

# Impaired Speed Perception but Intact Luminance Contrast Perception in People With One Eye

Krista R. Kelly,<sup>1,2</sup> Sarah R. Zohar,<sup>1</sup> Brenda L. Gallie,<sup>2,3</sup> and Jennifer K. E. Steeves<sup>1-3</sup>

<sup>1</sup>Centre for Vision Research and Department of Psychology, York University, Toronto, Canada

<sup>2</sup>The Hospital for Sick Children, Toronto, Canada

<sup>3</sup>Department of Ophthalmology and Vision Sciences, University of Toronto, Toronto, Canada

Correspondence: Jennifer K. E. Steeves, Centre for Vision Research and Department of Psychology, York University, 4700 Keele Street, Toronto, ON M3J 1P3; steeves@yorku.ca.

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**PURPOSE.** It is generally accepted that early visual deprivation from monocular enucleation (ME; the surgical removal of one eye) results in intact spatial vision. Yet, motion perception studies in this population yield inconsistent findings. Here, we investigated speed and luminance contrast perception in a group of ME individuals.

**METHODS.** Twelve ME participants (mean age = 24 years; mean age at enucleation = 24 months) and 17 controls (mean age = 25 years) viewing binocularly (BV) and monocularly (MV) completed a series of speed discrimination and luminance contrast detection and discrimination tasks. Stimuli consisted of 0.5 cpd vertical sine wave gratings varying in speed (3.8°/s–24°/s) or luminance contrast (0%–78%). A second set of luminance contrast tasks with 4 cpd gratings teased apart any spatial frequency effects.

**RESULTS.** The ME group exhibited elevated speed discrimination thresholds compared with BV ( $P = 0.001$ ) and MV ( $P = 0.027$ ) controls, but intact luminance contrast discrimination ( $P = 0.530$ ). Notably, both ME and MV groups displayed elevated luminance contrast detection thresholds compared with the BV group ( $P_s \leq 0.006$ ). However, the ME group exhibited slightly lower thresholds compared with MV controls for all 4 cpd tasks.

**CONCLUSIONS.** Our data indicate a disruption in the development of speed perception, but not luminance contrast perception with monocular enucleation. These data highlight the importance of receiving healthy binocular vision during postnatal development for the maturation of cortical regions associated with motion processing.

**Keywords:** monocular enucleation, luminance contrast perception, speed perception, visual development, monocular deprivation

The visual system is not fully developed at birth<sup>1</sup> and relies on normal levels of balanced visual input during postnatal maturation.<sup>2,3</sup> For example, imbalanced visual input from monocular deprivation during infancy due to congenital cataract, anisometropia, and strabismus results in deficits in spatial vision (e.g., contrast sensitivity, acuity) and motion perception (e.g., direction discrimination) that persist throughout life in both the deprived and nondeprived eye.<sup>4-12</sup> Considering that motion stimuli intrinsically possess spatial attributes, it is difficult to determine which aspect of vision underlies motion processing deficits in these disorders. In fact, one study has shown that motion processing deficits in amblyopia are related to contrast sensitivity impairments rather than poor local motion perception.<sup>13</sup> To determine how spatial vision and motion perception develop following visual deprivation, it may be helpful to examine populations that are impaired on only one of these aspects of vision, specifically a monocularly deprived population with intact contrast sensitivity.

One such population does exist, those who have experienced early monocular enucleation (ME; surgical removal of one eye) due to cancer of the retina (retinoblastoma), a disease with onset generally before 2 years of age. Enucleation provides a valuable model for examining the effects of early monocular deprivation on visual system development since it results in a

more complete form of monocular deprivation compared with other forms, such as strabismus or amblyopia, where disrupted patterned visual input is received by the deprived eye. Enucleated individuals demonstrate intact spatial vision compared with binocular viewing (BV) controls for contrast sensitivity,<sup>14</sup> luminance-defined (LD) contrast letter acuity,<sup>7,15,16</sup> and LD global shape discrimination.<sup>17</sup> Further, enucleated individuals actually have enhanced ability for the majority of these tasks compared with controls viewing monocularly with a patch over one eye.<sup>7,15-17</sup> Moreover, participants who underwent enucleation before 4 years of age have enhanced contrast sensitivity at 4 cpd compared with BV controls.<sup>14</sup> These data suggest cortical reorganization, which may compensate for the early loss of one eye.<sup>18,19</sup> It is important to note, however, that enucleated individuals exhibit mild deficits in face perception, suggesting that higher level spatial vision is somewhat disrupted in this group.<sup>20</sup>

