Oculomotor challenges in macular degeneration impact motion extrapolation

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Macular degeneration (MD), which affects the central visual field including the fovea, has a profound impact on acuity and oculomotor control. We used a motion extrapolation task to investigate the contribution of various factors that potentially impact motion estimation, including the transient disappearance of the target into the scotoma, increased position uncertainty associated with eccentric target positions, and increased oculomotor noise due to the use of a non-foveal locus for fixation and for eye movements. Observers performed a perceptual baseball task where they judged whether the target would intersect or miss a rectangular region (the plate). The target was extinguished before reaching the plate and participants were instructed either to fixate a marker or smoothly track the target before making the judgment. We tested nine eyes of six participants with MD and four control observers with simulated scotomata that matched those of individual participants with MD. Both groups used their habitual oculomotor locus—eccentric preferred retinal locus (PRL) for MD and fovea for controls. In the fixation condition, motion extrapolation was less accurate for controls with simulated scotomata than without, indicating that occlusion by the scotoma impacted the task. In both the fixation and pursuit conditions, MD participants with eccentric preferred retinal loci typically had worse motion extrapolation than controls with a matched artificial scotoma and foveal preferred retinal loci. Statistical analysis revealed occlusion and target eccentricity significantly impacted motion extrapolation in the pursuit condition, indicating that these factors make it challenging to estimate and track the path of a moving target in MD.

Introduction

Macular degeneration (MD) is a highly prevalent, often age-related condition that affects the central retina, including the fovea (Hubschman, Reddy, & Schwartz, 2009; Klein et al., 2011). When the central retina is affected in both eyes, it can lead to a binocular scotoma or region of central field loss. Under these conditions, individuals adopt an eccentric preferred retinal locus (PRL) for fixation and as a reference for eye movements (Cheung & Legge, 2005; Fletcher & Schuchard, 1997; Schoessow, Fletcher, & Schuchard, 2012; Schuchard, Naseer, & de Castro, 1999; Tarita-Nistor, Sverdlichenko, & Mandelcorn, 2023). Smooth pursuit is known to be impaired when individuals with MD use eccentric PRLs to track moving objects (Shanidze, Fusco, Potapchuk, Heinen, & Verghese, 2016; Shanidze, Heinen, & Verghese, 2017). Specifically, pursuit gain is significantly impacted compared with control participants viewing the same stimuli, with decreased and more variable gain in MD.

The impact that deficits in smooth pursuit have on functional vision in daily life is still being understood. Recently, Shanidze and Verghese (2024) showed that the impairment of smooth pursuit in MD affects dynamic visual acuity during pursuit, with target discrimination in the MD group depending on pursuit gain. Additionally, maintaining the PRL on moving objects during pursuit might help individuals with field loss due to MD keep obstacles or incoming objects in view and prevent collisions. In controls with intact vision, smooth pursuit has been associated with improved performance in an eye soccer motion

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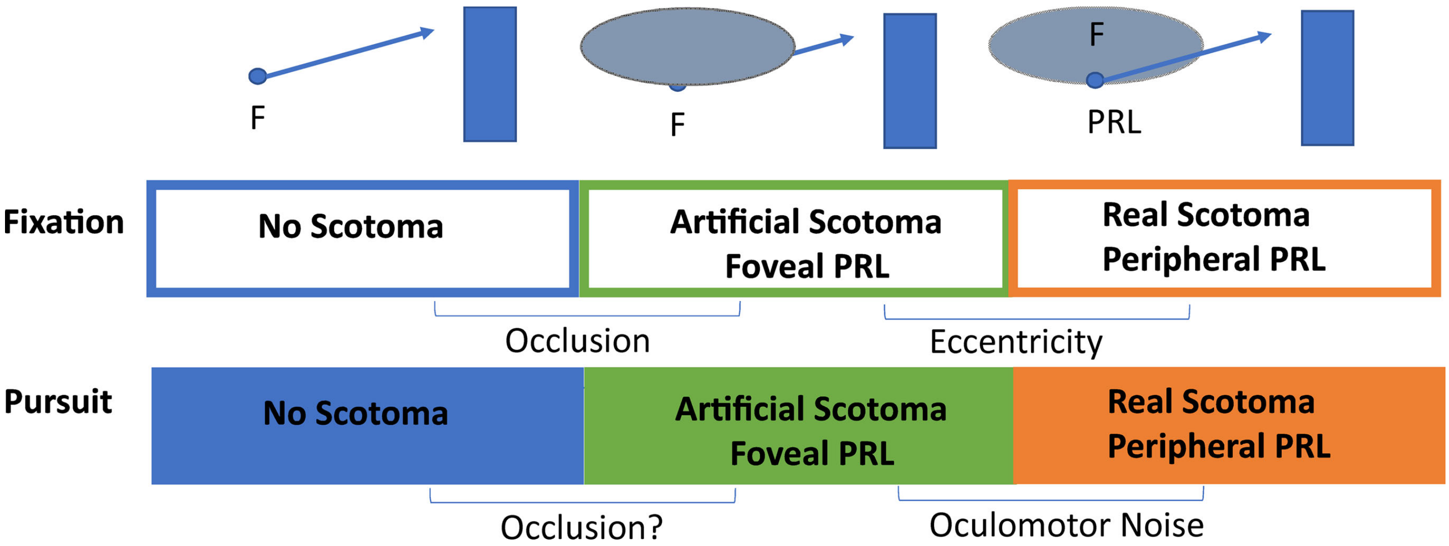

Figure 1. Schematic of experimental conditions. We used two experimental conditions (fixation and pursuit). Within each of these conditions, we compared three scotoma variants: no scotoma controls (blue), artificial scotoma in controls (green), and real scotoma in participants with MD (orange). The top row illustrates the fixation condition where observers maintain fixation and judge the end point of a trajectory that disappears before reaching the plate. We compare controls with no scotoma to those with a simulated scotoma to estimate the effect of occlusion due to the scotoma. The simulated scotoma matches the scotoma measured in the affected eye of an MD individual. A comparison of the simulated and real scotoma allows us to estimate the effect of target eccentricity as controls are fixating with their fovea and participants with MD are fixating with their PRL. The lower row shows the pursuit condition where the comparison between artificial and real scotomata allows us to examine the contribution of a non-foveal PRL to oculomotor noise.

extrapolation task, with pursuit gain correlating with the accuracy of motion prediction (Spering, Schütz, Braun, & Gegenfurtner, 2011). The use of pursuit eye movements has also shown to benefit motion prediction (Bennett, Baures, Hecht, & Benguigui, 2010). These studies suggest that, in addition to retinal information during pursuit, proprioceptive signals from eye muscles and efference copy of the motor command to drive the eye movement may influence motion extrapolation during occlusion. Thus, an impaired ability to pursue moving targets, as in MD, might also affect the ability to extrapolate the motion of a target. To further understand the factors that might affect smooth pursuit, and in turn affect performance in a motion extrapolation task, we used a task similar to ocular soccer (Spering et al., 2011).

There are several reasons why smooth pursuit may be impacted in MD. First and foremost is the loss of sensory input when the target enters the scotoma. Even though motion perception is generally intact in eccentric areas of healthy retina (Guénot et al., 2022; Shanidze & Verghese, 2019), the disappearance of a moving target under the scotoma could lead to a decrease in motion input to the visual system, and thus to a decrease in pursuit gain (Rashbass, 1961). Previous studies with normally sighted participants have shown that a temporary disappearance of the target behind an occluder leads to a decrease in pursuit gain (Barnes & Collins, 2008; Becker & Fuchs, 1985). Another factor affecting motion perception in central field loss is the added uncertainty in target position due to the more peripheral location of the PRL (Fahle & Schmid, 1988). As resolution declines with eccentricity (Virsu & Rovamo, 1979), the uncertainty in target position associated with a peripheral PRL increases with eccentricity. The third contributing factor that we consider is the challenge of using a non-foveal locus for fixation and for eye movements. An eccentric PRL is associated with increased fixation instability (Kumar & Chung, 2014; Verghese, Vullings, & Shanidze, 2021; White & Bedell, 1990; Whittaker, Budd, & Cummings 1988). Furthermore, White and Bedell (1990) demonstrated that only about one-third of their 21 participants with MD were able to use the PRL consistently as a reference for saccadic eye movements. As for pursuit with an eccentric PRL in MD, the gain of smooth pursuit is lower (González, Tarita-Nistor, Mandelcorn, Mandelcorn, & Steinbach, 2018; Shanidze et al., 2016) and is accompanied by increased saccadic intrusions (Shanidze, Lively, Lee, & Verghese, 2022).

