Horizontal Saccade Dynamics After Childhood Monocular Enucleation

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Purpose. We investigated the effects of monocularity on oculomotor control by examining the characteristics of the horizontal saccades of people with one eye, and comparing them to those of a group of age-matched controls who viewed the stimuli monocularly and binocularly.

Methods. Participants were tested in a no-gap, no-overlap saccadic task using a video-based remote eye tracker. One group consisted of unilaterally eye enucleated participants ($N = 15$; mean age, 31.27 years), the other of age-matched people with normal binocular vision ($N = 18$; mean age, 30.17 years).

Results. The horizontal saccade dynamics of enucleated people are similar to those of people with normal binocularity when they view monocularly and, with the exception of latency, when they view binocularly. The data show that the monocular saccades of control and enucleated observers have longer latencies than the binocular saccades of the control group, the saccades of the enucleated observers are as accurate as those of the controls viewing monocularly or binocularly, smaller saccades are more accurate than the larger ones, and abducting saccades are faster than adducting saccades.

Conclusions. Our data suggest that the true monocularity produced by early enucleation does not result in slower visual processing in the afferent (sensory) pathway, or in deficits in the efferent (motor) pathways of the saccadic system. Possible mechanisms to account for the effects of monocular vision on saccades are discussed.

Keywords: saccades, saccade latency, saccade amplitude gain, saccade peak velocity, monocular vision, binocularity, enucleation

While the functional and anatomic consequences of monocular deprivation in humans and primates[1,2] constitute interesting areas of study in their own right, they also provide valuable insights into the organization and function of the binocular brain. The complete deafferentation produced by unilateral eye enucleation provides a unique human model for examining the consequences of the loss of binocular vision in contrast with other forms of visual deprivation, such as amblyopia and cataracts, that frequently produce abnormal visual inputs.[3–5]

Behavioral studies of visual performance in people who have lost one eye before the end of the critical period for binocularity show evidence consistent with the notion of recruitment by the remaining eye of some of the resources of the removed eye. This plasticity, in addition to the removal of inhibitory binocular interactions and the absence of binocular competition, appears to lead to the preservation, and in some conditions to the enhancement, of contrast-defined visual abilities, such as acuity, contrast sensitivity, and global shape discrimination, especially at low contrast (see the reviews of Kelly et al.,[6] Steeves et al.,[7] and Steinbach and González[8]). Enucleation, however, seems to have adverse effects on the maturation of functions, such as motion[9–11] and face perception.[12]

When evaluating the characteristics of monocular vision, the question arises as to the contribution of oculomotor control to the visual functions investigated. To this day, however, only fixation stability and optokinetic nystagmus (OKN) have been measured in one-eyed observers to our knowledge. In terms of fixation stability, the main finding is that their fixation stability is not different from that of controls.[13] In terms of OKN, a small majority of enucleated observers show significant asymmetries favoring nasally-directed motion in the visual field.[14] Day also found that early enucleated people show asymmetries in motion visual evoked potentials that are larger compared to those of people who lost vision as adults or were congenitally monocular.[15] These findings are consistent with the disruption by enucleation before the end of the critical period for binocularity; specifically, of the visual cortical mechanisms involved in the development of symmetrical OKN[16] and with the earlier maturation of nasal-ward motion perception.[17]

The objective of our study was to evaluate the so far unknown features of the horizontal saccades of one-eyed people in terms of latency, amplitude gain, and asymptotic peak velocity. To this end, we compared a group of unilaterally

Table 1. Characteristics of Participants in the Enucleated and Control Groups

Enucleated Group				Control Group	
Viewing Eye	Age, y	AAE, mo	Diagnosis	Monocularly Viewing Eye	Age, y
RE	7	25	Unilateral	RE	8
RE	13	20	Unilateral	RE	15
RE	14	75	Unilateral	RE	18
LE	15	71	Unilateral	LE	19
LE	17	8	Unilateral	RE	19
LE	21	16	Unilateral	RE	21
RE	29	12	Bilateral	RE	22
RE	31	10	Unilateral	LE	24
LE	31	4	Unilateral	RE	24
RE	34	20	Unilateral	RE	25
LE	37	24	Unilateral	RE	27
LE	44	18	Unilateral	LE	29
RE	50	27	Unilateral	LE	34
RE	54	9	Unilateral	RE	34
RE	72	14	Unilateral	RE	42
				RE	54
				RE	60
				RE	68
Mean	31.27	23.53			30.17
SD	17.99	21.16			16.16
Median	31	18			25

RE, right eye; LE, left eye; AAE, age at enucleation in months.

enucleated children and adults to a group of age-matched binocularly normal controls.

Methods

Participants

This research was approved by the University Health Network's Research Ethics Board and conducted in accordance with the tenets of the Declaration of Helsinki. Informed consent was obtained from all adult participants, and from the parents or guardians of minors. Children 7 to 15 years old also gave their verbal assent.