Despite the generally intact or enhanced spatial vision ability following ME, small motion perception deficits are found for motion-defined form<sup>21</sup> and the perception of motion in depth.<sup>22</sup> This dissociation in visual ability suggests a greater vulnerability during atypical postnatal visual development of cortical regions associated with motion processing, likely the middle temporal/medial superior temporal (MT/MST) complex (MT+).<sup>23</sup> However, not all aspects of motion are disrupted,

enucleated participants demonstrate intact relative velocity detection<sup>24</sup> and direction discrimination for coherent motion<sup>21</sup> compared with controls. Binocular, more than monocular, congenital cataracts (corrected during the first year of life) disrupt global motion perception, suggesting that normal visual input from one eye spares some vision.<sup>9</sup> Thus, normal visual input from the remaining eye in the enucleated population may result in a relative sparing of motion perception for some tasks, but not others. Nonetheless, response asymmetries have been shown in enucleated individuals favoring lower over upper hemifield motion for relative velocity discrimination,<sup>24</sup> as well as nasalward over temporalward motion for coherent motion discrimination<sup>21</sup> and for eye movement responses to full field motion, specifically optokinetic nystagmus (OKN).<sup>25,26</sup> The OKN asymmetry indicates a disruption in the earlier developing subcortical regions that mediate OKN (e.g., nucleus of the optic tract [NOT]), whereas motion asymmetries point to a higher level cortical disruption and are consistent with evidence for an earlier maturation period for the processing of nasalward motion.<sup>27,28</sup>

Given the inconsistent nature of previous findings, it is worthwhile to further examine the effects of ME on motion perception development. One aspect of motion processing not yet studied in this population, the perception of speed, has real world applications such as playing sports, crossing the road, and driving. While research implicates visual areas such as cortical area MT in the coding of speed perception,<sup>29,30</sup> other studies suggest extrastriate visual areas V3 and V3a are also involved.<sup>31,32</sup> Further, speed processing occurs in cortical regions distinct from those for processing coherent motion.<sup>32</sup> The development of speed perception appears to have a number of sensitive periods with fast speeds (e.g., 6°/s and 9°/s) maturing earlier than slow speeds (e.g., 1.5°/s).<sup>33-37</sup> Consistent with developmental data, individuals who experienced binocular and monocular congenital cataracts exhibit stronger deficits in direction discrimination for slow compared with fast speeds,<sup>11</sup> indicating an earlier critical period for the development of neural regions sensitive to speeds that have not yet reached their optimal sensitivity.

We compare speed discrimination and luminance contrast detection and discrimination performance of a group of early ME participants to that of controls viewing binocularly and monocularly. We predict speed discrimination deficits as well as the presence of nasotemporal asymmetries in the enucleated group compared with controls, similar to disruptions observed in other tasks of motion processing with this population.<sup>21</sup> We also predict that these impairments will be more pronounced for slow than high speeds, consistent with developmental<sup>33-37</sup> and cataract<sup>11</sup> research. However, since some aspects of

motion processing are not impaired in enucleated participants,<sup>21,24</sup> we may find no speed perception deficits. For luminance contrast perception, we predict intact performance compared with controls, consistent with previous findings.<sup>14-17</sup> Finally, we correlate speed and luminance contrast perception performance within individuals to determine whether spatial vision and motion perception development are affected independently by enucleation as the previously described dissociation in visual ability would suggest. Data from these experiments will contribute to our understanding of the role that binocular vision plays in visual system development.

## METHODS

### Participants

**Monocular Enucleation (ME) Group.** Twelve adults ( $n_{\text{male}} = 8$ ) from The Hospital for Sick Children in Toronto who had one eye ( $n_{\text{right}} = 7$ ) enucleated due to retinoblastoma were tested. Mean age was  $23.9 \pm 2.4$  years (range, 17-43 years) and mean age at enucleation (AAE) was  $24.3 \pm 5.0$  months (range, 4-60 months). Participants had normal or corrected to normal Snellen acuity (Precision Vision, La Salle, IL). Enucleated participants are regularly seen by their ophthalmologist and no known ocular abnormalities were reported in the remaining eye. The Table lists individual patient histories.