In this study we set out to examine the effect of each of three factors on motion extrapolation in central field loss: (1) loss of visibility of the target due to occlusion by the scotoma, (2) eccentricity-dependent noise due to the use of non-foveal PRL, and (3) the

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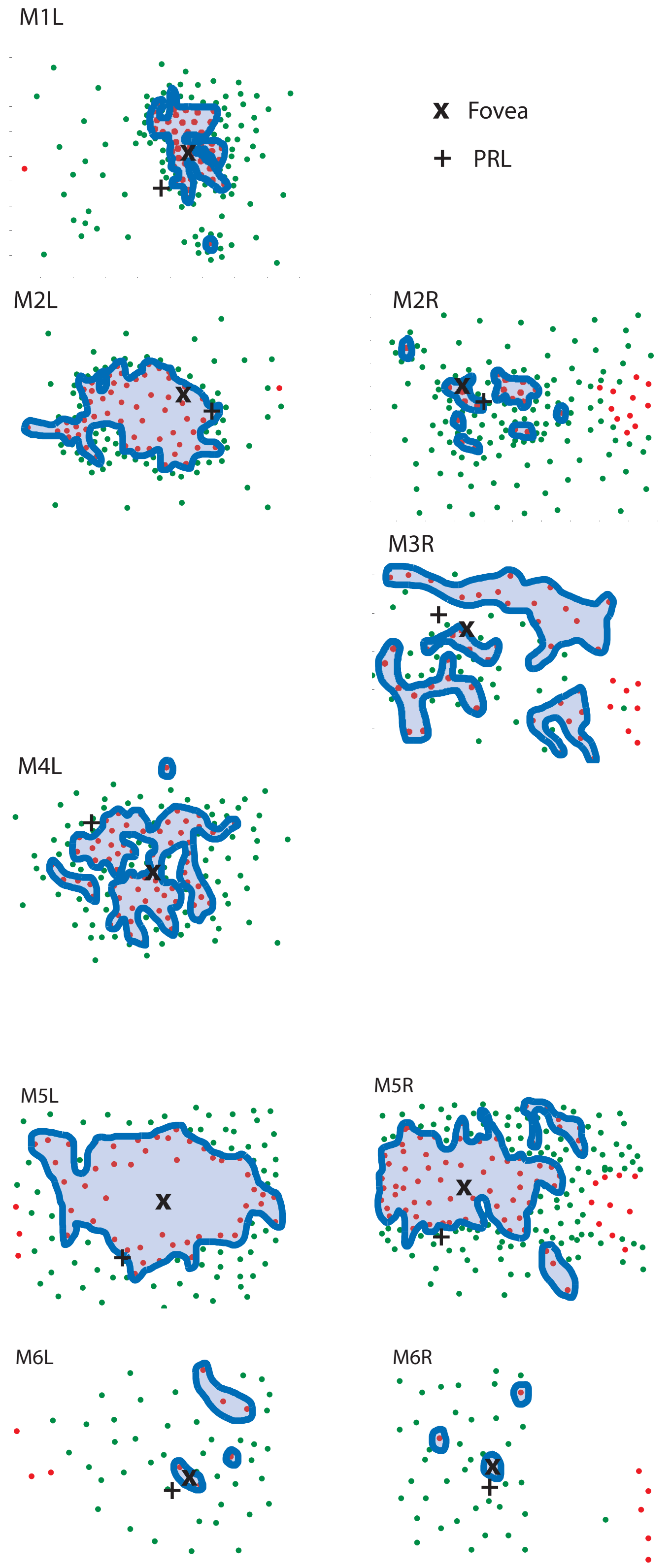

Figure 2. Scotoma maps of individual eyes that we tested, with left eyes and right eyes in the first and second columns, respectively. The “x” and “+” symbols indicate the fovea and PRL, respectively. The green and red dots indicate flash locations that were detected and missed, respectively, during microperimetry. The red symbols on the left of the first column → ← and the right of the second column mark the blind spot and are not included as scotomata due to MD.

challenge of using an eccentric PRL as an oculomotor reference. We adapted the baseball tasks of Fooken and Spering (2019), Kim, Badler, and Heinen (2005), where observers were required to extrapolate the path of a moving target that was extinguished before it reached a plate and to make a go/no-go decision: an eye movement or a manual interception of the target if it crossed a plate (strike) and withhold a response if it missed the plate (ball). Even though their task required a manual response, Fooken and Spering (2019) showed that the go/no-go decision in their task could be predicted by participants’ eye movements. In our version of the task, observers made a perceptual judgment of a ball/strike when they were instructed to fixate the starting position of the target, and while actively following the target with pursuit eye movements. We compared the performance of controls with no scotoma, controls with a non-foveal scotoma, and observers with MD with a scotoma that encompassed their fovea.

Figure 1 illustrates our experimental approach to evaluate the contribution of occlusion, increased target eccentricity in the presence of a peripheral PRL, and the oculomotor noise associated with a non-foveal PRL. We had three scotoma conditions (no scotoma, artificial scotoma and real scotoma) and two task conditions (fixation and pursuit). The artificial scotomata in controls were matched to the shape and location of the monocular scotoma in individual observers with MD with the artificial scotoma being placed at the analogous location with respect to the control’s fovea as the scotoma–PRL arrangement in an individual observer with MD’s scotoma. In the fixation task (top), the comparison of the no-scotoma and scotoma conditions in controls was designed to evaluate the effect of occlusion on target visibility, whereas the comparison of the artificial scotoma in controls and the real scotoma in participants with MD was designed to examine the effect of increased uncertainty in target position due the more peripheral location of the target in MD.

In the pursuit task (Figure 1, bottom) the comparison of the no-scotoma and artificial scotoma in controls was designed to investigate the effect of occlusion on target visibility, whereas the comparison of the artificial scotoma in controls and the real scotoma in MD was designed to investigate the effect of using a non-foveal locus for eye movements, as controls and participants with MD had matched scotoma, but controls had a foveal PRL, whereas participants with MD an eccentric PRL. Although smooth pursuit with an eccentric target has been demonstrated for targets moving horizontally

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in a predictable sinusoidal path both in the presence (Pidcoe & Wetzel, 2006) and absence of a compact circular scotoma (Winterson & Steinman, 1978), we wanted to test our participants with MD and controls with their natural PRLs as the target in our experiment moved along unpredictable linear or curved trajectories through actual, non-compact scotomata (see Figure 2).

As with a prior study (Guénot et al., 2022), the artificial scotoma in controls matched the scotoma of individual eyes in participants with MD, allowing us to use the fixation task to estimate the effect of the scotoma on visibility and the effect of uncertainty due to increased target eccentricity. In addition, by comparing pursuit in the presence of the same scotoma, in participants with MD with an eccentric PRL to controls with foveal PRL, we can investigate the impact of an eccentric PRL on eye movements. By isolating comparisons along these three factors associated with the functional impact of central field loss, we demonstrate that the loss of visibility due to the scotoma and increased target eccentricity have a significant impact on motion extrapolation in the pursuit condition, but not in the fixation condition.

Methods

Participants

Ten participants took part this study: six with MD (four female) and four participants with intact vision (one female). Microperimetry was performed on all participants with MD and a total of nine affected eyes were included in this study. The left eyes of all controls participants were tested, although we have limited right eye data for some participants. Participants were tested with their habitual correction for 1 m, if used. Most participants with MD chose not to wear glasses for viewing at this distance. The research protocol was reviewed by an independent ethical review board and conformed with the principles and applicable guidelines for the protection of human subjects in biomedical research, as stated in the Declaration of Helsinki. All participants provided their written consent to participate.

Apparatus

Stimuli were generated using PsychoPy (Pierce, 2007; Pierce et al., 2019) and rear projected on a large screen (40.36° × 30.27°), by a BenQ HT2050A DLP projector. Participants were seated at a distance of 1 m and viewed the display monocularly with their heads braced in a forehead and chin rest. Eye movements were sampled continuously with an EyeLink 1000 (SR Research Ltd., Ontario, Canada) in the tower-mount configuration at 1,000 Hz. A 5-point eye tracker calibration was performed before each block of 50 trials. The participant was asked to fixate each of five points in turn with their fovea or PRL. The size of the calibration annulus was increased to 1.5° diameter to improve visibility for participants with MD. In cases where the calibration could not be completed with five points, we used a three-point calibration.

Procedure

Visual function

Monocular visual acuity was measured with a Bailey Lovie chart (Berkeley School of Optometry, Berkeley, CA) at a distance of 3 m, and stereoacuity was measured with the RanDot Stereo test (Stereo Optical, Chicago, IL).

Microperimetry and PRL

For individuals with MD, we estimated the extent of functional vision loss in each eye using microperimetry as described in Vullings, Lively, & Verghese (2022). Briefly, we used the Optos (Optos Inc., Marlborough, MA) optical coherence tomography/scanning laser ophthalmoscope (OCT/SLO) to perform monocular microperimetry and to measure fixation stability, within a square window of 29.7°. We manually selected the test flash locations to probe each participant's functional scotoma (see Figure 2 for all nine scotoma maps). The absolute scotoma was measured with unattenuated 0-dB flashes with a dot luminance of 125 cd/m^2 and a Weber contrast of 12.5. For one participant (M3), we also measured the relative scotoma by attenuating the contrast of the flash in 2-dB steps until the flashes were no longer detected. Fixation stability and the PRL for static fixation were also measured monocularly, using a 10-second fixation target in the SLO. A custom MATLAB (MathWorks, Natick, MA) script was used to generate a border around the scotoma so that the shape of each affected eye's scotoma could be replicated as an artificial scotoma in controls.

