american physiological society
JNP JOURNAL OF NEUROPHYSIOLOGY

J Neurophysiol 133: 3–13, 2025.
First published November 25, 2024; doi:10.1152/jn.00123.2024

RESEARCH ARTICLE

Control of Movement

Latency and amplitude of catch-up saccades to accelerating targets

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Abstract

To track moving targets, humans move their eyes using both saccades and smooth pursuit. If pursuit eye movements fail to accurately track the moving target, catch-up saccades are initiated to rectify the tracking error. It is well known that retinal position and velocity errors determine saccade latency and amplitude, but the extent to which retinal acceleration error influences these aspects is not well quantified. To test this, 13 adult human participants performed an experiment where they pursued accelerating/decelerating targets. During the ongoing pursuit, we introduced a randomly sized target step to evoke a catch-up saccade and analyzed its latency and amplitude. We observed that retinal acceleration error (computed over a 200 ms range centered 100 ms before the saccade) was a statistically significant predictor of saccade amplitude and latency. A multiple linear regression supported our hypothesis that retinal acceleration errors influence saccade amplitude in addition to the influence of retinal position and velocity errors. We also found that saccade latencies were shorter when retinal acceleration error increased the tracking error and vice versa. In summary, our findings support a model in which retinal acceleration error is used to compute a predicted position error ~100 ms into the future to trigger saccades and determine saccade amplitude.

NEW & NOTEWORTHY When visually tracking object motion, humans combine smooth pursuit and saccadic eye movements to maintain the target image on the fovea. Retinal position and velocity errors are known to determine catch-up saccade amplitude and latency, however, it is unknown if retinal acceleration error is also used to predict future target position. This study provides evidence of a small but statistically significant contribution of retinal acceleration error in determining saccade amplitude and latency.

catch-up saccades; eye movement coordination; saccade programming; saccade trigger; smooth pursuit

INTRODUCTION

Humans utilize two complementary eye movement types to track moving objects - smooth pursuit and saccades. Smooth pursuit is primarily driven by visual motion, but occasionally, tracking errors can accumulate, necessitating a catch-up saccade to realign the gaze with the target and maintain foveation. The mismatch between the eye and target during tracking results in a position error that is used to determine the latency and amplitude of the resulting catch-up saccade (1–4). Recently, Coutinho et al. (5) and Nachmani et al. (6) proposed that the eye movement system predicts position error ~100 ms into the future through motion extrapolation using position and velocity tracking errors. This predicted position error is used both to determine saccade latency and compute saccade amplitude. They propose a saccade decision variable based on Bayesian inference and predictive extrapolation of noisy sensory signals. The decision variable, saccade confidence, is sensitive to the mean and uncertainty of predicted position error and fits within a theoretical framework for optimal Bayesian decision making (7, 8).

In the natural world, objects often accelerate or decelerate due to various factors such as gravity, drag, friction, or applied forces. Furthermore, even constant linear motion in three-dimensional (3-D) space will appear to have angular acceleration in retinal coordinates. This results in accelerating or decelerating retinal images. Humans therefore require the ability to accurately track and act on object acceleration to accomplish everyday tasks such as navigation or object interception.

It is known that in addition to velocity and position inputs, target acceleration is also used in the smooth pursuit

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Submitted 25 March 2024 / Revised 14 November 2024 / Accepted 17 November 2024

system; however, it is not well understood how acceleration affects saccades. In studies involving the tracking of sinusoidal target movements by both humans and monkeys, it was observed that eye acceleration correlated with velocity error, while smooth pursuit gain was influenced by target acceleration. Higher maximum target accelerations were also associated with lower pursuit gain (9). Results of this experiment suggest that tracking behavior worsens with higher accelerations.

In studies using transient occlusion, target acceleration influenced the control of pursuit before and during the occlusion, but the accelerating target needed to be presented for at least 500 ms before the occlusion; eye velocity at the end of the occlusion was scaled to target acceleration (10–12). Findings from these studies indicate that target acceleration can be extracted and used by the pursuit system, and this capability is enhanced with longer presentation times. More recently, other studies using occlusion tasks have shown that, while humans can accurately pursue accelerating targets as predictive pursuit scales with target acceleration, manual target interception is not influenced by target acceleration but instead uses an extrapolation of preocclusion velocity (13). Studies that have investigated the behavior of eye movements to perturbations in target velocity have also provided evidence for the use of target acceleration in influencing pursuit (14, 15).

In sum, there is experimental evidence that target acceleration is used to modulate pursuit responses. Furthermore, image motion models of smooth pursuit also use visual input signals related to target acceleration (16–19). Given that the saccadic and pursuit systems are synergistic and share signals both at the neurophysiological (20) and the behavioral levels (21), it follows logically that target acceleration could also be used by the saccadic system for catch-up saccade planning.

Although previous studies have investigated the influence of occlusion, sinusoidal, and circular target acceleration tracking with respect to saccades, an understanding of how constant target acceleration is used in computing catch-up saccades is lacking. In the occlusion study discussed earlier, saccadic eye displacement was modulated by target acceleration only when presented for at least 500 ms (15). These researchers also found that saccadic eye displacement during transient occlusion changed proportionately to target acceleration under these conditions. The results of this study suggest that target acceleration information can be extracted and used to predict the occluded target's trajectory.

Another target occlusion study also investigated the influence of accelerating target motion on predictive saccades (17). Different levels of target acceleration were not shown to have scaled with the landing time of the predictive saccade after temporal occlusion, however, saccades landed later for accelerating motion than they did for decelerating motion (17). The landing times of these predictive saccades suggest that target acceleration was not taken into account during occlusion, and instead were computed based on the last available velocity information preocclusion. Although participants' predictive saccades landing times did not scale to target acceleration, it is unknown how target acceleration affected saccade amplitude or latency in this study. Furthermore, as these were predictive saccades during an occlusion period, they do not reflect the behavior of saccades when tracking uninterrupted target motion.

The purpose of the current study is to investigate whether participants use retinal acceleration error in computing the latency and amplitude of catch-up saccades during ongoing smooth pursuit. We hypothesized that retinal acceleration error would be a significant predictor for both the latency of catch-up saccades and the computation of catch-up saccade amplitudes. We expect that retinal acceleration error will modulate catch-up saccade latencies depending on how retinal acceleration changes the predicted position error. We also predict that acceleration error will be a significant regressor along with velocity and position error in determining saccade amplitude. We tested these hypotheses in the context of targets that are continuously changing speed to ensure enough time for the brain to estimate target acceleration. We then introduced a sudden position step (jump) in the motion trajectory of the target to trigger a catch-up saccade.