**Binocular (BV) and Monocular (MV) Viewing Controls.** Seventeen adults ( $n_{\text{male}} = 6$ ) were recruited who were approximately age-matched to the ME group. Participants were tested binocularly (BV) and monocularly (MV) on two separate occasions with semitransparent medical tape over their nondominant eye ( $n_{\text{left}} = 12$ ) to reduce the effects of binocular rivalry. Mean age was  $25.2 \pm 1.6$  years (range, 19-40 years). Participants had normal or corrected to normal Snellen acuity and normal stereoacuity (Stereo Optical Co., Inc., Chicago, IL). Acuity and the Porta test<sup>38</sup> were used to assess eye dominance for the MV condition.

### Stimuli

Stimuli were created based on previously described methods<sup>39-41</sup> using VPixx v.2.71 software (VPixx Technologies Inc., Saint-Bruno, QC, Canada). Gabor patches consisted of a 0.5 cpd vertical sine wave grating within a 19° aperture with 1° Gaussian blur, which was applied to minimize edge effects.

**Speed Discrimination.** Leftward and rightward moving stimuli retained a constant luminance contrast of 20%. Base

TABLE. Patient Histories for Monocularly Enucleated Participants Including Age, Sex, Snellen Acuity, Enucleated Eye, and Age at Enucleation (AAE)

Patient	Age, y	Sex	Acuity	Enucleated Eye	AAE, mos
ME01	27	Male	20/16	Right	4
ME02	43	Female	20/12.5	Right	18
ME03	20	Male	20/20	Right	39
ME04	34	Female	20/12.5	Left	18
ME05	21	Male	20/20	Right	23
ME06	18	Female	20/16	Left	48
ME07	18	Male	20/16	Right	13
ME08	17	Male	20/20	Right	9
ME09	18	Male	20/20	Left	60
ME10	29	Female	20/20	Left	11
ME11	24	Female	20/16	Right	35
ME12	30	Male	20/20	Left	13

speed values, the speed levels to which an increment was added, were 3.8°/s, 6.2°/s, 10°/s, 16.2°/s, and 24°/s.

#### Luminance Contrast Detection and Discrimination.

Luminance contrast stimuli were static versions of the gratings described for speed discrimination. Base luminance contrast values were 0% for detection and 5%, 11%, 22%, 44%, and 78% for discrimination. Since individuals who were enucleated prior to 4 years of age have shown higher contrast sensitivity at 4 cpd compared with BV controls,<sup>14</sup> we also administered a set of luminance contrast detection and discrimination tasks at 4 cpd using 0%, 5%, and 11% base luminance contrasts. All other parameters were similar to those above.

#### Procedure

This research was conducted according to the doctrine of the Declaration of Helsinki and was approved by the research ethics boards of both the Hospital for Sick Children and York University. Informed consent was obtained from all participants prior to testing. Participants completed the tasks in a darkened room and sat 50 cm from the computer display with their chin resting on a chinrest. Stimuli were presented on a 17.5 inch Viewsonic G90fb CRT monitor (Viewsonic Corporation, Walnut, CA) with a refresh rate of 80 Hz. The monitor was driven by an Apple Macintosh Pro computer (Apple, Cupertino, CA). Participants' responses were recorded with a keyboard.

The sets of speed and luminance contrast perception tasks were blocked and counterbalanced. Leftward and rightward trials were interleaved in the speed discrimination tasks. A three-down one-up staircase procedure with a two-interval forced choice task was used to determine thresholds for each of the base speeds and luminance contrasts. The value of the target stimuli decreased with three consecutive correct answers and increased with one incorrect answer by an increment of 30% of the difference between the base and target on the previous trial. The staircase ended after 12 reversals so that all participants performed at 79.4% accuracy. Thresholds were calculated by analyzing the last nine reversals. Four practice trials were provided prior to completing each set of tasks to ensure participants understood the procedure. Speed and luminance contrast discrimination thresholds are expressed as a just noticeable difference (JND) or Weber Fraction ( $\Delta X/X$ ). Luminance contrast detection thresholds are expressed as a percent contrast.