Task

Observers viewed the display monocularly and performed an ocular baseball task similar to that of Fooken and Spering (2019) where they judged whether the extrapolated path of a target crossed the plate (strike) or missed the plate (ball). Figure 3A shows a schematic of our experimental display. A circular

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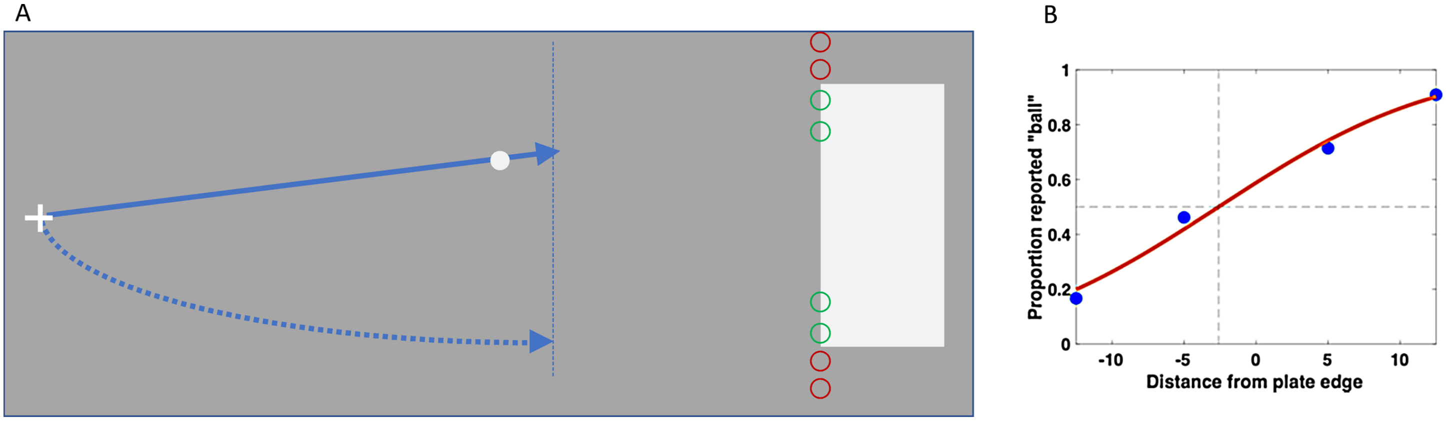

Figure 3. (**A**) Schematic of the experiment with a straight and curved (shown dotted) trajectory, illustrating potential end points on the plate. Green locations indicate strikes and red locations indicate balls. (**B**) Sample psychometric function from a control observer.

target 0.3° in diameter started from a fixation point 8° from the center of the display and moved toward a plate that was 8° on the other side of the display center, resulting in a distance between the starting point and the center of the plate of 16° (Figure 3A).The plate was 4° high and 2° wide, and could be on the left or right of the display with the corresponding starting point of the ball on the opposite side of the display. The target traveled a horizontal distance of 9.6 ° in 1.3 seconds, and disappeared at a distance of 5.4° from the nearest edge of the plate. On each trial, the target was programmed to hit the near edge of the plate at one of eight locations: ±0.2° or ±0.47° from the upper or lower edges of the plate (with negative values indicating a strike). The ball either followed a linear or a curved trajectory, always starting at a fixed location at a horizontal distance of 16° from the vertical center of the plate with the extrapolated trajectory ending at one of the eight locations mentioned above (Figure 3A). The probability of a curved path on any given trial was 67%. The curved path was created by randomly picking a vertex with a horizontal and vertical location within 1° of the midpoint between the starting and ending position of the target. A curved trajectory was created by fitting a parabola that passed through the starting point, the randomly selected vertex, and the end point for the trial.

Observers performed the task under two conditions that were blocked, but presented in randomized order: *fixation*, where they were required to maintain fixation on the starting point throughout the trial (if the eye deviated more than 1° from fixation, they received a warning), or *pursuit*, where they were asked to actively follow the target with eye movements. For each of the fixation and pursuit conditions, the location of the plate was blocked to be on either the left or the right, and the target correspondingly moved leftward or rightward. In the fixation condition, the distance of the plate from the fovea (16°) caused it to fall in the blind spot in the temporal visual field especially for controls with a foveal PRL; thus, for the fixation condition we only report rightward motion when left eyes were tested (all controls and M1, M2, M4, M5, and M6), and leftward motion when the right eye was tested for participants with MD (M2,M3, M5, and M6). This was not an issue for the pursuit condition because observers were free to move gaze with the target. Thus, we tested leftward and rightward motion for the pursuit condition. Each fixation and pursuit condition was run in a block of 50 trials.

Simulated scotoma

As described in a preceding section, we did microperimetry in the SLO to map out the scotoma in the affected eyes of each MD participant. We also measured fixation stability with a 10-second fixation target. We then used the OCT to locate the foveal pit (Verghese, Tyson, Ghahghaei, & Fletcher, 2016) and used the software developed by Ghahghaei and Walker (2015) to align fixation stability, perimetry, and OCT images and superimpose the fixation locus and the foveal pit on the perimetry map. In Figures 2 and 4, the fixation locus is the PRL and is marked with a "+" symbol while the fovea is marked with an "x" symbol. We then created a scotoma map that outlined the scotoma regions and used this outline to render a gaze-contingent scotoma for controls. Controls were tested with the scotoma from each MD eye that we included. The scotoma boundary was not visible, and the region within the scotoma was set to be the same gray as the background, rendering the target invisible when it was under the scotoma (see Supplementary Movies 1 and 2 to visualize trials in the no-scotoma and simulated scotoma conditions; Supplementary Movie 3 is for visualization purposes only and shows the outline of the simulated scotoma). Participants with

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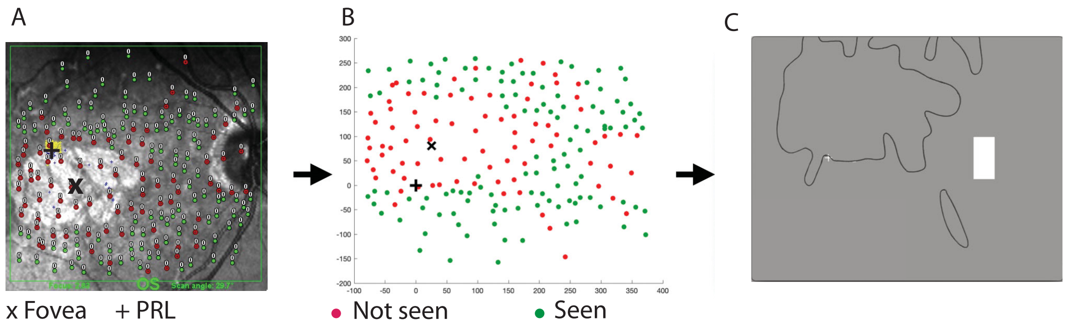

Figure 4. Creating a scotoma outline. (**A**) Microperimetry for the right eye of participant M5 showing the microperimetry overlaid on his retinal scan. The x and + symbols plot the locations of the fovea and PRL, respectively. (**B**) Seen and missed flash locations without the retinal scan. These points have been flipped vertically to compensate for the inversion of the retinal image. The outline of the real scotoma is used to simulate a scotoma in controls. (**C**) A visualization of the simulated scotoma, superimposed on the screen. The outline is shown for purposes of illustration only. In the experiment, the scotoma outline was invisible, and the target disappeared when it entered the scotoma region.

ID	Sex	Age	OS acuity	OS PRL (°)	OD acuity	OD PRL (°)	Stereoacuity
Patients							
M1	M	78	**0.6**	**3.21**	0.5	0	>30
M2	F	80	**0.81**	**1.07**	**0.4**	**1.06**	>30
M3	F	73	0.18	0.85	**0.84**	**3.14**	1.67
M4	F	81	**0.42**	**6.89**	0.11	1.80	>30
M5	M	60	**1.1**	**5.82**	**1.2**	**5.1**	19.2
M6	F	81	**0.74**	**1.89**	**0.36**	**1.08**	3.33
Controls							
C1	F	60	**0.0**	**0**	0.1	0	<0.67
C2	M	29	**0.0**	**0**	0.0	0	<0.67
C3	M	23	**0.0**	**0**	0.0	0	<0.67
C4	M	23	**−0.1**	**0**	−0.1	0	1.75

Table 1. Monocular acuity (logMAR), PRL distance from fovea, and stereoacuity. Tested eyes are in bold.

MD (M1, M3, and M4) (Table 1) had foveal scotomata in only one eye, so we only tested their affected eyes. We tested all eyes with foveal scotomata leading to a total of nine eyes. A total of four controls took part in the experiment. All controls were tested in the no-scotoma condition and three controls were tested with simulated versions of each of the nine foveal scotomata (C1, C2, and C3 for M1, M2, M3, and M4; and C1, C2, and C4 for M5 and M6).

Data analysis

Participants' ability to judge whether the target crossed the plate was measured as a function of the distance of the target from the upper and lower edge of the plate for straight and curved trajectories, for pursuit and fixation. From the observer's response after each trial, we used the proportion of hits and false alarms to calculate d′ as a measure of participant's performance for each condition. We also analyzed data for curved and straight paths for individual observers within each condition, and found that across participants with MD and controls, there was not a significant difference in d′ between straight and curved trajectories. Thus, we report a single d′ for each observer and condition. We also plotted the proportion of "ball" responses as a function of the distance from the edge of the plate and fit these data with a cumulative Gaussian to determine bias and sensitivity (1/standard deviation of the Gaussian fit). The example psychometric function shown in Figure 3B is a fit to a control observer's data in the no-scotoma condition. It combines data from the lower and upper edges and shows that the observer had a slight tendency (a bias of 2.5 pixels, or 0.1°) to underestimate the size of the plate—the point of subjective equality is shifted to negative values that indicate locations inside the edge of the plate.