MATERIALS AND METHODS

Sampling Plan and Participants

The study's procedures were approved by the Queen's University General Research Ethics Board in accordance with the Declaration of Helsinki. A power analysis based on effect sizes from previous work done in our laboratory (6) indicated the minimum number of participants needed is 12. To anticipate attrition, 15 adult participants were recruited from the Queen's University Centre for Neuroscience Studies graduate pool. Participants provided informed consent and received compensation at a rate of $10 per hour for their involvement. To qualify for participation, individuals needed to be at least 18 yr old and possess either normal vision or corrected-to-normal vision. Two participants opted to withdraw from the study, resulting in a final analysis sample size of 13 participants. This group had an average age of 21 yr, comprising 8 females and 5 males.

Experimental Procedure

We used a previously established double step-ramp task (1, 4) generated using custom Matlab code (MathWorks, Inc), with the Psychophysics Toolbox (22) into which we introduced a new acceleration component. This task involved an abrupt change in target position used to trigger catch-up saccades. Head-restrained participants viewed stimuli displayed on a ViewPixx screen (VPixx Technologies, 120 Hz refresh rate, resolution 1,920 × 1,200, strobed backlight). The screen was positioned 50 cm away from the participant spanning 60° of their visual field. Eye movements from the right eye were recorded using an Eyelink 1000 video-based recording system (SR Research, Mississauga, ON, Canada) at 1,000 Hz. Participants underwent a standard nine-dot calibration (Eyelink) every three blocks to ensure accurate eye position recording. Trials were configured in one of two ways, either an accelerating or decelerating trial, with an initial fixation target positioned 20° to either the left or right side of the visual field. The visual stimulus was a white dot on a black screen that moved horizontally. Target acceleration was a random integer variable between −80 to 80 deg/s^2.

Regardless of the initial fixation target position, two scenarios would occur as described in Fig. 1.

Accelerating trials began with an initial velocity of 0, continuously accelerating in the direction opposite to the fixation position after a 750–1,250 ms fixation period. After a random period between 300 and 500 ms, the target jumped (position step) randomly between −6 and 6 degrees, while target acceleration remained the same for another 500–700 ms, followed by a 500-ms fixation period. Decelerating trials consisted of a first position step of 6° and a starting velocity of −40 deg/s if the initial fixation was positive (right side of screen), and −6 degrees and a velocity of 40 deg/s if the initial fixation was negative (left side of screen). This was done to initiate pursuit with minimal occurrence of catch-up saccades (1). The targets continued to decelerate, while an additional position step randomly chosen between −6 and 6 degrees occurred after 300–500 ms, followed by another 500–700 ms of target motion and ending with a 500 ms fixation period.

The logic of having accelerating and decelerating conditions allowed disentangling the effects of velocity and acceleration errors. As acceleration values increase, the faster the eye falls behind when tracking. As a result, acceleration errors and velocity errors increase proportionally. Only by having different directions of velocity and acceleration errors, such as what we obtain by combining accelerating and decelerating trials, can we disentangle both. The initial fixation positions, initial target velocities, position steps, and acceleration values varied randomly between each trial (Note: rightward positions are positive values). The values for target acceleration and target step size were discrete but uniformly sampled.

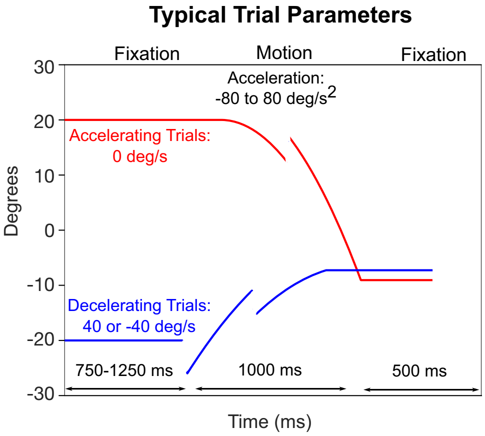

Figure 1. Experimental paradigm. This task was completed by 13 participants. The red trace depicts an example trial with an accelerating target; the blue trace shows an example trial with a decelerating target trajectory. Trials started with a 20-deg left or right initial fixation target. Target acceleration was a random integer variable between −80 and 80 deg/s^2. Accelerating trials (blue) began with an initial velocity of 0 deg/s, and continuously accelerated in the direction opposite to the fixation position after a 750–1,250 ms fixation period. Decelerating trials consisted of a 6 deg outward target step (away from the screen center) and a starting velocity of 40 deg/s toward the center of the screen. For both trial types, after a random period between 300–500 ms, the target jumped (position step) randomly between −6 and 6 deg, while target acceleration/deceleration remained the same for another 500–700 ms, followed by a 500-ms fixation period.

Data Preprocessing

Each participant undertook five data collection sessions of ∼30 min on different days. Each session consisted of 10 blocks each with 50 trials, resulting in 2,500 trials per participant and an overall total of 32,500 trials. Eye position was low-pass filtered using an autoregressive forward-backward filter with a cut-off frequency of 50 Hz. Eye velocity and acceleration were derived from position signals using a central difference algorithm (±10 ms window), and saccades were detected using an acceleration threshold of 750 deg/s^2. Saccades were measured and removed using the same process (4). Saccade removal consisted of a linear interpolation of the eye velocity 24 ms before saccade onset to 24 ms after saccade. The commands for saccades and pursuit have been shown to add together during catch-up saccades, so to correct saccade amplitude we needed to remove the smooth component (4). Therefore, we required a measure of eye velocity with the saccadic component removed to compute the pursuit velocity used to correct saccade amplitude. A more detailed description of the saccade correction process will follow in the *Eye Movement Parameters*.

We visually inspected all trials for errors using a custom-made analysis interface in Matlab. Trials in which the target was not tracked by the participant (e.g., due to distraction), that contained blinks between 100 ms before the step and the first catch-up saccade, that consisted of catch-up saccades where there was more than one velocity peak, saccades which occurred during the target jump during target motion, or trials that were missing eye tracking data were discarded from the analysis. To ensure the analysis did not include saccades that were planned before the target step or may have been influenced by the cancellation of a prior planned saccade, we discarded trials that had catch-up saccades with a latency relative to the target jump of less than 90 ms. A total of 7,678 trials were discarded from the analysis, with 24,822 remaining (76.4% of total trials). Each participant had between 1,089 and 2,269 trials with a mean of 1,904 trials each.

Eye Movement Parameters

The saccades of interest were the first saccades that occurred after the target step during target motion. It is well-established that visual stimuli do not exert any influence on saccades during the ∼100-ms period immediately preceding saccade onset (21). Therefore, all statistical analyses pertaining to saccade amplitude were conducted using data from the 100-ms time point before the onset of the saccade. Position errors were determined by subtracting the eye's position 100 ms before the saccade initiation from the corresponding target position at that moment.