Participants viewed two sequentially presented gratings, one base and one target, and were asked to indicate which of the two intervals contained: (1) a grating moving at a faster speed (speed discrimination), (2) a grating (luminance contrast detection), or (3) a grating of higher contrast (luminance contrast discrimination). The presentation sequence of the base and target was randomized and trials began with a "ping" sound. Each grating was presented for 250 ms with an interstimulus interval of 200 ms. The second grating was jittered to the right of the first by 0.7° in order to prevent point by point comparisons between the two stimuli. A fixation window 15° × 15° in size was presented for 200 ms before the first and second intervals in order to focus participants' attention to the center of the display, but not cause afterimages on the region where the gratings appeared.

One ME and one MV participant did not complete the speed discrimination tasks due to time constraints. All control participants completed the set of 4 cpd tasks at all contrasts in both BV and MV conditions. Nine participants from the original ME group also completed the 4 cpd discrimination tasks at 5% and 11% contrasts, and eight completed the 4 cpd detection task at 0% contrast.

## RESULTS

### Leftward/Rightward Speed Discrimination

An omnibus three-way ANOVA with group (BV, ME) as the between-groups variable, and direction (left, right) and base speed (3.8°/s, 6.2°/s, 10°/s, 16.2°/s, 24°/s) as the within-groups variables revealed no significant interactions ( $P_s \geq 0.146$ ). Significant main effects of group ( $F_{1,26} = 13.68$ ,  $P = 0.001$ ), speed ( $F_{2,1,54,1} = 38.32$ ,  $P < 0.001$ ), and direction, ( $F_{1,26} = 12.54$ ,  $P = 0.002$ ), were found. Both groups showed the typical pattern of lower thresholds for fast compared with slow speeds.<sup>36,37</sup>

Collapsed across direction, post hoc pairwise comparisons (Bonferroni-adjusted alphas = 0.01) revealed that the ME group exhibited significantly elevated thresholds (i.e., lower sensitivity) compared with the BV group for 10°/s ( $P = 0.004$ ) and 24°/s ( $P = 0.003$ ). The ME group also displayed tendencies for elevated thresholds compared with the BV group that approached significance for 3.8°/s ( $P = 0.032$ ), 6.2°/s ( $P = 0.015$ ), and 16.2°/s ( $P = 0.037$ ). Collapsed across speed, post hoc pairwise comparisons (Bonferroni-adjusted alphas = 0.025) revealed that the ME group exhibited significantly elevated thresholds compared with the BV group for both leftward ( $P = 0.003$ ) and rightward ( $P = 0.001$ ) motion. Further, the ME group exhibited significantly elevated thresholds for rightward compared with leftward motion ( $P = 0.005$ ), and the BV group exhibited only a tendency for the same pattern that approached significance ( $P = 0.074$ ). No simple effects analyses were conducted due to the lack of significant interactions. Figure 1 depicts leftward (A) and rightward (B) speed discrimination mean thresholds.

### Nasalward/Temporalward Speed Discrimination

An omnibus three-way ANOVA with group (MV, ME) as the between-groups variable, and direction (nasalward, temporalward) and base speed (3.8°/s, 6.2°/s, 10°/s, 16.2°/s, 24°/s) as the within-groups variables revealed a significant two-way speed by direction interaction ( $F_{2,4,60,7} = 3.10$ ,  $P = 0.043$ ). No other interactions were significant ( $P_s \geq 0.418$ ). Significant main effects of group ( $F_{1,25} = 5.56$ ,  $P = 0.027$ ) and speed ( $F_{4,100} = 45.42$ ,  $P < 0.001$ ), but not direction ( $F_{1,25} = 0.83$ ,  $P = 0.370$ ) were found. Both groups showed the typical pattern of elevated thresholds for slow compared with fast speeds.<sup>36,37</sup>

Collapsed across direction, post hoc pairwise comparisons (Bonferroni-adjusted alphas = 0.01) revealed tendencies for the ME group to have elevated speed discrimination thresholds compared with the MV group that approached significance for