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We also monitored eye position on every frame for both the fixation and pursuit conditions. For the fixation condition, participants received both an auditory and text warning on trials when their gaze exceeded a tolerance window of 1° radius around the fixation marker. We did not discard the trials, but retained them to determine whether the eye movement was due to fixation instability or was a strategy to fixate another location. Eye position in the pursuit condition was compared with the target position and used in the model to predict psychophysical performance in the task.

Models

We implemented two models: a generalized linear mixed effects (GLME) model to quantify the effects of occlusion, eccentricity and oculomotor noise on overall performance for the fixation and pursuit conditions, and a trial-by-trial decision model to predict ball/strike decisions based on visible target samples and on eye position in each trial.

GLME model

The GLME model had participants as a random effect factor, and fraction of the target occluded, target eccentricity from the fovea, and oculomotor noise as fixed effect factors. The model also includes pairwise interactions between fraction occluded, eccentricity and oculomotor noise. We ran a separate GLME model for the fixation and pursuit conditions. The fraction occluded was calculated on a trial-by-trial basis for each condition for each observer as the proportion of the target occluded, given the current eye position and scotoma. The fraction occluded was then averaged across all trials for each observer for each condition (fixation, leftward pursuit, and rightward pursuit). Target eccentricity was taken as the average distance of the target from the fovea on any given trial, given eye and target position. For participants with MD, the eccentric PRL adds further distance to the target. The values across trials for a condition were averaged to yield a mean eccentricity for each observer for that condition. As a measure of oculomotor noise in the fixation condition, we calculated the standard deviation of the eye positions during the trial. For the pursuit condition, we calculated the standard deviation of eye distance from the target during pursuit, for each trial. The oculomotor noise for a condition was taken as the mean of this standard deviation across trials for that condition. To account for open-loop pursuit latencies that are typically 150 ms, and to avoid eye deviations from the target at the end of the trial, we only considered oculomotor noise between 200 and 600 ms. For the pursuit model, we excluded the data from two participants (see Figure 7) because they did not follow instructions to pursue the target. Instead, they moved their fixation to a far peripheral location, so that they could view the entire trajectory in their periphery.

All statistical tests used an alpha level at 5%. We first checked the d′ distributions for normality, separately for controls and patients, and for fixation and pursuit conditions, and found these to be normal (Kolmogorov–Smirnov tests: fixation condition: controls, Kolmogorov–Smirnov = 0.11, $p = 0.84$; patients, Kolmogorov–Smirnov = 0.22, $p = 0.84$; and pursuit condition: controls, Kolmogorov–Smirnov = 0.13, $p = 0.26$; patients, Kolmogorov–Smirnov = 0.16, $p = 0.80$). We then checked for collinearity between the fixed-effect factors: no collinearity was strong enough to prevent analysis. In the fixation condition, eccentricity and fraction occluded correlated significantly (Kendall tau = 0.28; $p = 0.02$). Oculomotor noise was not correlated with eccentricity ($p = 0.92$), nor with fraction occluded ($p = 0.69$). In the pursuit condition, eccentricity correlated significantly with fraction occluded (Kendall tau = 0.27; $p = 0.0005$) and oculomotor noise (Kendall tau = 0.34; $p < 0.0001$), but fraction occluded and oculomotor noise did not correlate ($p = 0.89$).

Competing models included combinations of the mentioned factors but always included participants as a random-effect factor for the intercept (see GitHub link for details of competing models: https://github.com/Stereo-Boy/smooth_pursuit_MD_GLME). We compared all the competing models using the Akaike Information Criterion to select the best model, provided the residuals were normally distributed.

For the fixation condition, our best model (Akaike information criterion = 55.8, $R^2 = 31.7\%$, adjusted $R^2 = 29.7\%$, Kolmogorov–Smirnov test for normality of residuals: Kolmogorov–Smirnov = 0.13; $p = 0.54$) took the following form:

$$d' \sim 1 + (1|\text{participant}) + \text{fraction Occluded} : \text{oculomotor Noise}.$$

For the pursuit condition, our best model (Akaike information criterion = 138, $R^2 = 44.4\%$, adjusted $R^2 = 42\%$, Kolmogorov–Smirnov test for normality of residuals: Kolmogorov–Smirnov = 0.08; $p = 0.65$) took the following form:

$$d' \sim 1 + (1|\text{participant}) + \text{fraction Occluded} * \text{eccentricity (which includes main effects)}.$$

To interpret Cohen's f2 effect sizes, we used guidelines indicating that 0.02 is a small effect, 0.15 is a medium effect and 0.35 is a large effect (Cohen, 2013).

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Trial-by-trial decision models

To determine how the three factors that we proposed in the Introduction contributed to performance in the ocular baseball task, we explicitly included a decision model that predicted motion extrapolation on each trial based on visible target samples in that trial, perturbed by eccentricity-dependent noise. The visible target samples included only the trajectory points on each trial that were not occluded. To determine what target points were obscured by the scotoma, we recorded eye position on every frame and used the scotoma boundary to determine whether the target position was within the scotoma. This meant that the scotoma was largely stationary during the fixation condition and moved with gaze during pursuit. Next, to incorporate the effect of eccentricity on the uncertainty in target position, we added eccentricity-dependent noise in both the x and y dimensions to every visible target point as a function of eccentricity, using estimates of resolution from the data of Fahle and Schmid (1988). Eccentricity of the target from the fovea was calculated assuming a foveal oculomotor locus for controls, and by adding the offset of the PRL from the fovea for MD. We then fit the noisy data points to both curved and linear functions and chose the function that fit the data better (minimized sums of squared error). The model then extrapolated the best-fitting function toward the plate and made a ball or strike decision.

The decision model based on target position makes a prediction on the basis of noisy sensory data, but does not incorporate eye position directly. For the pursuit task, we also considered versions of the model that used eye position data on every frame and estimated the target trajectory by extrapolating the best-fitting curve to the eye-position data. A third variant of the decision model averaged target position and eye position on every frame and found the best-fitting curve. Finally, to incorporate the bias in observer decision, we added the bias value estimated from each observer's psychometric fit for each condition to the extrapolated model trajectory.

Results

Figure 6 plots the ability of observers to make the strike/ball judgment as d′ for the fixation and pursuit conditions. The plot includes average data from three controls for the no-scotoma condition (first column) with the results for the fixation condition on the left (open symbols) and the pursuit condition on the right (solid symbols). The fixation condition shows data for rightward motion, whereas the pursuit condition shows leftward and rightward motion of the left eye of controls. An inspection of these data shows that the pursuit condition is not significantly different from the fixation condition. This result indicates that keeping the fovea close to the target in the pursuit condition does not provide a significant benefit, at least for controls in the absence of a scotoma. Conversely, this finding implies that the eccentricity-dependent uncertainty in the position of the target in the fixation condition has little impact on motion extrapolation of an isolated target in the absence of a scotoma, when the entire trajectory is visible until it is extinguished.

The next nine columns are for the scotoma conditions indicated on the abscissa. Each column plots the data of one eye of an MD participant (in orange) alongside the average data from three controls with a simulated scotoma from that same MD participant (in green). Note that the scotoma was placed relative to the controls' foveal PRL (in green), so that the scotoma has the same relation to the observer's (control or MD) habitual PRL. The open and solid symbols plot data for the fixation and pursuit conditions, as before. The pursuit data (solid symbols) is further subdivided into directions where the trajectory was moving rightward or leftward.

Fixation with and without a scotoma

Performance in the fixation task allowed us to isolate the effects of loss of visibility due to the scotoma by comparing controls with no scotoma and controls with a simulated scotoma (open blue and green symbols in Figure 6). The presence of a scotoma impacted performance in the fixation task for control participants, except for the M3 and M5R scotomata.