Both velocity and acceleration error computations used averaging over windows that included information less than 100 ms before the saccade to obtain an accurate estimate of the signals of interest from noisy data. We required a larger window for acceleration compared with velocity because each time a derivative is taken, the noise in the signal is amplified. Therefore, we require different window time lengths for proper estimation due to the nature of velocity and acceleration. Velocity error (i.e., retinal slip) was computed by subtracting eye velocity from target velocity averaged over a

50 ms window centered on 100 ms before the saccade. Acceleration error was computed using the slope of a robust linear regression of the eye velocity with the saccadic component removed computed over a 200 ms range before the saccade (centered at 100 ms before the saccade). To account for heteroscedasticity and outliers in our data, we chose to use a robust linear regression. These are less sensitive to outliers than a standard linear regression. Instead of using ordinary least squares, robust regressions use a method called iteratively reweighted least squares to assign a weight to each data point (23).

Saccade amplitude was computed by subtracting the eye position at the beginning of the saccade from the eye position at the end of the saccade. Following the methods described by de Brouwer et al. (4), saccade amplitude was then corrected to remove the smooth pursuit component; saccade duration and pursuit velocity during the saccade were multiplied and subtracted from the total amplitude to correct for the contribution of pursuit.

$$\text{Corrected } S_{AMP} = S_{AMP} - S_{dur} * V_{PURS}$$

For all statistical analyses related to saccade latency, we evaluated position, velocity, and acceleration errors at the time of the target step rather than 100 ms before the saccade. This was because saccade latency is always relative to the time of the step and thus sensory variables at the step predominantly determine saccade latency (5, 6, 24). Bayesian statistics were conducted using JASP (25).

As has previously been suggested, a predicted position error extrapolated to some time interval into the future is correlated with saccade latency and amplitude (5, 6). Instantaneous predicted position error used in our saccade latency analyses was thus calculated as:

$$PEpred_t = PE_t + \tau * VE_t$$

where retinal position error ("PE") is the difference between target and eye positions and retinal velocity error ("VE") is the difference between target and eye velocities. The variable "t" represents sampling time and "τ" is the extrapolation duration of 150 ms, which was chosen based on the results of previous work done in our laboratory (6). Predicted position error is an instantaneous measure – target motion is being extrapolated 150 ms into the future at any given point in time. The 100 ms before a saccade is the last time information can be used for regular saccades (4), so when predicted position error is evaluated at this time, it overcomes the 100 ms sensory delay and then takes another 50 ms or so to make the saccade if required, resulting in around 150 ms time extrapolation duration as described by Nachmani et al. (6).

Hypotheses

For our first hypothesis, we expected retinal acceleration error to be a significant factor involved in computing catch-up saccade amplitude. If retinal acceleration error was taken into account by the saccadic system, saccade amplitude should increase or decrease accordingly to ensure more accurate tracking. Thus, we assessed the influence of retinal position, velocity, and acceleration errors in computing catch-up saccade amplitude using a multiple linear regression analysis, similar to De Brouwer et al. (4).

Our second hypothesis was that acceleration should also modulate saccade latency; retinal acceleration error should influence the error accumulation that is used to determine whether a saccade is triggered (5). Specifically, depending on the relative sign, retinal acceleration error would either increase or decrease the predicted position error, and thus saccade latencies should be shorter when the predicted position error is increased by retinal acceleration error and vice versa. This is because the same acceleration magnitude adding versus subtracting from the predicted position error should increase versus decrease the certainty with which a saccade is needed, thus leading to shorter versus longer saccade times, respectively. Therefore, we assessed the influence of estimated predicted position error on saccade latency. We used a repeated-measures ANOVA with the signed retinal acceleration error and predicted position error binned at four sizes as the independent variables and saccade latencies as the dependent variable.

As per our hypotheses, if retinal acceleration error was in fact used to time saccades and compute saccade amplitudes, then the equation for calculating predicted position error should be updated to include the additional acceleration error term as follows:

$$PEpred_t = PE_t + \tau * VE_t + \tfrac{1}{2}\tau^2 * AE_t$$

This effect of retinal acceleration error is expected to be small, even with large acceleration values, based on its contribution in the above equation.

RESULTS

Our study aimed to build on our current understanding of how saccade amplitude and latency are computed by assessing the influence of accelerating motion. Participants tracked a horizontal moving dot in an accelerating step ramp paradigm. Trials consisted of either accelerating (Fig. 2*A*) or decelerating target motion (Fig. 2*D*). As can be seen, in both conditions, participants were able to make fairly accurate catch-up saccades to foveate the target after the first step during target motion. Specifically, we looked at saccades that were made to the first (and only) target step for accelerating trials and the second target step for decelerating trials. In panel A in the accelerating trial condition, corrected saccade amplitude (pursuit component removed; see MATERIALS AND METHODS) was 11.75° while the position error 100 ms before the saccade was 9.76° (denoted by vertical double arrow). Saccade amplitude was similarly larger in magnitude than position error in the decelerating condition in panel D, with a corrected saccade amplitude of −5.27° and position error 100 ms before the saccade being −4.73°. Considering that the magnitude of position error was less than saccade amplitude, we can assume that velocity and/or acceleration errors 100 ms before the saccade were also taken into account when computing saccade amplitude (Hyp. 1), as we will later describe. Specifically, the accelerating trial condition displayed in Fig. 2 had velocity and acceleration errors of 18.50 deg/s and 33.30 deg/s^2 when sampled 100 ms before the saccade, respectively. These same errors in the decelerating trial condition were −6.88 deg/s and 1.54 deg/s^2. If these velocity and acceleration errors were not in fact taken into