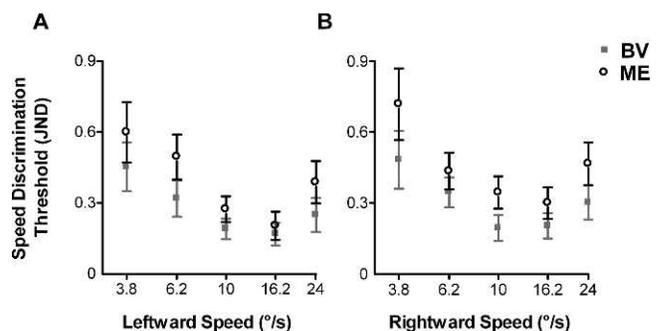


FIGURE 1. Speed discrimination thresholds (JND) for BV (filled gray square) and ME (open circle) groups for leftward (A) and rightward (B) motion. In general, the ME group exhibited elevated speed discrimination thresholds compared with the BV group. Error bars represent 95% confidence intervals (CIs).

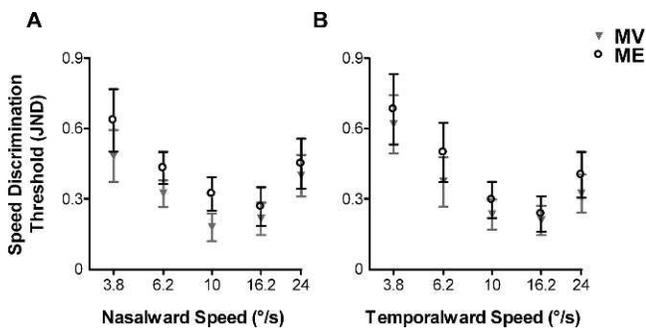


FIGURE 2. Speed discrimination thresholds (JND) for MV (filled gray triangle) and ME (open circle) groups for nasalward (A) and temporalward (B) motion. The ME group exhibited elevated speed discrimination thresholds compared with ME group for nasalward speeds only. Error bars represent 95% CIs.

6.2°/s ( $P = 0.044$ ) and 10°/s ( $P = 0.018$ ). The significant speed by direction interaction allowed a simple effects analysis (Bonferroni-adjusted alphas = 0.01), which revealed that the ME group had significantly elevated nasalward thresholds for 10°/s ( $P = 0.001$ ) and tendencies for elevated nasalward thresholds that approached significance for 3.8°/s ( $P = 0.081$ ) and 6.2°/s ( $P = 0.018$ ) compared with the MV group. The ME group showed no nasotemporal asymmetries at any speed ( $P_s \geq 0.221$ ), but the MV group showed tendencies for elevated temporalward compared with nasalward thresholds that approached significance for 3.8°/s ( $P = 0.065$ ) and 10°/s ( $P = 0.057$ ), but tendencies for lower temporalward compared with nasalward thresholds that approached significance for 24°/s ( $P = 0.033$ ). Figure 2 depicts nasalward (A) and temporalward (B) speed discrimination mean thresholds.

**Luminance Contrast Detection**

Luminance contrast detection thresholds could not be converted into JNDs and were, thus, analyzed independently from those for contrast discrimination using separate one-way ANOVAs for 0.5 cpd and 4 cpd spatial frequency with group (BV, MV, ME) as the between-groups variable. Significant main effects of group were found for 0.5 cpd ( $F_{2,43} = 22.73, P < 0.001$ ) and for 4 cpd ( $F_{2,39} = 11.16, P < 0.001$ ). All groups showed the typical pattern of significantly elevated thresholds for 0.5 cpd compared with 4 cpd ( $P_s < 0.001$ ).

Post hoc pairwise comparisons (Bonferroni-adjusted alphas = 0.017) revealed that the ME and MV groups exhibited significantly elevated detection thresholds compared with the BV group for 0.5 cpd and 4 cpd ( $P_s \leq 0.006$ ). However, the MV group exhibited a tendency for an elevated detection threshold compared with ME group that approached significance for 4 cpd ( $P = 0.070$ ). Figure 3 depicts 0.5 cpd (A) and 4 cpd (B) mean luminance contrast detection thresholds.

