be insufficient to account for the much flatter slopes under dichoptic viewings. It is likely that the spatial noise from amblyopic eye plus the temporal noise from high variability<sup>12,13</sup> of the interocular delay may contribute to the much shallower slope of dichoptic viewings compared to monocular viewing in amblyopia.

In conclusion, our observations confirm that trajectory extrapolation computations transfer between the eyes of normal observers. However, such transfer may be impaired in amblyopia. The smaller FLE magnitude when the flashes are presented to the FE and the rotating bar to the AE

than in the opposite way around in patients with amblyopia could be due to an interocular delay in the amblyopic visual system. Furthermore, the observation that normal controls present a smaller FLE in binocular conditions raises a question whether a larger FLE is or is not an indicator of better motion processing and extrapolation.

### Acknowledgments

Supported by the National Natural Science Foundation of China Grants NSFC 82070996, and Post-Doctor Research Project, West China Hospital, Sichuan University (2020HXBH167).

Disclosure: **X. Wang**, None; **Y. Song**, None; **M. Liao**, None; **R.F. Hess**, None; **L. Liu**, None; **A. Reynaud**, None

### References

- Hess RF, Howell ER. The threshold contrast sensitivity function in strabismic amblyopia: evidence for a two type classification. *Vision Res.* 1977;17(9):1049–1055.
- Levi DM, Harwerth RS. Spatio-temporal interactions in anisometropic and strabismic amblyopia. *Invest Ophthalmol Vis Sci.* 1977;16(1):90–95.
- Bedell HE, Flom MC, Barbeito R. Spatial aberrations and acuity in strabismus and amblyopia. *Invest Ophthalmol Vis Sci.* 1985;26(7):909–916.
- Birch EE, Swanson WH. Hyperacuity deficits in anisometropic and strabismic amblyopes with known ages of onset. *Vision Res.* 2000;40(9):1035–1040.
- Huang CB, Zhou J, Lu ZL, Feng L, Zhou Y. Binocular combination in anisometropic amblyopia. *J Vis.* 2009;9(3):17, 11–16.
- Husk JS, Hess RF. Global processing of orientation in amblyopia. *Vision Res.* 2013;82:22–30.
- Spang K, Fahle M. Impaired temporal, not just spatial, resolution in amblyopia. *Invest Ophthalmol Vis Sci.* 2009;50(11):5207–5212.
- Eisen-Enosh A, Farah N, Burgansky-Eliash Z, et al. A dichoptic presentation device and a method for measuring binocular temporal function in the visual system. *Exp Eye Res.* 2020;201:108290.
- Tao C, Wu Y, Gong L, et al. Abnormal Monocular and Dichoptic Temporal Synchrony in Adults with Amblyopia. *Invest Ophthalmol Vis Sci.* 2019;60(14):4858–4864.
- Kosovicheva A, Ferreira A, Vera-Diaz FA, Bex PJ. Effects of temporal frequency on binocular deficits in amblyopia. *Vision Res.* 2019;163:52–62.
- Tredici TD, von Noorden GK. The Pulfrich effect in anisometropic amblyopia and strabismus. *Am J Ophthalmol.* 1984;98(4):499–503.
- Reynaud A, Hess R. An Unexpected Spontaneous Motion-In-Depth Pulfrich Phenomenon in Amblyopia. *Vision.* 2019;3:54.
- Wu Y, Reynaud A, Tao C, et al. Two Patterns of Interocular Delay Revealed by Spontaneous Motion-in-Depth Pulfrich Phenomenon in Amblyopes with Stereopsis. *Invest Ophthalmol Vis Sci.* 2020;61(3):22.
- Chadnova E, Reynaud A, Clavagnier S, Hess RF. Latent binocular function in amblyopia. *Vis Res.* 2017;140:73–80.
- St John R. Judgements of visual precedence by strabismics. *Behav Brain Res.* 1998;90(2):167–174.
- Huang PC, Li J, Deng D, Yu M, Hess RF. Temporal synchrony deficits in amblyopia. *Invest Ophthalmol Vis Sci.* 2012;53(13):8325–8332.
- Nijhawan R. Motion extrapolation in catching. *Nature.* 1994;370(6487):256–257.