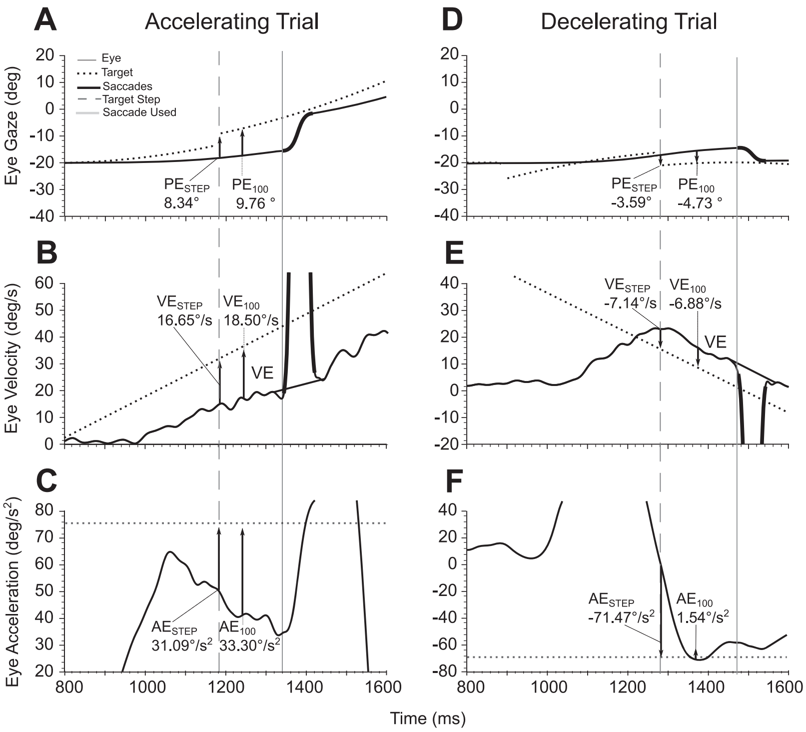

Figure 2. Typical trials. Example of a typical accelerating (*left*) and decelerating (*right*) trial from one participant. Eye and target position, velocity, and acceleration, respectively, are plotted against time. Filled lines denote the eye, dashed lines denote the target. Bolded sections indicate a saccade. Eye and target position (*A* and *D*), velocity (*B* and *E*), and acceleration versus time (*C* and *F*) for accelerating (*A*–*C*) and decelerating (*D*–*F*) trial conditions. Vertical arrows denote the difference between the eye and target positions, velocities, and accelerations used to compute position, velocity, and acceleration errors at both the target step and when centered 100 ms before the saccade.

account, saccade amplitude should be the same size as the position error.

Saccade latency was calculated as the time at which the saccade occurred relative to the target step, indicated by the gray vertical solid line (Fig. 2). In the accelerating trial condition example (Fig. 2*A*), saccade latency was 160 ms. In the decelerating trial condition example (Fig. 2*D*), saccade latency was 190 ms. Predicted position error was computed using position and velocity error parameters at the target step (vertical gray dashed line), and is thought to be used to determine the latency of when the saccade is triggered relative to the target step which will be later described (Hyp. 2; see *Catch-Up Saccade Latency*). Our aim was to determine if an acceleration component should be included in the computation of predicted position error. In Fig. 2, position, velocity, and acceleration errors at the target step in the accelerating trial condition example were 8.34 deg, 16.65 deg/s, and 31.09 deg/s^2. Decelerating was −3.59 deg, −7.14 deg/s, and −71.47 deg/s^2.

Catch-Up Saccade Amplitude

First, we wanted to examine whether retinal acceleration error was used to compute the amplitude of catch-up saccades. It is well known that retinal position and velocity errors ∼100 ms before saccade occurrence are used to compute saccade amplitude. We used multiple linear regression to test if saccade amplitude also correlates with retinal acceleration in conjunction with position error and velocity error sampled 100 ms before saccade onset. Saccade amplitude was corrected to remove the pursuit component (see MATERIALS AND METHODS, *Eye Movement Parameters*).

All participants were included in the regression.

The fitted regression model was:

$$\text{Corrected amplitude} = \beta_{PE} * PE + \beta_{VE} * VE + \beta_{AE} * AE \tag{1}$$

Retinal position error (PE), velocity error (VE), and acceleration error (AE) significantly predicted saccade amplitude ($\beta_{PE} = 0.8373$, $P < 1.10^{-100}$; $\beta_{VE} = 0.0791$, $P < 1.10^{-100}$; $\beta_{AE} = 0.0018$, $P = 2.029724\text{e-}09$; $R^2 = 0.893$). See Table 1 for more detail on regression results, including the standard errors and the upper and lower bounds on coefficients using a 95% confidence interval. The coefficients in *Eq. 1* can be interpreted as follows. The coefficient of PE ($\beta_{PE} = 0.8373$) is the proportion of position error that is corrected by the saccade. The coefficient of VE ($\beta_{VE} = 0.07910$) is the time extrapolation duration that is multiplied by a given VE, ie. $\tau_{VE.}$ The coefficient of AE ($\beta_{AE} = 0.0018$) can also be solved for the time extrapolation duration (τ_{AE}), computed by solving for τ: $\beta_{AE} = ½(\tau_{AE})^2$. The resulting time extrapolation durations for velocity and acceleration errors were $\tau_{VE} = 79.1$ ms and $\tau_{AE} = 60.0$ ms (see *Eq. 1*). This extrapolation begins at 100 ms before saccade occurrence, the last time information can be used before a saccade is triggered (4). In our equation for predicted position error ($PEpred_t$), we interpret each fit parameter as a gain value and extrapolation duration, meaning that the difference in extrapolation time between VE and AE could be interpreted as the same time but a different gain.

Table 1. *Multiple linear model regression results*

Variable	Coefficient	Standard Error	*P* Value	95% Confidence Interval	
				0.025	0.975
β_{AE}	1.78e-03	2.97e-04	2.029724e-09	1.20e-03	2.37e-03
β_{VE}	7.91e-02	1.01e-03	0.000000e + 00	7.71e-02	8.11e-02
β_{PE}	8.37e-01	2.37e-03	0.000000e + 00	8.33e-01	8.42e-01

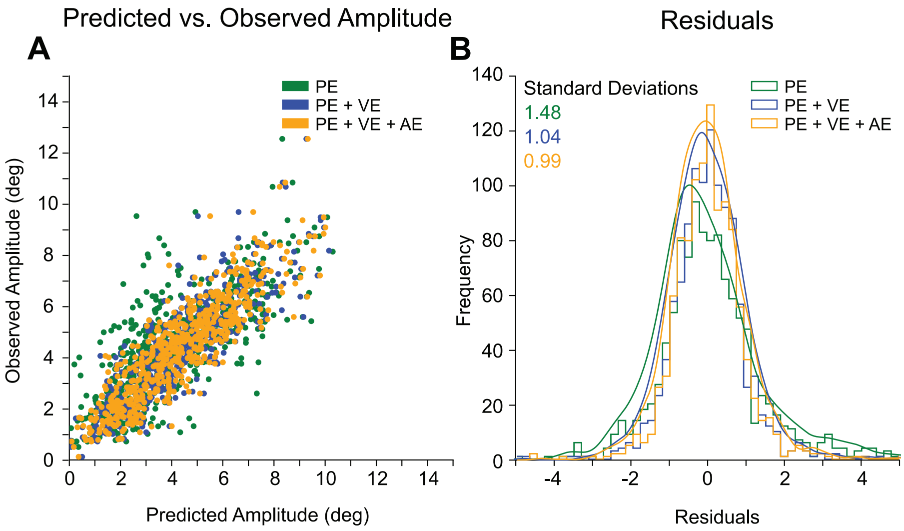

Figure 3. Regression results. Visualization of how the regression model developed as each variable was added for an individual participant. *A*: predicted versus observed amplitude. Green: predicted versus observed saccade amplitude values when position error was the only independent variable used for computing saccade amplitude. Blue: same with the addition of velocity error. Yellow: same including acceleration error. *B*: histogram of residuals between predicted and observed saccade amplitudes, including kernel density estimates with each addition of a new variable. Residuals and standard deviations decrease with the addition of each variable. All analyses were performed using signals centered 100 ms before saccade onset.