**Luminance Contrast Discrimination**

A two-way ANOVA with group (BV, MV, ME) as the between-groups variable and base contrast (5%, 11%, 22%, 44%, 78%) as the within-groups variable for luminance contrast discrimination at 0.5 cpd spatial frequency revealed no significant group by contrast interaction ( $F_{2,1,92.9} = 0.48, P = 0.767$ ) and no significant main effect of group ( $F_{2,43} = 0.64, P = 0.530$ ). However, a significant main effect of luminance contrast was found ( $F_{2,1,92.9} = 59.71, P < 0.001$ ). All groups showed the typical pattern of decreasing thresholds for increasing luminance contrast.

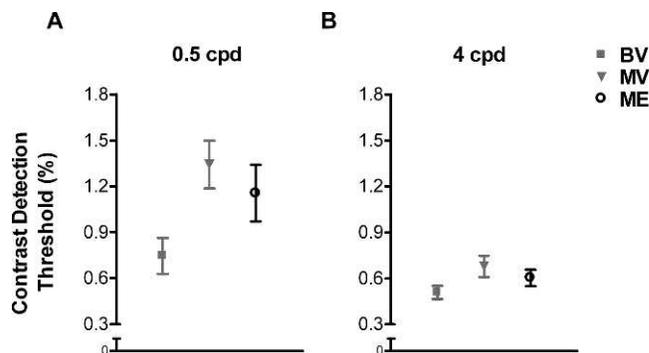


FIGURE 3. Contrast detection thresholds (%) for BV (filled gray square), MV (filled gray triangle), and ME (open circle) groups for 0.5 cpd (A) and 4 cpd (B) gratings. The MV and ME groups exhibited elevated luminance contrast detection thresholds compared with the BV group for both 0.5 and 4 cpd gratings. The MV group showed a tendency for elevated luminance contrast detection thresholds at 4 cpd compared with the ME group. Error bars represent 95% CIs.

Another two-way ANOVA with group (BV, MV, ME) as the between-groups variable and base contrast (5%, 11%) as the within-groups variable for luminance contrast discrimination at 4 cpd spatial frequency revealed no significant group by contrast interaction ( $F_{2,40} = 0.53, P = 0.593$ ). A significant main effect of luminance contrast ( $F_{1,40} = 19.82, P < 0.001$ ), and a marginally significant main effect of group ( $F_{2,40} = 3.21, P = 0.051$ ) were observed. All groups showed the typical pattern of elevated thresholds for 5% compared with 11% contrast ( $P_s \leq 0.06$ ).

Post hoc pairwise comparisons (Bonferroni-adjusted alphas = 0.025) revealed that the MV group exhibited tendencies for elevated thresholds compared to the ME group that approached significance for 5% ( $P = 0.056$ ) and 11% ( $P = 0.090$ ) at 4 cpd spatial frequency. Figure 4 depicts 0.5 cpd (A) and 4 cpd (B) luminance contrast discrimination mean thresholds.

**Timing of Deprivation**

Partial correlations controlling for age revealed no significant correlations between AAE in the ME group and their luminance contrast detection and discrimination, or speed discrimination thresholds ( $P_s \geq 0.123$ ).

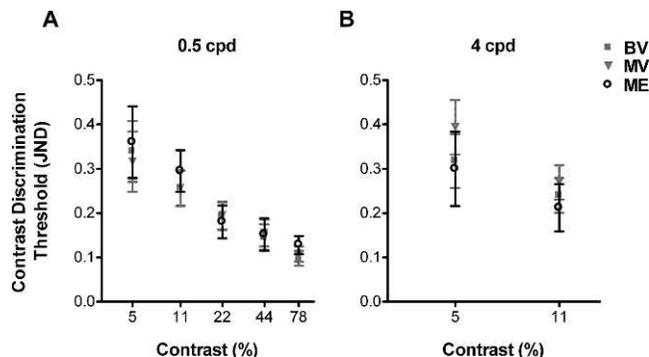


FIGURE 4. Contrast discrimination thresholds (JND) for BV (filled gray square), MV (filled gray triangle), and ME (open circle) groups for 0.5 cpd (A) and 4 cpd (B) gratings. No significant differences were found between groups for 0.5 cpd, but the MV group exhibited tendencies for elevated luminance contrast discrimination thresholds compared with the ME group at 4 cpd. Error bars represent 95% CIs.