Monocularly Enucleated Group

We tested 15 observers (12 women and 3 men; mean age, 31.27; SD, 17.99 years; range, 7–72 years) who had been unilaterally eye enucleated early in life due to retinoblastoma, a rare pediatric cancer of the eye. Of these participants, 14 were unilateral cases and had a normal remaining eye. The single observer with a bilateral diagnosis had a clear macula and tumor scars only in the far periphery. Age at enucleation for this group ranged from 4 to 75 months (median, 18 months).

Control Group

The control group consisted of 18 participants (13 women and 5 men; mean age, 30.17; SD, 16.17 years; range, 8–68 years) closely age-matched to the enucleated group. They all had normal or corrected to normal visual acuity and stereopsis of at least 40 seconds as measured by the Fly Stereotest (available in the public domain at http://www.stereooptical.com). For the monocular condition, they used their preferred eye and four viewed with the left eye.

Table 1 shows the demographic information of the two groups.

Stimuli

The saccadic stimulus was a white circle 0.25° in diameter presented on a black background at 5°, 10°, 20°, and 30° from fixation without a gap or overlap, and a duration of 1 second. The direction (left or right from fixation) and stimulus step size were randomized, and a total of 70 saccade stimuli presented in each testing condition.

Apparatus

A desktop remote EyeLink 1000 eye tracker (SR Research Ltd., Mississauga, Ontario, Canada) with a sampling rate of 250 Hz was used for recording the eye movements. This is a video–based eye tracker with a spatial resolution of 0.02° root mean square (RMS), and an average accuracy between 0.25° and 0.5°. Before data collection, the eye tracker was calibrated with its standard calibration and verification procedures.

Stimuli were presented on a Samsung monitor (Sync Master 900 NF; Samsung, Seoul, South Korea) with a 34.4 × 26 cm useful field of view, a resolution of 1024 × 768 pixels, and a refresh frequency of 120 Hz. For monocular viewing, an infrared (IR) long-pass filter, which appeared black to the observer, allowed the eye tracker to record the movements of the viewing and the covered eye (open loop) simultaneously. This setup ensured that the control observers had both eyes open during monocular testing.

The stimuli were generated by a Macintosh laptop computer (Apple, Inc., Reston, VA) using VPixx, a graphics and psychophysical testing software (VPixx Technologies, Inc., Montreal, QC, Canada). The laptop computer and the EyeLink's host computer were connected by means of a DATAPixx (available in the public domain at http://www.vpixx.com) interface, which sent time stamps and stimulus information to be stored in the eye movement data files.

Procedure

All participants were tested at a viewing distance of 60 cm. Testing was done in a well-illuminated room, and participants sat with their chin and forehead steadied by a headrest. All participants wore their optical correction, if any was needed. Control participants were tested monocularly and binocularly, in random order. After calibration, testing began with a central fixation cross and the eyes in primary position.

Data Analysis

Custom software written in Matlab (The MathWorks, Natick, MA) was used to obtain velocity data by differentiating eye position data with respect to time. Saccades were detected by software using a velocity threshold of 30°/sec and then visually verified. Only saccades made in response to a stimulus were analyzed. For this, a saccade had to be the first saccade after stimulus onset, it had to have been made in the appropriate direction, and had to have a latency between 80 and 500 msec. Saccadic accuracy, or amplitude gain, was obtained by dividing the amplitude of the saccade by the magnitude of the eccentricity of the stimulus from fixation, or stimulus step size. For each participant, peak velocity was plotted as a function of saccadic amplitude and the data fitted with an exponential function of the form:

Table 2. Summary of the Horizontal Saccade Dynamics of Enucleated and Control Observers

	Monocular	Binocular	Step Size	20° Temporal Target Effect	Nasotemporal Asymmetry
Latency					
Enucleated	NS	Binocular < enucleated	NS	*	NS
Monocular		Binocular < monocular	NS	*	NS
Binocular†			NS	NS	NS
Amplitude gain					
Enucleated	NS	Binocular > enucleated†	*	*	NS
Monocular		Binocular > monocular†	*	*	NS
Binocular‡			*	NS	NS
Asymptotic peak velocity					
Enucleated	NS	NS			Temporal > nasal
Monocular		NS			Temporal > nasal
Binocular‡					Temporal > nasal

NS, statistically nonsignificant difference.
* $P < 0.01$.
† For 20° temporal targets only.
‡ Preferred eye data during binocular viewing.

$$Y = V_{\max *}(1 - e^{-K*X}),$$

where V_{max} is the asymptotic peak velocity and K the slope at origin.

Univariate ANOVAs with a Greenhouse-Geisser correction are reported. An α level was set at 0.05 for all statistical tests and, for pairwise comparisons, family-wise error was controlled using a Holm's sequential Bonferroni approach.