This difference in gain could be due to the larger influence of velocity errors compared with acceleration errors on computing saccade amplitude. With respect to the range of values we used for target position (−6, 6 deg), velocity (−40, 40 deg/s), and acceleration (−80, 80 deg/s^2), we expected the relative contribution of acceleration to be small. For example, when computing saccade amplitude based on our coefficients in *Eq. 1* using the maximum values in our parameter ranges, a 6-degree position error would result in a 5.024-degree correction, a 40-degree/s velocity error would result in a 3.164-degree correction, and a 80-degree/s^2 acceleration error would result in a 0.144-degree correction.

The scatterplot in Fig. 3 demonstrates predicted versus observed saccade amplitude as each variable of interest is added for a single participant. As seen in Fig. 3*A*, the final addition of acceleration error as a regression term tightens the relationship between predicted and observed amplitude. Figure 3*B* displays the regression residuals as each variable is added. Like Fig. 3*A*, it is evident from the visual representation that incorporating acceleration error leads to the least amount of deviation from the diagonal line, i.e., the smallest difference between predicted and observed values. Standard deviations decrease and kernel density estimates tighten with the addition of each new variable and is lowest when acceleration error is included.

Although catch-up saccades correct for the majority of error and allow for the continuation of target tracking, they are not perfect. The "idealized" saccade would consist of the corrected amplitude used in the above regression added to the position error between the eye and target and the end of the saccade. To quantify the proportion of errors taken into account when planning an idealized saccade, we ran a multiple linear regression with the same sensory errors used in Table 1 used as independent variables (retinal position error, velocity error, and acceleration error sampled 100 ms before saccade onset), and the position error between the eye and target at the end of the saccade as the dependent variable. Retinal position error (PE), velocity error (VE), and acceleration error (AE) significantly predicted position error at the end of the saccade ($\beta_{PE} = 0.1551$, $P < 1.10^{-100}$; $\beta_{VE} = 0.0917$, $P < 1.10^{-100}$; $\beta_{AE} = 0.0095$, $P = 3.391218\text{e-}244$; $R^2 = 0.589$). See Table 2 for more detail on regression results, including the standard errors and the upper and lower bounds on coefficients using a 95% confidence interval.

We would expect the coefficients for the variables in Table 1 and Table 2 to be added together if the brain were to make an idealized saccade, which is rarely the case, as most saccades have a remaining position error at the end point. To calculate the proportion of the effect of each sensory error on computing an idealized saccade, the coefficients from Table 1 can be divided by the sum of these coefficients added to the coefficients in Table 2.

$$\text{Proportion of effect} = C_1/(C_1 + C_2)$$

The proportions of the effect of each sensory error on computing the exact saccade would therefore be 0.843 for position error, 0.463 for velocity error, and 0.158 for acceleration error. In other words, actual saccades compensated for ∼84% of the actual position error 100 ms before the saccade and accounted for ∼46% and ∼16% of the anticipated cumulative errors due to retinal velocity and acceleration error, respectively.

Although retinal acceleration error was a significant predictor of saccade amplitude when all participants data was compiled and used in the analysis, there was some variability between individual participants (Table 3). When examined individually, retinal acceleration error was not a significant predictor of saccade amplitude in addition to position and velocity error in five of the 13 participants when computing saccade amplitude. The eight other participants all reached statistical significance. Regression results for each individual

Table 2. *Multiple linear model regression results: sensory errors versus position error at end of saccade*

Variable	Coefficient	Standard Error	*P* Value	95% Confidence Interval	
				0.025	0.975
β_{AE}	9.51e-03	2.81e-04	3.391218e-244	8.96e-03	1.01e-02
β_{VE}	9.16e-02	9.59e-04	0.000000e + 00	8.98e-02	9.35e-02
β_{PE}	1.55e-01	2.25e-03	0.000000e + 00	1.50e-01	1.59e-01

Table 3. *Multiple linear model regression results for individual participants*

Participant ID #	β_{PE}	β_{VE}	β_{AE}	β_{AE} p	R^2
1	0.9056	0.0812	0.0017	0.015	0.965
2	0.8912	0.0342	0.0003	0.630	0.949
3	0.9191	0.0745	0.0043	0.000e + 00	0.927
4	0.8952	0.1064	0.0123	0.000e + 00	0.917
6	0.7892	0.0674	−0.0009	0.434	0.854
7	0.8522	0.0239	−0.0021	0.000e + 00	0.949
9	0.8740	0.0881	−0.0009	0.585	0.883
10	0.8292	0.0577	0.0031	0.016	0.886
11	0.8322	0.0659	0.0018	0.023	0.928
12	0.8466	0.0301	0.0005	0.442	0.947
13	0.8668	0.0851	0.0038	0.000e + 00	0.903
14	0.7413	0.0691	0.0019	0.161	0.801
15	0.9001	0.0815	0.0092	0.000e + 00	0.875

participant are described below in Table 3. Due to the variability in regression coefficients for each participant, the time extrapolation durations for velocity and acceleration errors also vary. The extrapolation durations for all participants; τ_{VE} (mean = 66.54 ms, sd = 23.49 ms) and τ_{AE} (mean = 60.55 ms, sd = 48.14 ms) showed different group means with τ_{VE} time being slightly longer. However, a paired samples t test indicated that there is no significant difference between the participants τ_{VE} and τ_{AE} [$t(12) = -0.5375$, $P = 0.6007$].

In summary, our findings align with both our initial predictions and the existing body of literature on saccadic responses to accelerating target motion, as detailed in the DISCUSSION. Notably, our study highlights the relatively modest yet statistically significant contribution of retinal acceleration error in the computation of catch-up saccade amplitudes.