## Relationship Between Luminance Contrast Detection/Discrimination and Speed Discrimination

Since the ME group did not exhibit nasotemporal asymmetries, nasalward and temporalward thresholds were averaged. Each speed discrimination threshold was then correlated with each luminance contrast detection and discrimination threshold using partial correlations controlling for age to determine if development of speed and luminance contrast processing are affected in the same way by ME. Only correlations that reached  $P < 0.05$  (uncorrected alpha) subsequent to outlier removal are reported. Only two positive correlations were found: (1)  $10^\circ/\text{s}$  speed and 44% luminance contrast perception ( $r_7 = 0.74$ ,  $P = 0.024$ ), and (2)  $24^\circ/\text{s}$  and 78% luminance contrast perception ( $r_8 = 0.75$ ,  $P = 0.013$ ). To compare against the ME group, the same correlations were conducted for the BV group with leftward and rightward thresholds averaged and for the MV group with nasalward and temporalward thresholds averaged. No significant correlations were found for the BV group; however, two positive correlations were found for the MV group: (1)  $24^\circ/\text{s}$  and 0% luminance contrast at 0.5 cpd ( $r_{11} = 0.58$ ,  $P = 0.047$ ) and (2)  $24^\circ/\text{s}$  and 0% luminance contrast at 4 cpd ( $r_{12} = 0.69$ ,  $P = 0.013$ ). These few correlations may be due to the problem of multiple comparisons when conducting many correlations and, thus, must be interpreted with caution.

## DISCUSSION

We demonstrate speed discrimination impairments in early ME individuals compared with BV controls for all speeds regardless of direction. This is consistent with previously reported motion processing deficits in this group.<sup>21,22</sup> Moreover, we also report the first instance of motion perception deficits for the early ME group compared with MV controls. While the ME group showed elevated speed thresholds at all speeds relative to BV controls, they only showed deficits at slower speeds when compared with MV controls. This finding supports research indicating later maturation for the perception of slow speeds<sup>11,33-37</sup> and suggests an interruption to this critical period with ME. Further, the enucleation group's speed processing deficits were less pronounced when compared with monocular rather than BV controls indicating that the control condition of MV with an eye patch over one eye appears to interfere with the visual processing of motion. This is likely due to inhibitory binocular interactions from the eye patch such as binocular inhibition or rivalry. Binocular inhibitory effects may also contribute to the mild nasotemporal asymmetries observed in our MV controls. Nonetheless, MV controls are better than ME participants at speed discrimination. This finding suggests that binocular inhibitory effects from eye patching disrupt speed perception minimally in controls, which is supported by the lack of asymmetry for global motion perception with eye patching.<sup>21</sup> Remarkably, enucleated observers displayed deficits for nasalward motion only compared with MV controls, suggesting that at least for the perception of speed, the earlier developing perception of nasalward motion may be more vulnerable to early visual deprivation when assessing local rather than global motion. Thresholds for temporalward motion appear to be slightly elevated (Fig. 2B), and perhaps there may exist a disruption in the development of processing temporalward motion as well; however, these elevations did not reach significance.

Motion perception deficits have been documented in developmental disorders affecting visual ability such as

Williams Syndrome and autism,<sup>42,43</sup> suggesting that a vulnerability of the dorsal motion processing system may exist with atypical development.<sup>27</sup> Deficits in speed perception for our enucleated group may also be attributed to a disruption in dorsal regions associated with processing speed that are beyond V1, such as V3/V3a and MT+.<sup>23,31,32</sup> Cells in MT+ and V3a are also tuned to binocular disparity and there is considerable functional overlap between stereopsis and motion processing.<sup>44-46</sup> Indeed, strabismic individuals with weak stereopsis exhibit similar deficits in speed judgements as our ME group.<sup>47</sup> Thus, a common physiologic link between motion perception and binocular integration may account for the motion deficits in our enucleated group, for whom no binocular interaction in the visual cortex is possible. Consequently, intact binocularity may be required for the normal maturation of motion systems.