Results

Upon graphic inspection of the latency data from the enucleated group and the controls' monocular data, we noticed that participants exhibited slower saccades when the target appeared at an eccentricity of 20° from fixation, but only if this stimulus step was in the temporal direction; that is, near the blind spot in the visual field (i.e., rightward saccades made by participants whose monocularly viewing eye was the right eye, or leftward saccades made with a viewing left eye). This led us to reorganize the monocular saccade data in terms of whether they were temporal (abducting) or nasal (adducting). This analysis also was consistent with literature that found an asymmetry for these directions in OKN and motion direction discrimination.[11,14,15] For consistency, the binocular data of the control group were organized similarly, although analysis in terms of rightward or leftward directions yielded results similar to that of the temporal versus nasal analysis. No analyses involving the open loop and the nonpreferred eye data are presented. A summary of the results is shown in Table 2.

Latency

Binocular saccades had shorter latencies than the monocular saccades of enucleated and control observers, who had similar saccadic latencies. Excluding the saccades to temporal stimuli at 20°, the mean latency of the enucleated observers' saccades was 1.19 (SD, 0.16) times longer than the mean of the binocular saccades. For the control observers, the latency of their monocular saccades was, on average, 1.1 (SD, 0.11) times longer than their binocular saccades.

The enucleated observers and the monocularly viewing controls also exhibited increased latencies to temporal stimuli at 20° eccentricity. This effect was found in 8 the 15 (53.33%) enucleated observers and in 12 of the 18 controls (66.67%). No other nasotemporal asymmetries in monocular saccade latencies were found (Fig. 1).

Enucleated Group. Analysis of the temporal saccades of the enucleated group and the monocularly viewing controls with a 2×4 between/within ANOVA for two groups and four stimulus step sizes (5°, 10°, 20°, and 30°) yielded a nonsignificant effect of group, a significant effect of step size, $F_{(1.42,93)} = 7.63$, $P < 0.01$, partial $\eta^2 = 0.20$, and a nonsignificant interaction between these two effects. Comparisons of the latency differences among the 5°, 10°, 20°, and 30° steps yielded statistically significant differences between the 10° and 20° ($P = 0.01$), and between the 20° and 30° ($P < 0.01$) steps only. For the nasally-directed saccades, a 2×4 between/within ANOVA for two groups and four stimulus step sizes (5°, 10°, 20°, and 30°) yielded no significant effects of group, step size, or of the interaction between them.

For temporal saccades, the comparison between the enucleated group and the binocularly viewing controls yielded a significant effect of group, $F_{(1,31)} = 13.66$, $P < 0.01$, partial $\eta^2 = 0.31$, and nonsignificant effects of step size and group x step size interaction. Similarly, for nasally-directed saccades, there was a significant group effect, $F_{(1,31)} = 11.00$, $P = 0.002$, partial $\eta^2 = 0.26$, and nonsignificant effects of step size or a group x step size interaction.

Control Group. For the temporal saccades, ANOVA of viewing condition (monocular/binocular) and stimulus step size (5°, 10°, 20°, and 30°) yielded significant effects of viewing condition, $F_{(1,17)} = 11.43$, $P < 0.01$, partial $\eta^2 = 0.40$; stimulus step size, $F_{(1.31,22.22)} = 6.08$, $P = 0.02$, partial $\eta^2 = 0.26$; and the interaction between these two main effects, $F_{(1.26,51)} = 6.71$, $P = 0.01$, partial $\eta^2 = 0.28$. Post hoc analysis of the interaction showed that temporal binocular latencies were shorter than temporal monocular latencies only at an eccentricity of 20° ($P = 0.01$).

For the nasal saccades, ANOVA of viewing condition (monocular/binocular) and stimulus step size (5°, 10°, 20°, and 30°) only yielded a significant effect of viewing condition, $F_{(1,17)} = 24.28$, $P < 0.01$, partial $\eta^2 = 0.59$, showing that the latency of nasal binocular saccades was shorter than that of nasal monocular saccades.

For the binocular saccades, a 2×4 repeated measures ANOVA for direction (temporal/nasal) and stimulus step size (5°, 10°, 20°, and 30°) yielded no significant effects of direction, stimulus step size, or the interaction between the two.