18. Blom T, Liang Q, Hogendoorn H. When predictions fail: Correction for extrapolation in the flash-grab effect. *J Vis.* 2019;19:3.
19. Hogendoorn H. Motion Extrapolation in Visual Processing: Lessons from 25 Years of Flash-Lag Debate. *J Neurosci.* 2020;40(30):5698–5705.
20. Jancke D, Erhagen W, Schonher G, Dinse HR. Shorter latencies for motion trajectories than for flashes in population responses of cat primary visual cortex. *J Physiol.* 2004;556(Pt 3):971–982.
21. Subramaniyan M, Ecker AS, Patel SS, et al. Faster processing of moving compared with flashed bars in awake macaque V1 provides a neural correlate of the flash lag illusion. *J Neurophysiol.* 2018;120(5):2430–2452.
22. Ekman M, Kok P, de Lange FP. Time-compressed preplay of anticipated events in human primary visual cortex. *Nature Commun.* 2017;8:15276.
23. Wang X, Reynaud A, Hess RF. The Flash-lag Effect in Amblyopia. *Invest Ophthalmol Vis Sci.* 2021;62(2):23–23.
24. Wang X, Liao M, Song Y, Liu L, Reynaud A. Delayed Correction for Extrapolation in Amblyopia. *Invest Ophthalmol Vis Sci.* 2021;62(15):20.
25. van Heusden E, Harris A, Garrido M, Hogendoorn H. Predictive coding of visual motion in both monocular and binocular human visual processing. *J Vis.* 2019;19:3.
26. Watt RJ, Hess RF. Spatial information and uncertainty in anisometric amblyopia. *Vision Res.* 1987;27(4):661–674.
27. Wang H, Levi DM, Klein SA. Spatial uncertainty and sampling efficiency in amblyopic position acuity. *Vision Res.* 1998;38(9):1239–1251.
28. Levi DM, Klein SA. Equivalent intrinsic blur in amblyopia. *Vision Res.* 1990;30(12):1995–2022.
29. Simmers AJ, Bex PJ, Hess RF. Perceived blur in amblyopia. *Invest Ophthalmol Vis Sci.* 2003;44(3):1395–1400.
30. Levi DM, Klein SA. Noise provides some new signals about the spatial vision of amblyopes. *J Neurosci.* 2003;23(7):2522–2526.
31. Felius J, Wang YZ, Birch EE. The accuracy of the amblyopia treatment study visual acuity testing protocol. *J AAPOS.* 2003;7(6):406–412.
32. Richards MD, Goltz HC, Wong AMF. Optimal Audiovisual Integration in the Ventriloquism Effect But Pervasive Deficits in Unisensory Spatial Localization in Amblyopia. *Invest Ophthalmol Vis Sci.* 2018;59(1):122–131.
33. Ernst MO, Banks MS. Humans integrate visual and haptic information in a statistically optimal fashion. *Nature.* 2002;415(6870):429–433.
34. Legge GE. Binocular contrast summation—I. Detection and discrimination. *Vision Res.* 1984;24(4):373–383.
35. Meese TS, Georgeson MA, Baker DH. Binocular contrast vision at and above threshold. *J Vis.* 2006;6(11):1224–1243.
36. Baker DH, Lygo FA, Meese TS, Georgeson MA. Binocular summation revisited: Beyond  $\sqrt{2}$ . *Psychol Bull.* 2018;144(11):1186–1199.
37. Cagenello R, Arditi A, Halpern DL. Binocular enhancement of visual acuity. *J Opt Soc Am A Opt Image Sci Vis.* 1993;10(8):1841–1848.
38. Bearse MA, Jr., Freeman RD. Binocular summation in orientation discrimination depends on stimulus contrast and duration. *Vision Res.* 1994;34(1):19–29.
39. Minke B, Auerbach E. Latencies and correlation in single units and visual evoked potentials in the cat striate cortex following monocular and binocular stimulations. *Exp Brain Res.* 1972;14(4):409–422.
40. Blake R, Martens W, Di Gianfilippo A. Reaction time as a measure of binocular interaction in human vision. *Invest Ophthalmol Vis Sci.* 1980;19(8):930–941.
41. Wakayama A, Matsumoto C, Ohmure K, Inase M, Shimomura Y. Influence of target size and eccentricity on binocular summation of reaction time in kinetic perimetry. *Vision Res.* 2011;51(1):174–178.
42. Opoku-Baah C, Wallace MT. Binocular Enhancement of Multisensory Temporal Perception. *Invest Ophthalmol Vis Sci.* 2021;62(3):7.
43. Richard B, Chadnova E, Baker DH. Binocular vision adaptively suppresses delayed monocular signals. *Neuroimage.* 2018;172:753–765.
44. Pardhan S, Gilchrist J. Binocular contrast summation and inhibition in amblyopia. The influence of the interocular difference on binocular contrast sensitivity. *Doc Ophthalmol.* 1992;82(3):239–248.
45. Thompson B, Richard A, Churan J, et al. Impaired spatial and binocular summation for motion direction discrimination in strabismic amblyopia. *Vision Res.* 2011;51(6):577–584.
46. Fornaciai M, Park J. Serial dependence in numerosity perception. *J Vis.* 2018;18(9):15.