Unlike previous research,<sup>21,25,26</sup> no nasotemporal asymmetries were observed in our ME group. Attending to speed rather than direction has been shown to activate different neural regions for motion<sup>32</sup> and could account for the lack of asymmetry in our study. It is also possible that a nasotemporal asymmetry does not manifest during tasks where motion is easily determined by local cues such as speed. Individuals who have experienced early-onset strabismus show larger nasalward biases for the perceived speed of sine wave gratings,<sup>47,48</sup> though this is a very different form of deprivation than enucleation. A lack of nasotemporal asymmetries may also reflect a brief period of binocular vision with normal input through the removed eye prior to enucleation since the majority of our participants underwent enucleation later than 6 months of age. However, central vision is usually obstructed approximately 6 months prior to when retinoblastoma is diagnosed and the eye is enucleated, therefore, this brief period of normal vision is likely even shorter. It is possible that complete deafferentation of one eye with enucleation is fundamentally different from other forms of monocular deprivation and results in speed discrimination deficits but no nasotemporal asymmetries.

The ME group exhibited substantially elevated luminance contrast detection thresholds regardless of spatial frequency compared with the BV group, which is consistent with a previously reported elevated threshold for luminance contrast letter acuity at 4% contrast compared with BV controls.<sup>15</sup> More importantly, these deficits disappear when performance in the ME group is compared with MV controls in our study. This indicates a binocular advantage when viewing with two eyes (i.e., binocular summation) compared to one. Binocular summation effects have been implicated in the superior resolution of vernier acuity as well as luminance contrast detection and discrimination and its effect is strongest at lower luminance contrasts.<sup>49-51</sup> Therefore, the reduction in luminance contrast detection in our study for both the MV and ME groups can be largely attributed to the lack of binocular summation and not to a deficit in the development of luminance contrast perception.

Despite the lack of binocular summation, the ME group nonetheless had a tendency for superior luminance contrast detection and discrimination of 5% and 11% luminance contrast 4 cpd gratings compared with the MV group. This finding is consistent with previous luminance contrast tasks in this population.<sup>7,14-17</sup> Several suggestions have been put forth to account for the superior performance of ME patients compared to MV controls at low contrast visual tasks<sup>18</sup> including: (1) binocular interference of binocular rivalry when wearing an eye patch for the MV controls, which of course is absent in the ME group, (2) years of monocular practice for the ME group, and (3) compensatory reorganization within visual cortex of ME patients in favor of the remaining eye. For

instance, the complete removal of one eye eliminates binocular inhibitory interactions and binocular competition for cortical space during postnatal visual development. Consequently, neurons in the visual pathway that would otherwise have been allocated to the enucleated eye may be recruited by the remaining eye at various levels of the visual system such as the lateral geniculate nucleus and V1.<sup>52,53</sup> Recruitment within V1 may prevent spatial vision deficits following ME, and in some cases may actually enhance this ability.

No timing of deprivation effects were found for luminance contrast detection and discrimination. This finding is consistent with previous studies of spatial vision in enucleation, which have not found an effect of age at enucleation.<sup>7,15-17,19</sup> Apart from two individuals, all of our participants had their eye surgically removed before 44 months of age, which may be outside developmental critical periods or may not span a large enough period in early development to be sensitive to developmental critical period effects. Further, when we removed participants who underwent eye enucleation after 24 months of age from our analyses, we found the same pattern of results. The relative lack of relationships between luminance contrast detection and discrimination and speed discrimination for either group, coupled with the dissociation in visual ability, suggests that early ME affects the development of the motion perception and spatial vision pathways differently.

## CONCLUSIONS

In conclusion, our study shows that enucleated observers have deficits in speed but not luminance contrast processing, which is consistent with the previously reported dissociation in visual ability. This is the first study to measure both luminance contrast and speed processing in the same individuals. These findings, coupled with a relative lack of correlations between the sets of speed and luminance contrast tasks, point to independent effects of enucleation on these two systems. It is possible that the visual system undergoes compensatory reorganization in response to the loss of one eye during infancy for spatial vision to remain intact. Yet, such reorganization may not be sufficient for the development of motion perception. This study highlights the importance of normal and balanced levels of binocular postnatal visual input for the normal development of the motion processing systems.

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