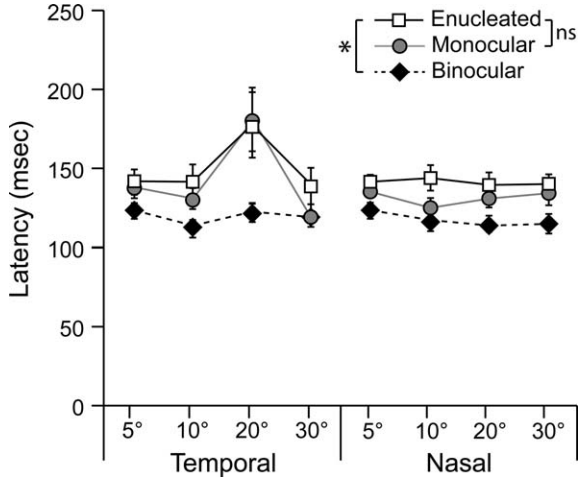

FIGURE 1. Mean saccadic latency as a function of stimulus step size (5°, 10°, 20°, and 30°) and direction (temporal/nasal). Stimulus step size was not a statistically significant effect and, for monocular viewing (enucleated and monocular control), saccadic latency was longer than for binocular viewing. *Error bars* are ±1 SE and all significant differences (*asterisks*) have a probability value $P < 0.01$. Only the data for the preferred eye are shown for the binocular condition.

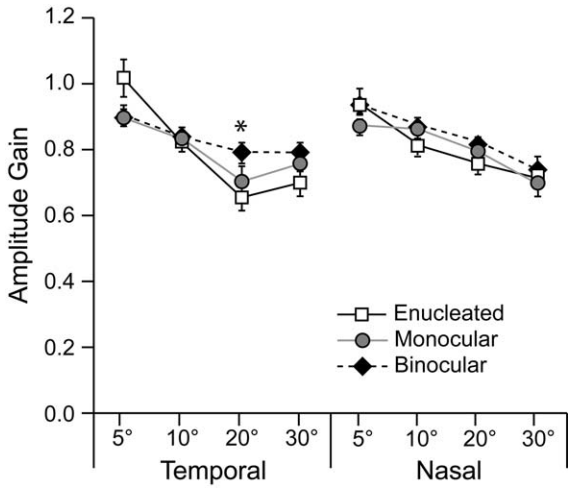

FIGURE 2. Mean saccadic amplitude gain as a function of stimulus step size (5°, 10°, 20°, and 30°) and direction (temporal/nasal). Stimulus step size was a statistically significant effect and, for monocular viewing (enucleated and monocular control), the amplitude gain for temporal stimuli at 20° was reduced compared to binocular performance. *Error bars* are ±1 SE and all significant differences (*asterisks*) have a probability value $P < 0.01$. Only the data for the preferred eye are shown for the binocular condition.

Amplitude Gain

There was a significant inverse relationship between saccadic size and accuracy; that is, the smaller saccades were more accurate than the larger ones. In addition, and consistent with the latency data, the amplitude gain of the monocular saccades for temporal stimuli at 20° appeared to be affected by the proximity of the blind spot in the visual field: the enucleated observers' saccades to 20° temporal stimuli were 13.54% (SD, 15.68) more hypometric than the controls' binocular saccades and the control group's monocular saccades were 8.54% (SD, 17.90) more hypometric than their binocular saccades. This effect was present in 86.67% of the enucleated observers and in 61.11% of the monocularly viewing controls. There were no other significant differences between temporal and nasal saccades.

Enucleated Group. For this group, there was a significant effect of step size, $F_{(1.99,27.79)} = 36.96$, $P < 0.01$, partial $\eta^2 = 0.73$, and a significant step size x direction interaction, $F_{(2.18,30.54)} = 3.94$, partial $\eta^2 = 0.22$. Analysis of the significant interaction showed that all the pairwise comparisons among steps for the temporal saccades were statistically significant ($P < 0.01$), and only that between 20° and 30° was nonsignificant. All the pairwise comparisons among steps for the nasal saccades were statistically significant ($P < 0.01$). There were no significant differences between temporal and nasal saccades at any step size.

The comparison between the temporal saccades of the enucleated group and the monocularly viewing controls was made with a 2 × 4 between/within ANOVA for two groups and four stimulus step sizes (5°, 10°, 20°, and 30°), which yielded a significant effect of step size, $F_{(2.26,70.23)} = 36.26$, $P < 0.01$, partial $\eta^2 = 0.54$, and no significant effects of group or of group x step size interaction. All pairwise comparisons among the step sizes were statistically significant ($P < 0.01$) with the exception of the 20° vs. 30° comparison.

For the nasal saccades, a second 2 × 4 between/within ANOVA for two groups (enucleated/monocular control) and four stimulus step sizes (5°, 10°, 20°, and 30°) yielded a significant effect of step size, $F_{(1.94,60.25)} = 36.32$, $P < 0.01$, partial $\eta^2 = 0.51$, and no significant effects of group or of group x step size interaction. All pairwise comparisons among the step sizes were statistically significant ($P < 0.01$).

The comparison between the temporal saccades of the enucleated group and the binocularly viewing controls yielded a significant effect of step size, $F_{(2.35,72.91)} = 33.92$, $P < 0.01$, partial $\eta^2 = 0.52$, and a significant interaction of step size x group, $F_{(2.35,72.91)} = 8.22$, $P < 0.01$, partial $\eta^2 = 0.21$. For the enucleated group, all pairwise comparisons of the steps were statistically significant ($P < 0.01$) with the exception of the 20° vs. 30° comparison. For the binocularly viewing controls, only the pairwise comparisons involving the 5° step were significant ($P < 0.05$). None of the group comparisons at each of the four step sizes was statistically significant despite the apparent groups differences at 5° and 20° in Figure 2.

