View metadata, citation and similar papers at core.ac.uk
brought to you by CORE
provided by University of Birmingham Research Portal

UNIVERSITY OF BIRMINGHAM

Research at Birmingham

Eye movement accuracy determines natural interception strategies

Fooken, Jolande; Yeo, Sang-Hoon; Pai, Dinesh; Spering, Miriam

DOI:
10.1167/16.14.1

License:
Creative Commons: Attribution-NonCommercial-NoDerivs (CC BY-NC-ND)

Document Version
Publisher's PDF, also known as Version of record

Citation for published version (Harvard):
Fooken, J, Yeo, S-H, Pai, D & Spering, M 2016, 'Eye movement accuracy determines natural interception strategies', Journal of Vision, vol. 16, no. 14, 1. https://doi.org/10.1167/16.14.1

Link to publication on Research at Birmingham portal

General rights
Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of ‘fair dealing’ under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy
While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

Download date: 01. Feb. 2019

Eye movement accuracy determines natural interception strategies

Jolande Fooken
Ophthalmology & Visual Sciences,
University of British Columbia, Vancouver, Canada
Graduate Program in Neuroscience,
University of British Columbia, Vancouver, Canada

Sang-Hoon Yeo
Sport, Exercise and Rehabilitation Sciences,
University of Birmingham, Birmingham, UK

Dinesh K. Pai
Computer Science, University of British Columbia,
Vancouver, Canada
Institute for Computing,
Information and Cognitive Systems,
University of British Columbia, Vancouver, Canada
Centre for Brain Health, University of British Columbia,
Vancouver, Canada

Miriam Spering
Ophthalmology & Visual Sciences,
University of British Columbia, Vancouver, Canada
Institute for Computing, Information and Cognitive Systems,
University of British Columbia,
Vancouver, Canada
Centre for Brain Health, University of British Columbia,
Vancouver, Canada
International Collaboration on Repair Recoveries,
University of British Columbia, Vancouver, Canada

Eye movements aid visual perception and guide actions such as reaching or grasping. Most previous work on eye-hand coordination has focused on saccadic eye movements. Here we show that smooth pursuit eye movement accuracy strongly predicts both interception accuracy and the strategy used to intercept a moving object. We developed a naturalistic task in which participants ($n = 42$ varsity baseball players) intercepted a moving dot (a "2D fly ball") with their index finger in a designated "hit zone." Participants were instructed to track the ball with their eyes, but were only shown its initial launch (100–300 ms). Better smooth pursuit resulted in more accurate interceptions and determined the strategy used for interception, i.e., whether interception was early or late in the hit zone. Even though early and late interceptors showed equally accurate interceptions, they may have relied on distinct tactics: early interceptors used cognitive heuristics, whereas late interceptors' performance was best predicted by pursuit accuracy. Late interception may be beneficial in real-world tasks as it provides more time for decision and adjustment. Supporting this view, baseball players who were more senior were more likely to be late interceptors. Our findings suggest that interception strategies are optimally adapted to the proficiency of the pursuit system.

Introduction

It is well known that eye movements aid visual perception and guide actions such as reaching or grasping. An important goal of movement is accurate interception of moving objects, both for evolutionary advantage (e.g.,

Citation: Fooken, J., Yeo, S.-H., Pai, D. K., & Spering, M. (2016). Eye movement accuracy determines natural interception strategies. *Journal of Vision*, *16*(14):1, 1–15, doi:10.1167/16.14.1.

doi: 10.1167/16.14.1 Received May 27, 2016; published November 1, 2016 ISSN 1534-7362

prey capture) and in everyday activities such as sports. Interception requires estimation of an object's trajectory from a brief glance at its motion, and a decision when to intercept it (Brenner & Smeets, 2015). This requires a fundamental tradeoff, related to "optimal stopping" in decision theory. An early interception strategy could allow the animal to quickly seize an opportunity but at the risk of an inaccurate strike, whereas a late interception strategy allows more time to extract visual information and make a decision. Perhaps for this reason, athletes are instructed to "keep their eyes on the ball."

Indeed, there is a tight coupling between motion perception and smooth pursuit eye movements—continuous, slow movements that keep the eyes close to a moving visual target (Kowler, 2011; Lisberger, 2015; Spering & Montagnini, 2011). These movements enable better motion perception and improved ability to predict object trajectories in space (Spering, Schütz, Braun, & Gegenfurtner, 2011) and time (Bennett, Baures, Hecht, & Benguigui, 2010). Most previous studies on interception, however, have focused on saccadic eye movements. It is not known how smooth pursuit accuracy affects interception accuracy and strategy.