Fixation with real and artificial scotomata

A comparison of performance with the real and artificial scotomata allowed us to examine the contributions due to the increased positional uncertainty of the target due to an eccentric PRL in MD. An examination of the fixation condition (Figure 6, open orange and green symbols for real and artificial scotoma, respectively) shows that observers M1, M3, and M4 with MD performed worse than controls with matched scotomata relative to their fovea (their d′ is outside the standard error across control observers). We do not plot the fixation data for MD participant M2 because she did not follow the instructions to keep gaze on the fixation mark during the fixation condition. The poorer performance in the fixation condition for participants M1, M3, and M4 suggests that the increased eccentricity of the target from the fovea resulting from their use of a peripheral PRL impacts performance compared with

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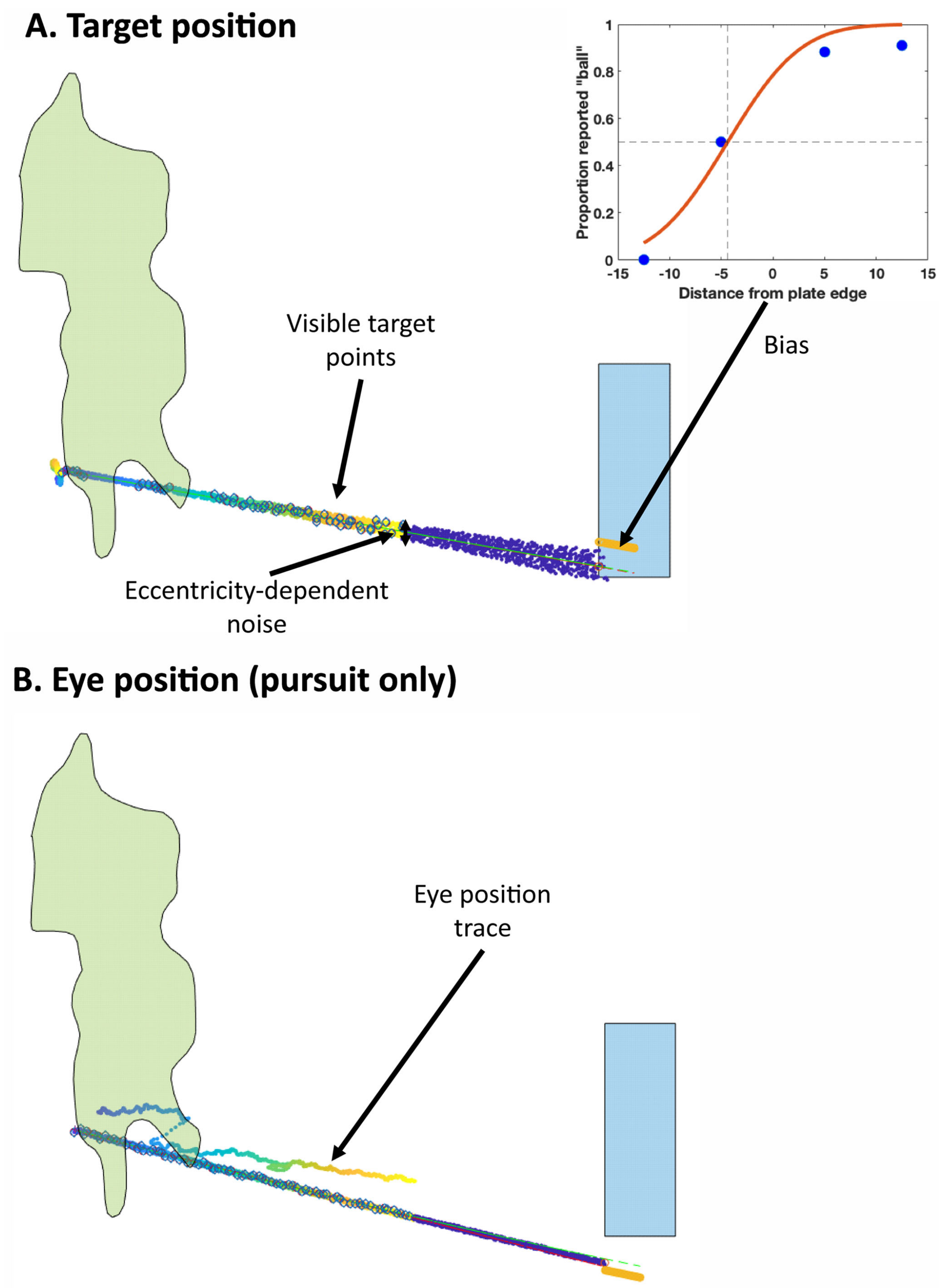

Figure 5. Model schematic. (**A**) Target position–based model uses target samples (circles) not occluded by the scotoma with added eccentricity-dependent noise. The best fit to the noisy samples (line or curve) is extrapolated to the plate and the bias estimated from the observer's psychometric function for that condition is added to get the model prediction for that trial. (**B**) Eye position based model is similar to (**A**), except that the prediction is based on the best fit to the eye-position samples (the blue to yellow color range depicts samples from the beginning to the end of the trial). A variant of this model is the mixed model that averages the target and eye samples and estimates the trajectory.

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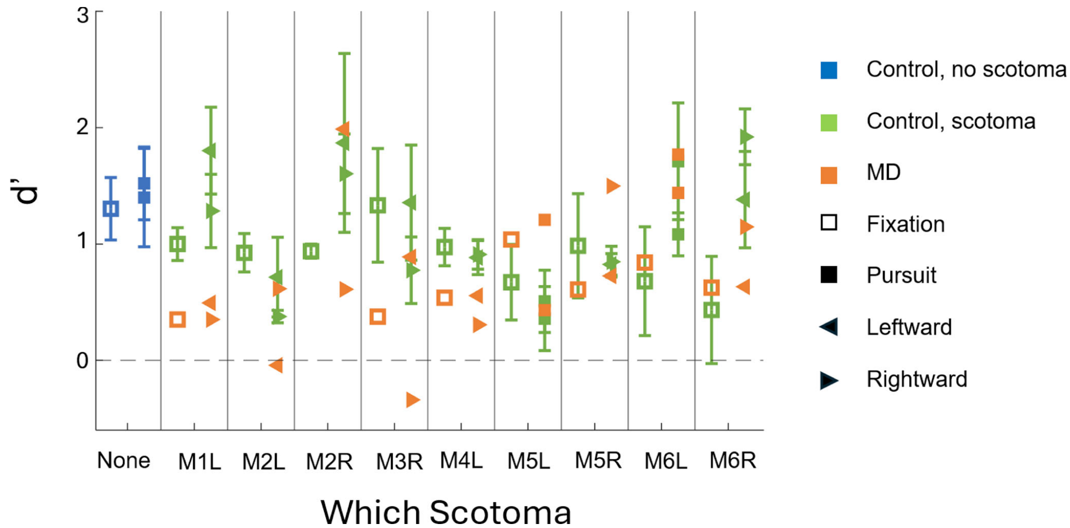

Figure 6. Discrimination between strike and ball trajectories (d′) plotted for various scotoma conditions. The no-scotoma condition is shown in the first column. Subsequent columns illustrate the scotomata of individual participants with MD and the average performance of three controls when using the corresponding scotoma. The no scotoma, artificial and real scotoma conditions are shown in blue, green and orange, respectively. Open symbols indicate fixation and closed symbols indicate pursuit. Error bars represent standard error across all control participants when tested with a given scotoma.

controls who had matched scotomata, but a foveal PRL. Interestingly, M5 and M6 have comparable performance to controls for different reasons. M6 has PRLs very close (approximately 1°) to the fovea, whereas M5 has juvenile MD and had long-standing experience with eccentric PRLs.

Pursuit with and without a scotoma

The pursuit condition allows us to determine whether pursuit could mitigate the effect of occlusion by the scotoma. A comparison of controls with and without a scotoma (filled green and blue symbols in Figure 6) shows that in the pursuit condition, d′ with most artificial scotomata (with the exception of M2's left eye scotoma and M5's large bilateral scotoma) is comparable with d′ without a scotoma, suggesting that pursuit is able to compensate for occlusion by the scotoma, at least for controls with a foveal PRL.

Pursuit with real and artificial scotomata

The comparison of real scotoma with an eccentric PRL to a matched artificial scotoma with a foveal PRL allows us to evaluate the impact of an eccentric PRL on eye movements. An inspection of the filled orange and green symbols in Figure 6 shows that performance in the motion extrapolation task is worse than controls for some observers with MD (M1, M2, M3, and M4) and is comparable with controls for others (M5 and M6).

We also evaluated whether task performance was related to the ability to track the target by measuring the average distance between target and PRL on every trial and plotting the distribution of these distances for individual MD eyes and their matched controls (Figure 7). Pursuit gain is a more standard measure of smooth pursuit, but MD eyes rarely showed periods of constant velocity in our task (see Supplementary Figure S1), so we plot distance from the target instead. The average eye-to-target distance in each trial was estimated in the interval from 200 to 600 ms, to avoid open-loop pursuit at the beginning of the trial and deviations of gaze at the end of the trial. The distribution of these distances across trials for leftward and rightward pursuit (Figures 7A and 7B) was compared between each observer with MD and three controls with matched scotomata. In general, observers with MD (except M3) had PRL positions that were more variable and further from the target than controls with matched scotomata and foveal PRLs. The exception to the lower variability of distances for controls is for M5's scotomata. In this case, the larger range of the control distributions is largely due to control C4, who had poor pursuit with M5's large simulated scotomata. A closer inspection of pursuit distances indicates that three MD eyes (M2R, M5L, and M5R) maintained a very large but consistent distance from the target (rightward pursuit, Figure 7B). They adopted the strategy of moving their gaze (PRL) to a location away from the target and observing