Catch-Up Saccade Latency

We also aimed to investigate the potential impact of retinal acceleration error on saccade latency. More specifically, our inquiry centered on whether retinal acceleration error would influence the predicted position error, and subsequently, saccade latencies. This would result in shorter saccade latencies when the predicted position error aligns with the direction of acceleration error and longer latencies when they oppose each other. This effect occurs because the addition or subtraction of the same acceleration magnitude to the predicted position error can enhance or diminish the certainty of the need for a saccade, therefore leading to shorter or longer saccade latencies depending on the relative sign.

Figure 4 illustrates the relationship between saccade latencies and predicted position error across different bin sizes, showing how they differ depending on the sign of acceleration error. In panels A and B, we can see that saccade latencies are shorter when predicted position errors are larger, as well as shorter when acceleration error has the same direction (sign) as predicted position error. This can be seen by a slight difference in the shape of latency distributions in panel A as well as by the difference in median latencies in panel B. Our interpretation is that these latencies are shorter due to there being less uncertainty as to whether a saccade should be triggered. Panel C illustrates the latency differences between the sign of acceleration error for each bin of predicted position error.

We wanted to test whether latency differences for different sizes of predicted position error were statistically significant. To test this, we used a repeated-measures ANOVA with the sign of retinal acceleration error and predicted position error bin sizes as the independent variables and saccade latencies as the dependent variable. The ANOVA revealed a significant main effect of predicted position error [on saccade latencies $F(3, 36) = 40.975$, $P < 0.001$], but no main effect of the sign of acceleration error ($P > 0.05$). However, as expected there was a significant interaction between the effects of sign of acceleration error and size of predicted position error [$F(3, 36) = 4.333$, $P = 0.010$].

The effect of acceleration error on saccade latency was dependent on the size of predicted position error. As seen in Fig. 4, panels B and C display larger latency differences between positive and negative acceleration errors when the predicted position error was smaller versus larger. This is likely because with smaller predicted position errors, there is more uncertainty as to whether a saccade should be triggered, thus information about retinal acceleration error is used in the final decision. When predicted position errors are larger, there is greater certainty that a saccade is required, thus information about acceleration is not necessary to make a decision.

A paired sample t test was performed to compare saccade latencies for each of the four predicted position error bins. We have corrected for multiple comparisons using Bonferroni-adjusted α levels of 0.0125 per test. There was a significant difference in saccade latencies between positive and negative retinal acceleration error or the −5 to 0 deg small negative-predicted position error bin [$t(12) = 3.101$, $P = 0.009$), but no significant difference for the three other bins < −5 deg large negative [$t(12) = 0.770$, $P = 0.456$], 0 to 5 deg small positive [$t(12) = -1.562$, $P = 0.144$], and > 5 deg large positive [$t(12) = -0.907$, $P = 0.382$].

A Bayesian paired sample t test was also performed, revealing moderate evidence for a difference in saccade latencies between positive and negative acceleration error for small negative (−5 to 0 deg) predicted position errors (BF10 = 6.221), but no evidence for the other sizes of predicted position errors; < −5 deg large negative (BF10 = 0.359), 0 to 5 deg small positive (BF10 = 0.738), and > 5 deg large positive (BF10 = 0.395).

These results partially support our hypotheses; we did not expect the sign of acceleration error to have a main effect on saccade latencies as it averages out across all predicted position errors. However, we did expect a differential effect of sign of AE as a function of the predicted position error. If AE did not play a role in computing catch-up saccade latency, we would expect to see identical latency distributions for both positive and negative AEs. The results displayed in Fig. 4 show otherwise. Predicted position error either increased or decreased in the same direction as the sign of AE. We can also observe that saccade latencies are shorter when the predicted position error is in the same direction as AE for small predicted position error bins (though this did not reach significance for small positive predicted position errors). These findings affirm prior research on catch-up saccade triggering; longer saccade latencies were associated with smaller predicted position errors, while shorter latencies corresponded to larger predicted position errors (6).

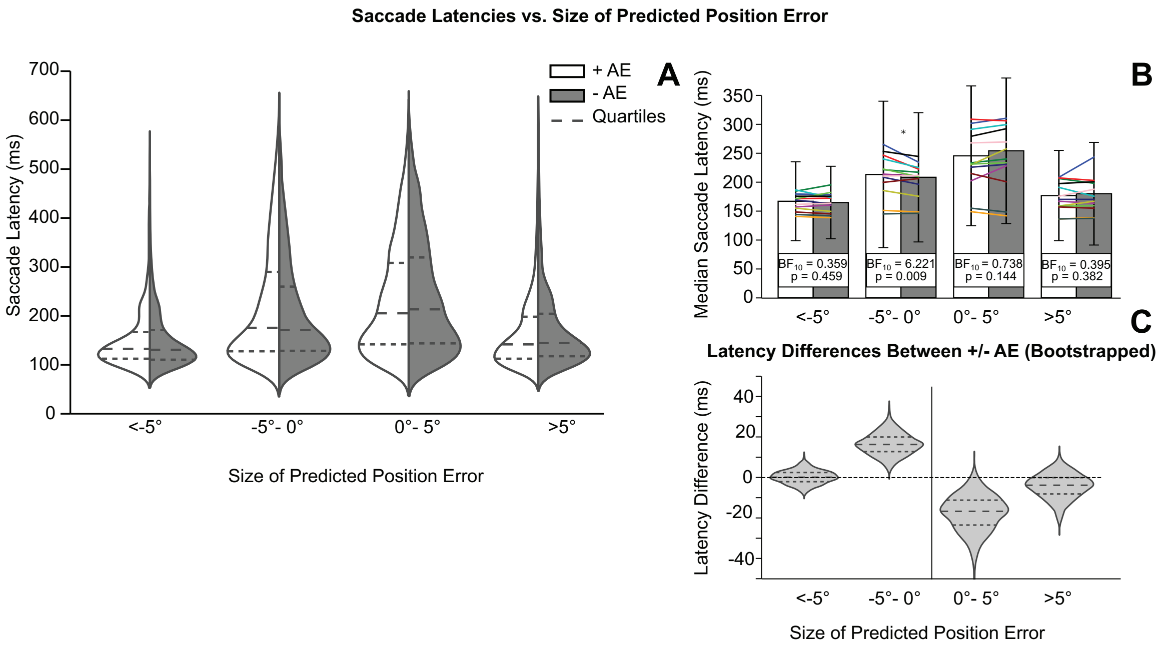

Figure 4. Saccade latency distributions. *A*: saccade latency distributions of all participants ($n = 13$) across four bins of predicted position error split into groups of positive versus negative retinal acceleration error. *B*: the magnification of the median saccade latencies across all participants of *A* including the individual participant medians (colored lines). *P* values and Bayes factor are from a paired *t* test and a Bayesian paired *t* test. Stars indicate statistical significance. *C*: bootstrapped median saccade latency differences between positive and negative acceleration errors across all participants for each bin size of predicted position error. Latency differences for each bin were calculated by subtracting the median latencies for negative acceleration error groups from the positives for each participant. Bootstrapped with 1,000 iterations using scikit learn (26).