For the nasal saccades, the comparison between the enucleated group and the binocularly viewing controls yielded a significant effect of step size, $F_{(1.95,60.53)} = 27.30$, $P < 0.01$, partial $\eta^2 = 0.47$, and no significant effects of group or of the group x step size interaction. All the pairwise comparisons among steps were statistically significant ($P < 0.01$).

Control Group. A 2 × 2 × 4 analysis of variance for viewing condition (monocular/binocular), direction (temporal/nasal), and saccadic step size (5°, 10°, 20°, and 30°) yielded a significant effect of viewing condition, $F_{(1,17)} = 5.76$, $P = 0.03$, partial $\eta^2 = 0.25$; a significant effect of step size, $F_{(1.26,21.48)} = 20.16$, $P < 0.01$, partial $\eta^2 = 0.54$; and a significant direction x step size interaction, $F_{(1.95,33.17)} = 6.28$, $P = 0.01$, partial $\eta^2 = 0.54$. This interaction was analyzed with two 2 × 4 ANOVAs for the binocular and monocular data, respectively.

For the monocular data, there were significant effects of step size, $F_{(1.44,24.45)} = 17.89$, $P < 0.01$, partial $\eta^2 = 0.51$, and of the direction x step size interaction, $F_{(1.68,28.61)} = 6.90$, $P = 0.01$, partial $\eta^2 = 0.29$. For the temporal saccades, the pairwise comparisons of the saccadic step sizes yielded statistically significant differences ($P < 0.01$), with the exception of the comparison between 20° and 30° step sizes. For the nasally-directed saccades, the pairwise comparisons of the differences among the saccadic steps were statistically significant ($P < 0.01$), with the exception of the comparison between 5° and

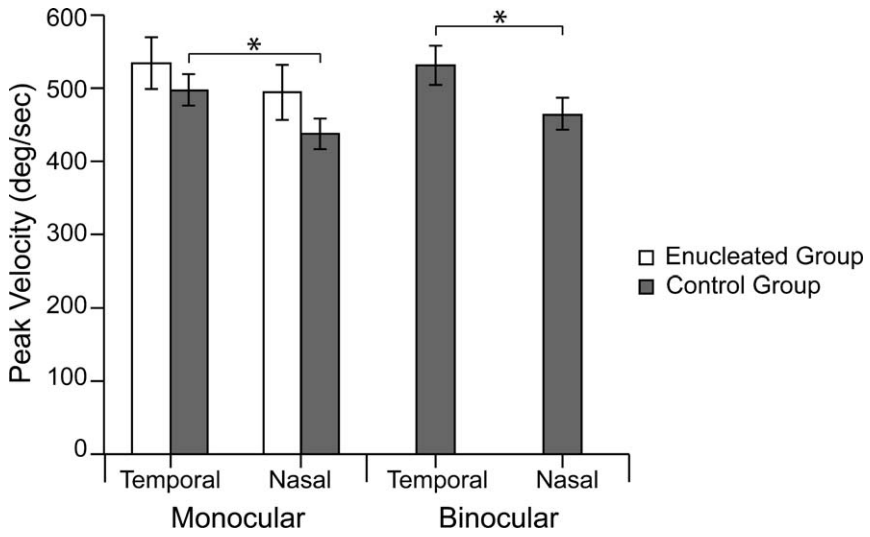

Figure 3. Collapsed across stimulus step size (5°, 10°, 20°, and 30°), asymptotic peak velocity (Vmax) as a function of stimulus direction (temporal/nasal). There were no significant differences between groups (enucleated/control) or viewing condition (monocular/binocular). *Error bars* are ±1 SE and all significant differences (*asterisks*) have a probability value $P < 0.01$. Only the data for the preferred eye are shown for the binocular condition.

10° step sizes. Temporal and nasal monocular saccades were only significantly different at 20° ($P = 0.01$).

For the binocular data, only the effect of step size was significant, $F_{(1.53,26.06)} = 14.19$, $P < 0.01$, partial $\eta^2 = 0.46$, and all the pairwise comparisons among steps were statistically significant ($P < 0.01$), with the exception of the 5° vs. 10° comparison.

Asymptotic Peak Velocity

For the enucleated and control groups, temporal saccades were faster than nasal saccades (Fig. 3).

Enucleated Group. The comparison between the enucleated group and the monocularly viewing controls yielded nonsignificant differences between groups, and significantly faster temporal than nasal saccades, $F_{(1,31)} = 19.48$, $P < 0.01$, partial $\eta^2 = 0.39$. Similarly, the comparison between the enucleated group and the binocularly viewing controls yielded nonsignificant differences between groups, and significantly faster temporal than nasal saccades, $F_{(1,31)} = 19.38$, $P < 0.01$, partial $\eta^2 = 0.38$).