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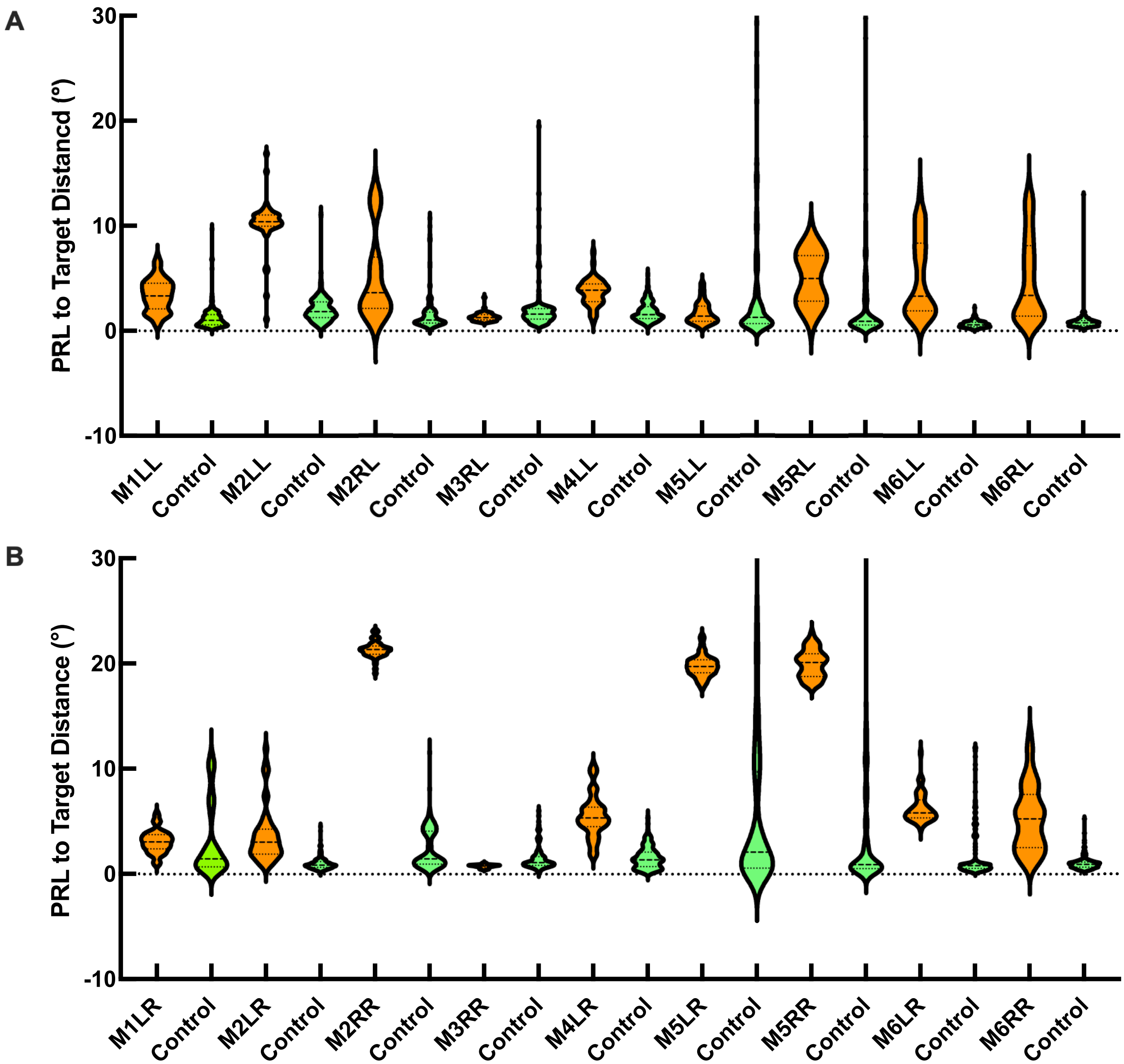

Figure 7. Violin plots of PRL-to-target distance in participants with MD (orange) and controls with matched scotomata (green). Data for left and rightward pursuit are shown in (**A**) and (**B**). Each symbol shows the mean (dashed line), upper and lower quartiles (dotted lines), and the range of the data. Abscissa labels such as M1LR indicate the MD participant (M1), the eye tested (left), and the direction of pursuit (rightward). Control data are pooled across three participants.

the target from this location. It is not clear why M2 adopted this strategy for the right eye, which had a small scotoma. Neither is it clear why M5 adopted this strategy, because the scotomata in both eyes were largely above the PRL. However, the strategy avoided the need to track the target and allowed him to view much of the target path from an eccentric location (panel M5 pursuit in Supplementary Figure S1). Only one MD eye maintained a similar median distance to the target as controls—M3, who had a PRL close to the

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fovea. Overall, controls with simulated scotoma were able to keep their fovea closer to the target than most MDs using a peripheral PRL.

Effect of occlusion, eccentricity, and oculomotor noise

To understand how the sensitivity to motion extrapolation (d′) was related to the three factors we considered in the Introduction, we specifically examined the relation of d′ to the proportion of the trajectory that was occluded by the scotoma, to the eccentricity of the target from the fovea, and to oculomotor noise. This last factor was determined by how steadily the participant fixated or pursued the target, that is, the variance of gaze position around the fixation target in the fixation condition and the variance of the gaze distance from the target in the pursuit condition. Each row of Figure 8 plots the data for each of these factors, looking at the data for fixation (Figure 8, left), and pursuit (Figure 8, right). In each panel the blue, green, and orange symbols denote the no-scotoma, artificial scotoma, and real scotoma conditions, respectively, with each symbol representing d′ for individual blocks for individual observers.

GLME models

We ran separate generalized linear mixed-effect models for fixation and for pursuit. The model for fixation did not show a significant contribution of any of the three factors on d′ (all $p > 0.82$). However the model for pursuit showed a large effect of fraction occluded on d′, $t(72) = -5.02$, $p = 3.5 * 10^{-6}$, Cohen's f2 = 0.4, with a small effect of eccentricity, $t(72) = -2.11$, $p = 0.038$, Cohen's f2 = 0.02, and a small interaction between fraction occluded and eccentricity, $t(72) = 2.31$, $p = 0.024$, Cohen's f2 = 0.05.

The GLME models for fixation and pursuit are consistent with a visual inspection of the data. If we look at d′ as a function of the average fraction of trajectory that was occluded for the fixation case (Figure 8A), there seems to be no consistent relationship between the fraction occluded and the ability to extrapolate motion and distinguish balls from strikes. In contrast, for the pursuit condition d′ seems to depend on how well the participant was able to track the target and keep it out of the scotoma (Figure 8B). This outcome suggests that participants were better able to extrapolate motion when they tracked the target with smooth pursuit eye movements, consistent with previous studies on the benefits of smooth pursuit for motion prediction (Bennett, et al., 2010; Spering et al. 2011).

If we consider the effect of eccentricity on d′, in the fixation case there is no clear relation between d′ and eccentricity (Figure 8C), whereas in the pursuit case d′ decreases with the eccentricity of the target (Figure 8D), consistent with the GLME model. If we compare the fixation and pursuit cases in the presence of a scotoma (artificial or real) the average eccentricity of the target is higher for pursuit than for fixation, indicating that gaze is paradoxically further from the target when observer tries to pursue the target in the presence of a scotoma. As for the effect of oculomotor noise, there is no clear relation between oculomotor noise and d′ for either the fixation or pursuit conditions (Figures 8E and 8F). One point to note is that individuals with real scotomata (MD) have much larger values of oculomotor noise in the fixation condition, indicating that they have difficulty fixating with their eccentric PRL.

Trial-by-trial decision models

In addition to the GLME model, which looks at the d′ for a condition as a function of the average value of the three factors for that condition, we formulated a decision model to predict ball/strike choice on a trial-by-trial basis. Model predictions were based on extrapolating noisy target samples, using only target samples that were visible depending on eye position and occlusion by the scotoma. Noise was added to target samples depending on their eccentricity (Fahle & Schmid, 1988). For the pursuit condition, we also considered versions of the model that estimated the trajectory based on eye position alone or combined with target position. Our measurements, with a larger PRL-to- target distance (Figure 7), and idiosyncratic strategies for some individuals. This finding is unsurprising because three of the nine eyes were the worse eye with a monocular PRL that may not be the oculomotor reference under everyday binocular viewing conditions. Given the poor pursuit of our participants with MD, we only compared the model predictions to the data of control observers with simulated scotomata and a foveal PRL.