There is also a close link between eye and hand movements. Many studies show that eye movements occur naturally when observers engage in reaching, grasping, pointing, or hitting (Diaz, Cooper, Rothkopf, & Hayhoe, 2013; Hayhoe & Ballard, 2005; Hayhoe, McKinney, Chajka, & Pelz, 2012; Land, 2006; Land & McLeod, 2000; Mrotek & Soechting, 2007; Ripoll, Bard, & Paillard, 1986; Soechting & Flanders, 2008). Professional athletes and other task experts show more accurate and less variable eye movements in the field. For instance, expert cricket batsmen make a saccade to the predicted bounce location of a consistently bowled ball; experts' saccades are more accurate and occur earlier than novices' saccades (Land & Furneaux, 1997; Land & McLeod, 2000). Moreover, eye and hand movements are spatially and temporally coordinated. Gaze leads the hand by up to 1 s (Ballard, Hayhoe, Li, & Whitehead, 1992; Land, 2006; Sailer, Flanagan, & Johansson, 2005; Smeets, Hayhoe, & Ballard, 1996) and gaze locations depend on task requirements during object manipulation (Belardinelli, Stepper, & Butz, 2016; Johansson, Westling, Bäckström, & Flanagan, 2001). Gaze is anchored on the target in pointing tasks (Gribble, Everling, Ford, & Mattar, 2002; Neggers & Bekkering, 2000) and when hitting, catching or tracking moving objects with the hand (Brenner & Smeets, 2011; Cesqui, Mezzetti, Lacquaniti, & d'Avella, 2015; van Donkelaar, Lee, & Gellman, 1994), presumably because of the beneficial effects of smooth pursuit on motion prediction (Bennett et al., 2010; Spering et al., 2011).

This behavioral evidence, however, is mostly based on observational and descriptive studies indicating a link between eye movements and the subject's expertise or skill level, and most of these studies are on saccades. We developed a novel paradigm to directly assess the functional importance of smooth pursuit for manual interception accuracy and strategy in a task manipulating eye movement quality. Observers had to track a small moving dot (the ball) with smooth pursuit eye movements and manually intercept (hit) it as accurately as possible after it entered a designated "hit zone." Critically, the ball disappeared briefly after its launch, requiring trajectory extrapolation akin to a real-life baseball scenario, where hitters have less than 300 milliseconds to decode a ball's trajectory (Adair, 2002). It is well known that tracking can be temporarily maintained after disappearance of a moving target, using a combination of saccades and smooth pursuit (Becker & Fuchs, 1985; Bennett & Barnes, 2005; Bennett, Orban de Xivry, Barnes, & Lefèvre, 2007). Motion trajectory information can be extracted from brief initial exposure and used to predictively drive pursuit (Bennett et al., 2007).

On one hand, we might expect beneficial effects of smooth pursuit on interception accuracy, based on the close link between pursuit and motion prediction, and pursuit's natural occurrence in interception tasks (Brenner & Smeets, 2011; Hayhoe & Ballard, 2005; Land, 2006; Soechting & Flanders, 2008). On the other hand, perception-pursuit dissociations have been reported frequently (Spering & Carrasco, 2015) and pursuit quality and catching performance have been reported to be uncorrelated on a trial-by-trial basis (Cesqui et al., 2015). Our data allow us to directly link spatio-temporal properties of smooth pursuit eye movements to interception accuracy and strategy, revealing distinct tactics used to intercept either early or late.

Material and methods

Observers

Observers were 42 males (mean age 19.4 ± 1.4 years), members of the UBC varsity baseball team, with normal or corrected-to-normal visual acuity; 37 were right-handed, five were left-handed (dominant hand was defined as hand used for writing). We included 32 participants in the main experiment and the remaining ten observers, who completed the same experiment, in testing a neural network model. All observers were unaware of the purpose of the experiment. The experimental protocol adheres to the Declaration of Helsinki and was approved by the UBC Behavioral Research Ethics Board; participants gave written informed consent prior to participation.