For the enucleated group, the difference between saccade directions was nonsignificant, even though for 11 the 15 participants (73.33%) temporal saccades were faster than nasal saccades (mean difference, 39.41; SD, 83.83°/sec). (A posteriori power analysis showed that the sample size required for this difference to be statistically significant would have had to be 38.[18])

Control Group. A 2 × 2 ANOVA for viewing condition (monocular/binocular) and direction (temporal/nasal) yielded only a significant effect of direction, $F_{(1,17)} = 53.12$, $P < 0.01$, partial $\eta^2 = 0.76$, which means that temporal saccades were faster than nasal saccades monocularly (mean difference, 59.07; SD, 40.18°/sec) and binocularly (mean difference, 66.21; SD, 51.85°/sec).

Figure 4 shows the main sequence data for the two groups as a function of saccadic direction.

Saccade Dynamics as a Function of Age

Similar to the data of Irving et al.,[19] the relationship between age and saccadic latency for the enucleated and control groups, with monocular and binocular viewing, followed a U-shaped pattern, with younger and older participants exhibiting longer latencies. The enucleated group showed a significant decrease in peak velocity as a function of age for temporal ($r_{[13]} = -0.47$, $P = 0.04$) and nasal ($r_{[13]} = -0.52$, $P = 0.02$) saccades, consistent with the data of Irving et al.,[19] for people within the same age range. The control group data showed no statistically significant correlations between asymptotic peak velocity and age for the temporal, nasal, monocular, or binocular saccades. Figure 5 shows the data collapsed across direction and stimulus step size.

Because most participants in the enucleated group were enucleated at an early age, age and time since enucleation followed the same patterns. No relationships were found between latency, amplitude gain, or asymptotic peak velocity and age at enucleation.

Discussion

The horizontal saccade dynamics of enucleated people are similar to those of people with normal binocularity when they view monocularly; the monocular saccades of enucleated and control observers have longer latencies than binocular saccades, and the saccades of enucleated observers are as accurate as those of controls viewing monocularly. We also found that temporal stimuli located at an eccentricity of 20° produced, for a majority of enucleated and control participants (viewing monocularly), an increase in latency and a decrease in amplitude gain compared to binocular viewing. These findings have little precedence in the literature, probably because measurements of left and right eye saccades sometimes are averaged, and most monocular recordings are collected with binocular viewing.

Research often has found left/right asymmetries in saccadic latencies to be idiosyncratic (see the reviews of Honda[20] and Vergilino-Perez et al.[21]), and in our study we found that classifying the saccades' direction as either temporal (abducting) or nasal (adducting) accounted for a larger proportion of the variance than classifying them as rightward or leftward. This type of analysis also was consistent with literature that found an asymmetry for these directions in OKN and motion