We first considered a decision model that only used information about visible target locations (Figure 5A), plus eccentricity-dependent noise. The noisy target samples were fit with straight and curved lines, and the best-fitting line was extrapolated to the plate. Even for large scotomata, the extrapolated noisy samples resulted in a d′ that far exceeded human performance (see Supplementary Figure S2). To address this, we added each observer's bias estimated from their psychometric function for each condition to extrapolated value. The data in the figure are in black and are taken from Figure 6, replotting only the control data with and without scotomata. With a

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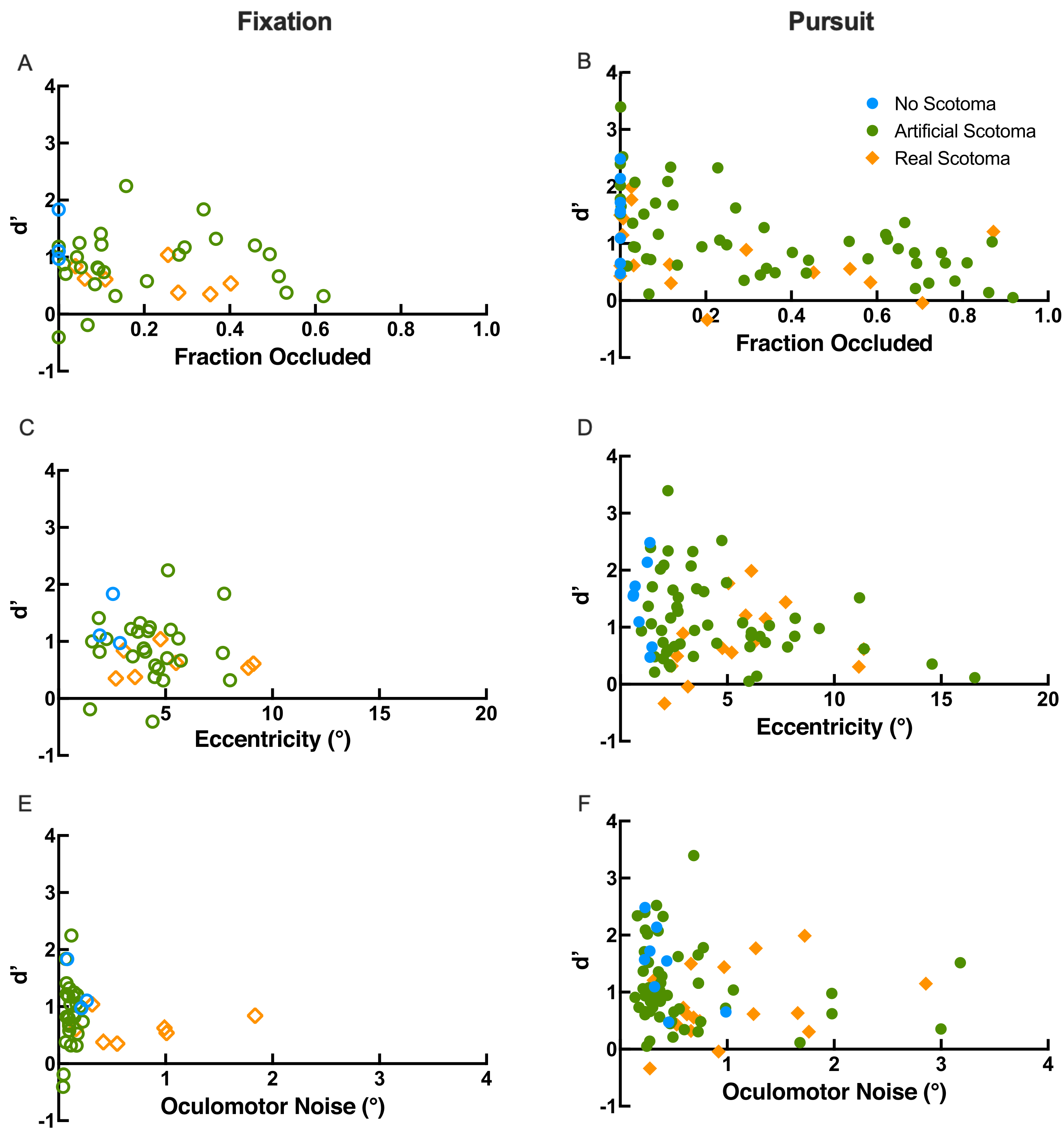

Figure 8. Discriminability d′ for ball/strike judgments is plotted as a function of three factors (rows) during the fixation condition (left) and the pursuit condition (right). The first row (**A** and **B**) plots d′ versus the mean fraction of trajectory occluded, the second row (**C** and **D**) plots d′ as function of the eccentricity of the target, and the third row (**E** and **F**) plots d′ as a function of oculomotor noise.

few exceptions the model predictions are within the interobserver values of d′ (Figure 9A).

We next considered predictions based on eye position for pursuit, rather than on target position (Figure 9B). The motivation here was to examine whether the observer's eye position during the trajectory was a reflection of their estimate of target position. This model examined whether corollary discharge signals accompanying an ongoing pursuit movement influence motion perception/extrapolation, as suggested by

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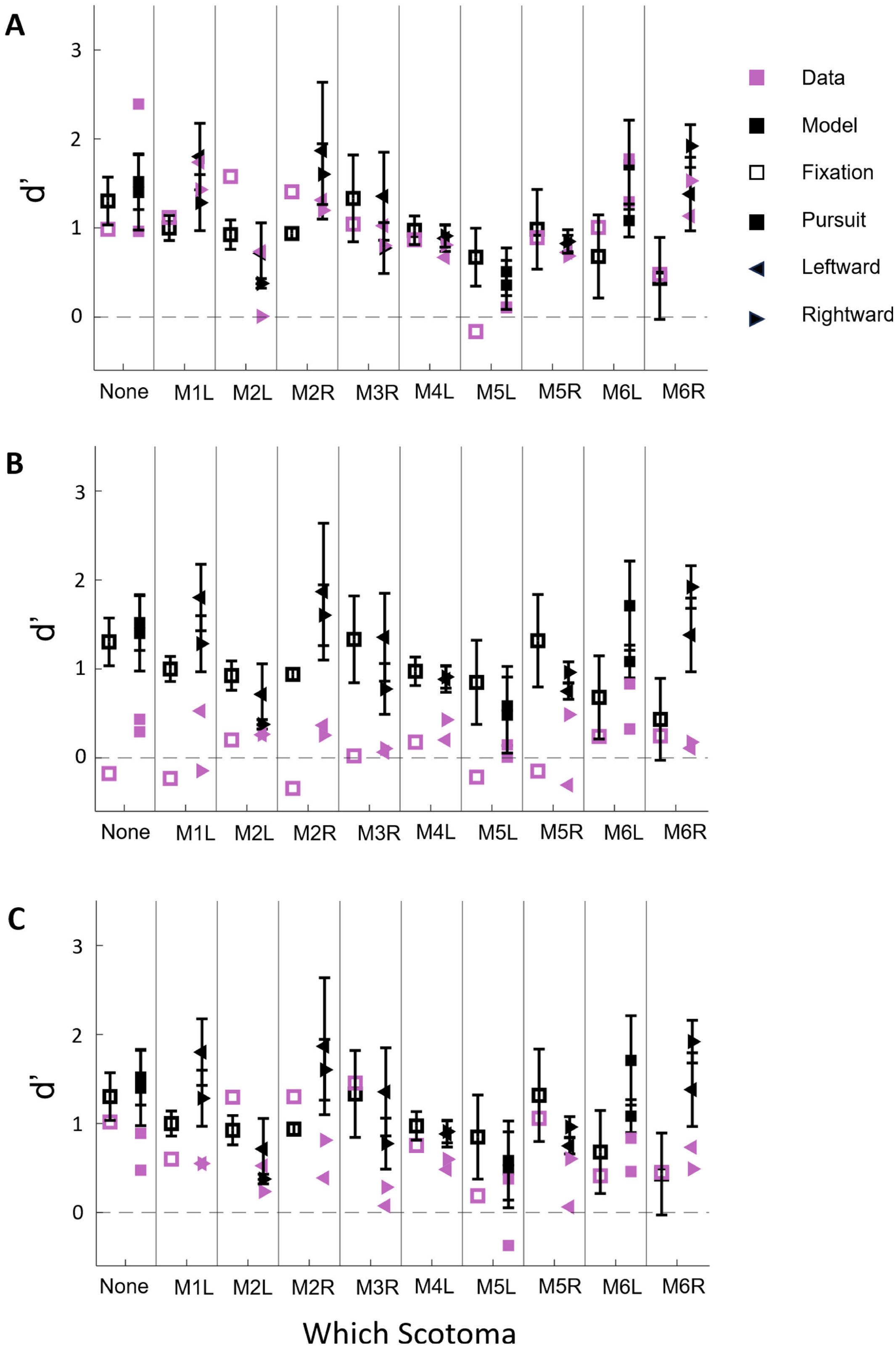

Figure 9. Comparison of decision model to control participant data. The black symbols replot control data without and with a scotoma matched to individual participants with MD from Figure 6. The purple symbols show corresponding model predictions. (**A**) The target position model finds the best fit (line or curve) to the visible data points that are jittered by eccentricity-dependent noise and extrapolates them to the plate. Each observer's bias value is added to the model prediction. (**B**) The eye position model fits the eye position data for the pursuit-condition only. Other aspects are similar to the target model. (**C**) The mixture model is similar except that it averages the target and eye position for the pursuit condition and finds the best fitting curve. Error bars represent standard error across all control participants when tested with a given scotoma.

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Bennett et al. (2010) and Spering et al. (2011). (The fixation data are plotted alongside for reference without the predictions of the eye-position model, as observers were instructed to keep their gaze on the fixation point.) We can see that the model prediction for pursuit is much worse than the actual data, indicating that the extrapolation of the best-fitting line to eye position data is less reliable than estimating the trajectory from visible target points.

Finally, we considered the predictions of a model that averaged the visible target and eye position samples (Figure 9C). This model's performance is intermediate between the target position–based model and the eye position–based model. The model that is most consistent with human data is the first version, which takes into account the visible portions of the trajectory, eccentricity-dependent noise, and each observer's bias for the corresponding condition, estimated from their psychometric function.

A comparison of the best GLME model for pursuit and the decision model most consistent with participant data indicate that target occlusion and eccentricity are the most important contributors to the ability to extrapolate target motion.