Finally, we wanted to further analyze the effects of both retinal velocity and acceleration on saccade latencies across a finer scale of position errors at target step. Figure 5 displays saccade latencies versus position error at the target step binned both by size of velocity error (Fig. 5*A*) and acceleration error (Fig. 5*B*), as a function of saccade amplitude (Fig. 5*C*), and position error alone (Fig. 5*D*). In panel A, data are binned by size of velocity errors. Large negative is <-10 deg/s, small negative is –10 to 0 deg/s, small positive is 0 to 10 deg/s, and large positive is >10 deg/s. Panel B is binned by size of acceleration errors. Large negative is <-20 deg/s^2, small negative is –20 to 0 deg/s^2, small positive is 0 to 20 deg/s^2, and large positive is >20 deg/s^2. In both analyses, we see that saccade latencies are longest when position errors are smallest due to increased uncertainty as to whether a saccade is required. There is a less pronounced effect when binned by acceleration error rather than velocity error. This aligns with our expectations, considering the smaller relative impact of acceleration error, as outlined in the kinematic equation described in our latency hypothesis (Hyp. 2).

We expect the biggest influence of acceleration on saccade latency for small position errors. This is because a change in velocity with small position errors results in greater uncertainty, which has a bigger influence on saccade confidence estimation with small position errors (5). If the velocity and acceleration errors increase the magnitude of predicted position error, then it is more certain that a saccade is needed, thus lower latencies. If they reduce the magnitude of predicted position error, there is less certainty a saccade is needed, thus longer latencies. It appears that the magnitude of velocity and acceleration errors also have an effect on saccade latency. Although all sizes of velocity and acceleration bins still show latencies peaking as position error as the target step approaches 0, Fig. 5, *A* and *B*, show that latencies are longest for the largest bins of velocity and acceleration error. Uncertainty is increasing as position error approaches 0, but large velocity and acceleration errors make predicting future target position even more difficult. Therefore, to take into account larger velocity and acceleration errors, the brain requires more time to decide whether a saccade is needed, and thus latencies increase.

The signed effect of retinal acceleration error on saccade latency is also correlated with saccade amplitude. Saccades with small amplitudes would have been triggered by small position errors and have longer latencies as there was more uncertainty as to whether a saccade is required. Saccades with larger amplitudes would have been triggered by large position errors, therefore there is little uncertainty that a saccade is required, resulting in short-latency saccades. Panel C displays a shift in latency distribution in that there are longer latencies when the sign of acceleration error is in the same direction as the sign of the amplitude. This panel displays how the sign of acceleration error can change predicted position error by visualizing the resulting shift in the relationship between amplitude and latency. The interpretation of this shift is that predicted position error must be using acceleration error to compute both saccade amplitude and latency.

Panel D is complementary to panels A and B and displays median saccade latencies as a function of position error with no other conditions and shows the isolated effect of position error on latency. Like in panels A and B, latencies are also longest close to 0 degree position errors.

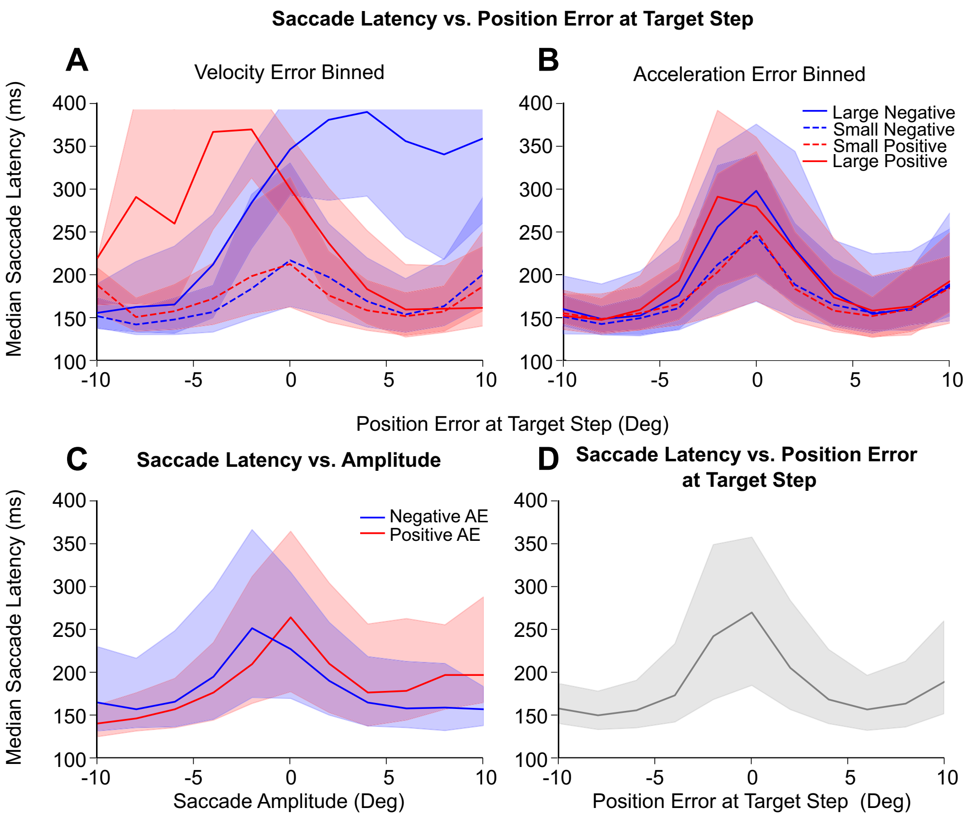

Figure 5. Median saccade latencies versus position error and saccade amplitude. Data from all participants ($n = 13$) are shown. *A*: saccade latencies as a function of position error at the step for different retinal velocity errors. Large negative: <-10 deg/s, small negative: -10 to 0 deg/s, small positive: 0 to 10 deg/s, large positive: >10 deg/s. *B*: same as *A* but for different retinal acceleration errors. Large negative: <20 deg/s^2, small negative: -20 to 0 deg/s^2, small positive: 0 to 20 deg/s^2, large positive: >20 deg/s^2. *C*: median saccade latencies versus saccade amplitude binned by sign of acceleration error. *D*: median saccade latencies versus position error at target step not binned by any conditions. Shaded areas display the 25th–75th percentile range of the data.