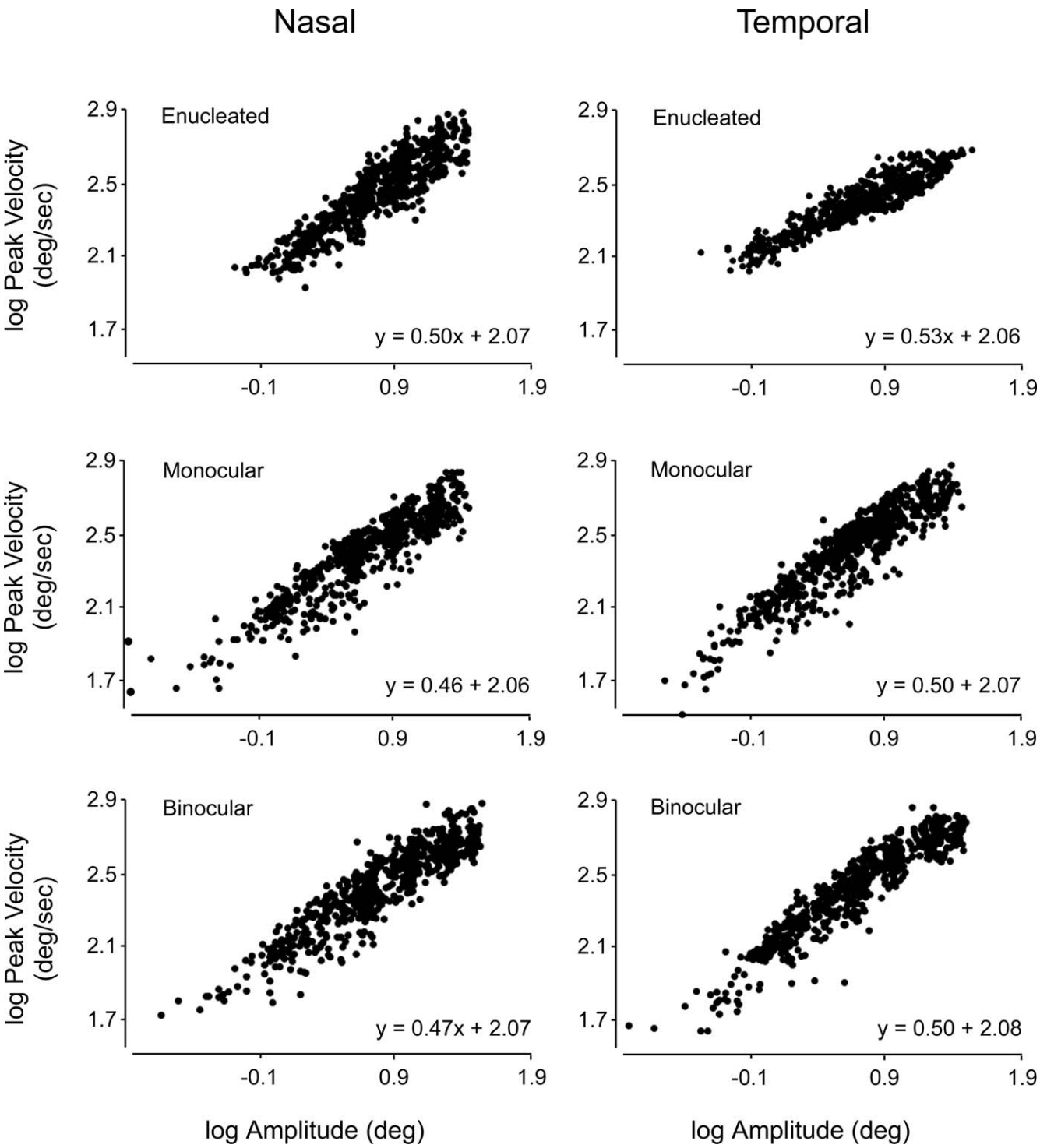

FIGURE 4. For the two groups, main sequence data in log–log coordinates as a function of saccadic direction (nasal/temporal). Only the data for the preferred eye are shown in the binocular condition.

direction discrimination.[11,14,15] No analysis of handedness could be made, since only one of our control participants was sinistral.

The design of our study did not allow us to investigate any amplitude–latency relationships. While the latencies of saccades starting from primary position increase with stimulus step size (amplitude–latency relation), the latencies of eccentrically initiated saccades decrease with stimulus step size (orbital position–latency relation), affecting the largest amplitudes the most.[22] In our study saccades could begin at any starting position, and were classified only in terms of their direction and stimulus step size. This allowed us to obtain the desired stimulus step sizes, while remaining within the recording range of the apparatus and the size of the display. It also minimized the recording time, which is an essential requirement when testing children. One drawback of this type of design[19] is that it requires averaging the latency of saccades

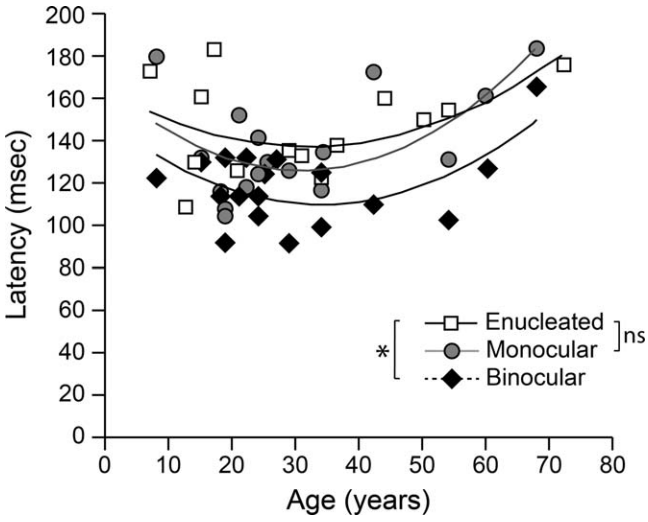

FIGURE 5. Collapsed across stimulus step size (5°, 10°, 20°, and 30°) and direction (temporal/nasal), latency as a function of age for the two groups: enucleated and control (viewing monocularly and binocularly). Data were fitted with second order polynomial functions that yielded the following equations: for the enucleated group, $y = 0.03x^2 - 1.81x + 165.94$ ($R^2 = 0.28$); for the monocularly viewing controls, $y = 0.04x^2 - 2.60x + 166.51$ ($R^2 = 0.41$); and for the binocularly viewing controls, $y = 0.04x^2 - 2.46x - 151.33$ ($R^2 = 0.37$). Only the data for the preferred eye are shown in the binocular condition. *Asterisk* refers to statistically significant differences at $P < 0.01$.

of the same amplitude regardless of starting position and cancels out any amplitude–latency relationships.