Discussion

Teasing apart factors that impact motion extrapolation in the presence of a central scotoma

Our focus was to understand how a central scotoma in each eye affected the visibility of a moving target and the ability to extrapolate its motion. Given that individual scotomata come in various sizes and shapes, we were interested in how a specific scotoma affects visibility and eye movements. Thus, we simulated scotomata that matched those of the affected eyes of individual participants with MD. Each real scotoma was replicated in three control observers to give us a measure of interindividual variability. Both observers with MD and controls with matched scotomata performed a motion extrapolation task under two conditions: while fixating a marker and while pursuing the target. Performance in the fixation task allowed us to isolate the effects of occlusion by comparing controls with and without a simulated scotoma. The presence of an artificial scotoma impacted performance in the fixation task, suggesting that occlusion by the scotoma impacts motion extrapolation. The fixation condition also allowed us to compare performance with an artificial and a real scotoma. This comparison shows that participants with MD with a real scotoma and an eccentric PRL typically performed worse than controls with a matched scotoma and a foveal PRL, raising the possibility that the increased retinal eccentricity of the stimulus or poorer fixation stability due to an eccentric fixation locus (Whittaker et al., 1988; Kumar & Chung, 2014) might affect motion extrapolation in the presence of a scotoma. Although our data show greater oculomotor noise for MDs with eccentric PRLs in the fixation condition (Figure 8E), this factor does not seem to impact the d′ for motion extrapolation. Overall, the GLME model shows no clear effect of any of the three factors (occlusion, eccentricity, and oculomotor noise) on d′ in the fixation condition.

In the pursuit condition, all observers used their habitual PRL—a non-foveal PRL in the affected eyes of participants with MD and a foveal PRL for control participants. The pursuit condition allowed us to determine whether pursuit could mitigate the effect of occlusion by the scotoma. A comparison of controls with and without a scotoma (filled green and blue symbols in Figure 6, respectively) shows that pursuit with smaller artificial scotomata (M1L, M2R, M3R, M6L, and M6R) is comparable with pursuit without a scotoma, suggesting that pursuit is able to compensate for occlusion by small scotomata, at least for controls with a foveal PRL. The pursuit condition also allowed us to examine the challenge of using a non-foveal PRL for eye movements. Several of our participants with MD, particularly M1, M3, and M4, perform much worse in the pursuit condition than controls with matched scotomata and foveal PRLs (we discuss possible reasons in the following paragraph). Other participants with MD performed similarly to controls with a matched scotoma (M2R, M5R, and M6). Although there was not a clear difference in motion extrapolation between individuals with a real or artificial scotoma (orange and green points in Figures 8B, 8D, and 8F), the GLME model showed that fraction occluded and target eccentricity contributed significantly to the d′ for motion extrapolation in the pursuit condition, indicating that it is likely these two factors that diminish the typical benefit of smooth pursuit to motion prediction (Bennett et al., 2010; Spering et al., 2011).

Other factors that impact pursuit in MD

We tested every eye with a central scotoma. Three of our observers with MD had a central scotoma in only one eye (M1, M3, and M4). Because the foveal region was largely intact in the other eye, they did not experience a binocular scotoma and did not need a peripheral PRL under binocular viewing conditions. Thus, by testing their worse eye we might have been testing them under conditions that did not match their everyday experience, specifically the lack of experience with a peripheral PRL for fixation and eye movements. Although a stable peripheral fixation

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locus can develop within 6 months of central field loss (Crossland, Culham, Kabanarou, & Rubin, 2005), eye movements with a peripheral PRL are particularly challenging (White & Bedell, 1990). This might explain why these participants did particularly poorly under pursuit conditions compared with the fixation condition.

Among the individuals who have central field loss in both eyes, M2 has very different patterns of loss in the two eyes, with a large scotoma to the left of her PRL in the left eye. The PRLs in the two eyes are in roughly corresponding locations, so the poorer performance in the left eye (Figure 6) is probably related more to the large size of the scotoma in that eye and less due to lack of experience with the PRL. Two other participants with MD (M5 and M6) had central field loss in both eyes and comparable performance under the pursuit condition as controls with a matched scotoma and a foveal PRL. M6 has patchy small scotomata in both eyes and PRLs quite close to the fovea. M5 has long-standing extensive central field loss resulting from juvenile MD. Thus, he likely has considerable experience using an eccentric PRL for eye movements. This factor might explain why, despite an eccentric PRL, the pursuit in his dominant right eye is comparable with that of controls with a foveal PRL. Furthermore, because he has PRLs in corresponding locations in the two eyes, his performance in the pursuit condition is good regardless of the eye tested.

Motion extrapolation for leftward versus rightward pursuit

For some participants, performance in the baseball task is more impacted for one direction of target movement than the other, although not necessarily worse for the rightward direction under binocular viewing conditions (González et al., 2018), or for the direction toward the scotoma under monocular viewing conditions (Shanidze et al., 2016). We measured performance for only two directions of motion as opposed to the 8 directions in Shanidze et al. (2016), so we did not have sufficient data to determine whether motion extrapolation was more impacted for motion toward the scotoma rather than away from it. Moreover, recall that we measured performance in a motion extrapolation task for two directions of motion, and not pursuit gain per se, as in Shanidze et al. (2016) and González et al. (2018).

Were patients always using a consistent PRL?

Previous studies suggest that individuals with MD switch fixational PRLs depending on the task (Lei & Schuchard, 1997; Duret, Issenhuth, & Safran, 1999; Sullivan, Jovancevic-Misic, Hayhoe, & Sterns, 2008; Crossland, Crabb, & Rubin, 2011). Our previous studies have directly visualized the target on the retina using an SLO (Shanidze et al., 2016; Shanidze & Verghese, 2024) to determine the retinal locus used for smooth pursuit. Shanidze et al. (2016) reported that for linear motion trajectories and a velocity of approximately 5°/s, the PRL used for static fixation was often the oculomotor reference for smooth pursuit. Four of the participants in this study (M1, M2, M4, and M5) also participated in the Shanidze et al. (2016) study and used the same locus for static fixation as they used for pursuit. Nevertheless, it is possible, particularly when only one eye is affected, that patients use multiple PRLs as they might not have experience with an eccentric locus for eye movements under everyday binocular viewing conditions. González et al. (2018) obtained a different result in a study that measured smooth pursuit in individuals with bilateral MD. They observed a systematic shift in gaze in the direction of upcoming target motion before pursuit was initiated, when viewing was binocular. For some participants with MD, we too see a shift in the monocular eye position away from the fixation marker when pursuit is initiated (see Supplementary Figure S1), but the shift is idiosyncratic and not always in the direction of target motion. It is possible that the difficulty of our task influenced pursuit strategy for each participant depending on the extent and location of their scotoma and their ability to consistently use an eccentric locus for eye movements.

Factors that determine motion extrapolation in MD

The classic study by White and Bedell (1990) shows that experience with using an eccentric PRL influences whether it can be consistently used as an oculomotor reference. This is certainly true in our study. Here the individual with the longest experience (M5) performs similarly to controls in most conditions and even exceeds their performance in other conditions. M2 also has a long-standing scotoma and does well for the saccade and pursuit conditions with her dominant right eye. At the other end of the spectrum are M1, M3, and M4, who do not have a binocular scotoma and thus have very little experience with the eccentric PRL in their weaker eye. Their performance in the motion extrapolation task is considerably worse for both fixation and for pursuit. Although scotoma size and the eccentricity of the PRL are known to contribute to fixation stability, we do not have a large enough pool of participants with MD to systematically investigate

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the role of scotoma size. For instance, M6 and M5 have scotomata at the small and large ends of the spectrum, respectively, but they do well in the motion extrapolation task for different reasons: M6's PRLs are close to the fovea, whereas M5's PRLs are approximately 5° to 6° eccentric; however, he has longstanding experience using these eccentric loci as oculomotor references.

Comparison with other motion estimation tasks in MD

Our results show that motion extrapolation of a single moving dot during fixation is impaired in MD. This might seem to contradict other studies that show that direction and speed discrimination are comparable between individuals with MD and aged-matched controls (Shanidze & Verghese, 2019), and that discrimination of the direction of optic flow for translation, rotation and expansion is unaffected in MD (Guénot et al., 2022). The key difference is that these two studies used a field of moving dots, so that the occlusion of a portion of the stimulus had a smaller impact than the occlusion of the single target dot in our study. In addition to the fixation condition, our smooth pursuit condition provided an opportunity to smoothly track the target and to prevent it from entering the scotoma. However, the smooth pursuit condition introduced the challenge of using an eccentric PRL for oculomotor control. Our results suggest that the efficient use of a non-foveal PRL depends on its proximity to the fovea and the duration of experience with the PRL.

Conclusions

The combination of oculomotor and visual deficits associated with MD complicates interpretation of difficulties associated with tracking moving objects. By examining each factor in isolation, we demonstrate that the loss of visibility due to the scotoma and the increased eccentricity of the target due to the PRL have a functional impact on vision in a dynamic task. Individual scotoma characteristics such as the extent and location of the scotoma and the experience with an eccentric locus for eye movements also determine the ability to track moving targets and determine their future position. These findings have direct implications for individualized training approaches for rehabilitation.

Keywords: motion extrapolation, scotoma, peripheral vision, smooth pursuit

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