DISCUSSION

General Discussion

In this study, we investigated whether retinal acceleration error is used by the brain in determining the latency and amplitude of catch-up saccades during smooth pursuit. To test this, we designed an accelerating target tracking task and quantified the influence of retinal position, velocity, and acceleration errors on the latency and amplitude of catch-up saccades during pursuit. We observed that retinal acceleration error influenced both the amplitude and latency of catch-up saccades, consistent with our hypotheses. In addition to position and velocity errors, acceleration error had a small influence on predicting saccade amplitude. Furthermore, when the direction of acceleration error and predicted position error was aligned, saccade latencies were shorter than when the signs opposed each other. These findings expand on the results of previous behavioral studies, which demonstrated that humans are able to perceive and discriminate object acceleration (15, 17, 27). In summary, we provide evidence that the brain uses target acceleration information to compute the amplitude and latency of catch-up saccades.

Comparison to the Literature

The results of our study are confirmatory to others that investigate the computation of catch-up saccade amplitude (4) and latency (6) in that we show that retinal position and velocity errors are used to predict catch-up saccade amplitude. In addition, our study provides new evidence that retinal acceleration error is included in these computations. Compared with the contribution of position and velocity errors, acceleration error has a small effect on predicting catch-up saccade amplitude. This can be explained by the scaling of our regression coefficients in *Eq. 1*. Indeed, given the temporal horizon of predicted position error, the expected amplitude correction that can be attributed to the position component is the largest, followed by velocity and acceleration being the smallest due to the nature of the kinematic equation.

There is also a relationship between these sensory errors and saccade latency. Schreiber and colleagues (28) demonstrated that the longer the catch-up saccade latency, the more influential velocity error becomes compared with position error. When there is a change in velocity after the target position step, the brain seems to require more time to take into account the target velocity before a saccade is programmed. In our experiment, we have a change in target velocity due to acceleration, which should similarly result in a larger influence of acceleration as well as velocity errors with longer saccade latencies.

In addition to this effect on catch-up saccade computations, acceleration has also been shown to influence the pursuit system. Kreyenmeier and colleagues' (17) recent occlusion study found that while acceleration is taken into account by the pursuit system leading up to target occlusion, it is not used in predicting time-to-contact when making an interceptive hand movement. These results suggest that acceleration signals are used differently when visually tracking compared with predicting manual interception.

The relatively small influence of acceleration error on saccade amplitude and latency could also be potentially linked to the difficulty humans have with perceiving acceleration, which has been a topic of debate. A prevalent theory posits that acceleration might be perceived indirectly through changes in speed (15, 27). This conclusion is supported by findings that the participants can perceive accelerating target movement based on a threshold of 25% change in velocity throughout a trial (29).

Hypothetical Neural Mechanisms

The oculomotor response to accelerating target motion has also been investigated from a neural perspective. Primate area MT is one of the core motion-processing areas of the brain. Evidence from electrophysiology studies from MT neurons in monkeys shows joint target acceleration and target speed coding (30, 31). These studies support theories that suggest acceleration is processed by the brain indirectly through changes in velocity. Furthermore, frontal eye field (FEF) activity has been shown to reflect a dynamic internal representation of target motion (32–34). It is possible that retinal acceleration error could be processed by one or both of these motion-processing areas in the brain, either directly or indirectly.

Limitations

A limitation of the present study, shared with many eye-tracking investigations conducted in controlled laboratory settings, is the challenge of generalizing findings to real-world conditions. In our study, participants were tasked with following a sparse stimulus, a dot that moved unpredictably across a restricted range of accelerations, limited by screen dimensions. This stimulus lacked salience for the observers and its simplicity limited the development of prior expectations akin to those formed with natural stimuli. Research has shown that the human visual system responds differently when processing dynamic, natural scenes as opposed to simplified artificial stimuli typically used in laboratory experiments (35). Indeed, the categorization of conventional laboratory stimuli demands more attentional resources compared with the relatively effortless processing of natural stimuli (36). Furthermore, humans learn and develop priors related to the laws of motion throughout their lifetime when interacting with natural stimuli, for example with gravity (37, 38). For example, in a naturalistic occlusion task portraying a virtual baseball game, humans track and predict fly-ball trajectories more accurately with natural gravity compared with manipulated gravity (39). Together, these findings highlight the fact that the human visual system is adapted to the properties of its everyday input, and therefore can only be fully understood within a naturalistic context.

Future Directions

Accounting for the influence of retinal acceleration error when designing target tracking tasks could be useful for various subfields of neuroscience. Our findings that catch-up saccades use retinal acceleration error independently of velocity and position errors can be studied more specifically from a modeling perspective. Specifically, models of catch-up saccades could now be updated to account for an independent influence of target acceleration involved in computing saccade amplitude and latency.

Next, we should investigate how retinal acceleration affects saccades to natural stimuli, allowing for more generalizable interpretations consistent with everyday life. Specifically, how does the brain take accelerating object motion in naturalistic environments into account, and how is this different than in laboratory environments? How does the oculomotor system differ in computing saccade latency and amplitude in natural scenes versus simple, artificial stimuli. For example, would the target acceleration have more of an influence on saccade latency and amplitude when observing naturally falling objects, accelerating cars, or running humans and animals compared with a simple dot accelerating across a screen? Naturalistic research will be useful in updating current models of catch-up saccade behavior and better understanding their function in everyday life.

Conclusions

Our study provides evidence that retinal acceleration error is used to compute the latency and amplitude of catch-up saccades to accelerating target motion in addition to retinal position and velocity errors. As expected, we found that the influence of retinal acceleration error on predicting catch-up saccade amplitude was small. We also found a signed effect of retinal acceleration error on saccade latency, in that latencies were shorter when retinal acceleration error and predicted position error were the same sign and longer when opposite.

DATA AVAILABILITY

The data that support this study are available at the link to OSF in "SUPPLEMENTAL MATERIAL".

SUPPLEMENTAL MATERIAL

Data is available on OSF (https://osf.io/d9mzc/).

Code is available on github (https://zenodo.org/records/10870399).

ACKNOWLEDGMENTS

The authors thank all the members of the Blohm lab for feedback and Emma Brooks for assisting in data collection.

GRANTS

This work is supported by Natural Sciences and Engineering Research Council of Canada and Canada Foundation for Innovation. S.D. was supported by a Queen's FHS Dean's Graduate Award.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.D. and G.B. conceived and designed research; S.D. performed experiments; S.D. analyzed data; S.D., J.C., and G.B. interpreted results of experiments; S.D. prepared figures; S.D. drafted manuscript; J.C., A.Z.K., P.L., and G.B. edited and revised manuscript; G.B. approved final version of manuscript.

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