For all ages, our latency values (using a 60 cm viewing distance and stimulus duration of 1 second) were shorter than the binocular data of Irving et al.,[19] who tested their participants at 2 m and 1 m, and used stimulus durations varying randomly between 1 and 1.5 seconds. This effect is a function of our shorter viewing distances[23,24] and of the constant stimulus probability,[25–27] which have been shown to produce shorter latencies.

Monocular Versus Binocular Viewing

A significant finding was that binocular saccades exhibit shorter latencies than the monocular saccades of enucleated and control observers. The binocular summation of latencies could represent an increase in the strength of the visual signal that controls the movements of the eyes. The underlying mechanism could be based on the fact that, for horizontal saccades, premotor eye movement control circuits encode monocular eye movement commands and binocular coordination is achieved by the calibration of the network of motoneurons and interneurons that innervate the extraocular muscles.[28] This calibration occurs initially with the development of stereopsis and incorrect, weak, or absent signals could disrupt it, and may even be a cause for strabismus.[29] If the neurons innervating the extraocular muscles exhibit a form of binocular summation, it is possible that monocular viewing, either permanent or temporary, provides a weak signal to their network resulting in delays to saccadic onset.

Effects of Temporal Stimuli at 20° of Eccentricity

Most participants exhibited an increased delay and a hypometric decrease in accuracy to temporal stimuli at 20°. Similar changes in the shape of the saccadic latency function have been reported previously.[30] Pirozzolo and Rayner[31] found a linear decrease in latency for saccades up to 10° and an increase for stimuli beyond 10° to 15° away from fixation, and attributed the differences in latencies to a functional division of the visual field, with short saccades being under the control of mechanisms in the geniculocalcarine pathway and longer saccades being driven by the superior colliculus (SC). Our data cannot be accounted for by this explanation, because the increase in latency only occurred for temporal saccades during monocular viewing.

We propose that a more likely source of the increase in latency and the decrease accuracy to temporal stimuli at 20° is the nearness of these saccadic targets to the blind spot, which, on average, is 15.5° ± 1.1° (range, 13.0°–17.9°) temporally from the fovea in the visual field.[32] We found that the number of saccades to temporal stimuli at 20° was not reduced, which means that the effect was not due to the image of the target falling on the optic disc. The delaying effect of the blind spot on latency is reminiscent of the remote distractor (RD) effect,[33] in which the presentation of a distractor significantly increases saccadic reaction time to a target. Models explaining this effect are based on the mutually inhibitory neural activities at the locations of target and distractor, and predict that the RD effect is more prominent when the distractor is far from fixation.[34] If we assume that the blind spot acts as a distractor, albeit an unconscious one,[35] during monocular viewing, its effects on saccadic reaction time and accuracy could be accounted for by a similar inhibitory mechanism.

Other Saccade Characteristics of the Saccades of Enucleated Observers

The saccades of both groups tended to fall short of their targets, a common feature that, nevertheless, can be made to change depending on the stimulus set and task.[36] Our data also replicated the finding of Irving et al. of an inverse relationship between amplitude gain and saccadic step size.[19]

Just as for the monocularly viewing control participants, the temporal-ward (abducting) saccades of enucleated observers are faster than nasal-ward (adducting) saccades, a finding that has been reported previously,[37,38] but not consistently.[39] That this difference is weaker for the enucleated group could be related to plasticity through recruitment by the remaining eye of the resources normally assigned to the missing eye.[6–8]

CONCLUSIONS

Recent models of saccadic latency incorporate combinations of goal-related (top–down or endogenous) and stimulus-related (bottom–up or exogenous) neural signals that map onto visual stimuli, and combine in the retinotopic maps of the intermediate layers of the SC, which then project to the premotor circuits in the brainstem that drive the saccades.[40] Furthermore, recent data have shown that exogenous spatial attention can be dissociated from consciousness and that subliminal spatial cues can affect ocular motor responses.[41] We proposed that monocular saccadic latency data are the product of the additive effects of two factors: a weaker input to the network of motoneurons and specialized interneurons that innervate the extraocular muscles, and the remote distractor effect related to the natural scotoma produced by the optic disc in the temporal visual field.

Finally, this exploration of the saccade dynamics of enucleated observers showed that, by itself, the lack of binocularity does not produce the saccadic deficits found in other people with reduced or absent stereoscopic vision, such as those with amblyopia. Amblyopia has been found to produce an increase in saccadic latency, and a reduction in

amplitude gain that depend on its degree and type.[42–45] These deficits are part of a number of visual and motor impairments absent in enucleated people who are not affected by the abnormal binocular interactions associated with amblyopia.[3,5] Our findings suggested that the true monocularity produced by early enucleation does not result in slower visual processing in the afferent (sensory) pathway, or in deficits in the efferent (motor) pathway of the saccadic system.

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