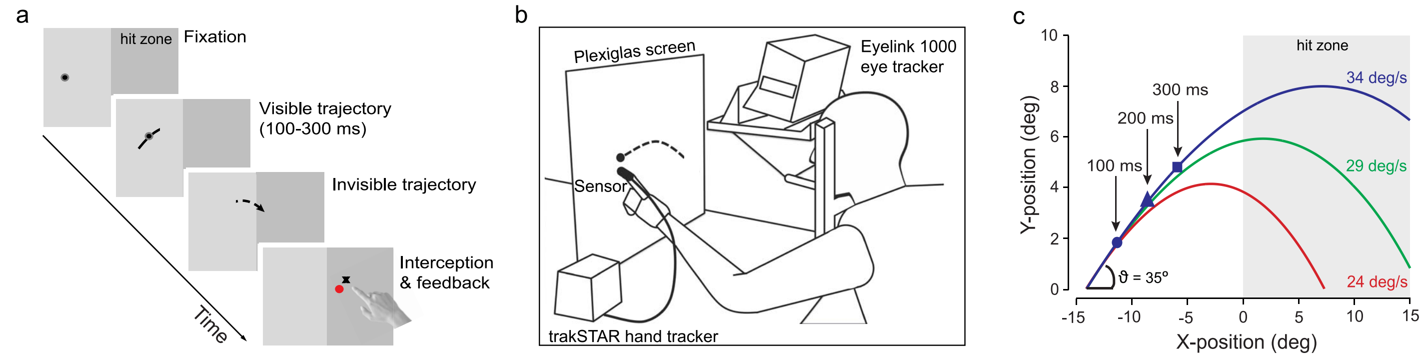

Figure 1. (A) Trial timeline; each trial starts with (1) fixation (random interval between 500–700 ms), followed by (2) a brief (100, 200, or 300 ms) stimulus presentation duration after which (3) the stimulus disappears until (4) the observer intercepts in the darker gray "strike zone." Performance feedback at the end of each trial showed true target position (black) relative to finger position (red). (B) Cartoon of set-up showing an observer intercepting with their left hand and relative positions of eye tracker, magnetic finger tracker, and translucent screen for back-projection. (C) Simulated trajectories for three target velocities launched at a common angle of 35°. Points of disappearance after 100, 200 and 300 ms are indicated by solid blue symbols exemplary for the fastest velocity. Gray area (right) indicates strike zone.

Visual stimuli and apparatus

The pursuit target was a black ball (Gaussian dot, $SD = 0.38°$) with luminance 5.4 cd/m^2, moving across a gray background equally divided into a lighter (35.9 cd/m^2) and darker (31.5 cd/m^2) zone, the "hit zone" (Figure 1a). The physical trajectory of the ball was simulated to be the natural flight of a batted baseball. In the following equations, $\ddot{x}$ and $\ddot{y}$ are the horizontal and vertical acceleration components, taking into account ball mass (m), gravitational acceleration (g), aerodynamic drag force (F_D), and Magnus force (F_M) as induced by the baseball's spin; ϑ is the angle between the velocity vector and the horizontal (for conditions and constants used in the simulation see Table 1).

$$\ddot{x} = -\frac{1}{m}\Big(F_D\cos(\vartheta) + F_M\sin(\vartheta)\Big) \qquad (1)$$

$$\ddot{y} = -g - \frac{1}{m}\Big(F_D\sin(\vartheta) - F_M\cos(\vartheta)\Big) \qquad (2)$$

The drag force (F_D) and the Magnus force (F_M) are defined as

$$F_D = (C_D A \rho v^2)/2, \qquad (3)$$

$$F_M = \gamma f v C_D, \qquad (4)$$

in which A is the cross sectional area of the baseball, ρ the air density, γ is an empirical constant determined by measurements of a spinning baseball in a wind tunnel by Watts and Ferrer (1987), f refers to the frequency with which the simulated ball spins, v denotes the ball's velocity, and C_D is the drag coefficient. The launch angle was constant ($\vartheta = 35°$).

Stimuli were back-projected onto a translucent screen (Figure 1b) with nondistorting projection screen material (Twin White Rosco screen, Rosco Laboratories, Markham, ON, Canada) clamped onto a solid glass plate and fixed in an aluminum frame with a Vivid LX20 LCD projector [Christie Digital Systems Inc., Cypress, CA; refresh rate 60 Hz, resolution 1280 (H) × 1024 (V) pixels]. The displayed window was 48.5 (H) × 38.8 (V) cm or 60° × 48° in size. Stimulus display and data collection were controlled by a PC (NVIDIA GeForce GT 430 graphics card), and the experiment was programmed in Matlab 7.1 using Psychtoolbox 3.0.8. Observers were seated in a dimly lit room at 46 cm distance from the screen with their head supported by a combined chin- and forehead-rest, and they viewed stimuli binocularly.

Procedure and design

We tested each observer's right-handed and left-handed interception in separate blocks of trials: In right-handed interception blocks, stimulus motion was from left to right (see example trial in Figure 1a); in left-handed blocks, stimulus motion was from right to left. Each trial started with fixation on a stationary ball presented 14° to the left or right from the screen center. During fixation, the eye had to be within a 1.4° radius of the fixation target (drift correction). We introduced a set of conditions to increase task difficulty, varying only stimulus speed and presentation duration. The ball moved at one of three speeds (24°/s, 29°/s, or 34°/s) and disappeared after one of three visible durations (100, 200, 300 ms, denoted with solid symbols in Figure 1c); conditions were randomly interleaved within each block of trials.

Variable	Value
Air density (20°C, sea level)[1]	$\rho = 1.204\ \text{kg/m}^3$
Baseball cross section[2]	$A = 2\pi \cdot 0.0365\ \text{m}^2$
Drag coefficient[3]	$C_D = 0.3$
Mass of baseball[4]	$m = 0.145\ \text{kg}$
Initial angle of flight[4]	$\vartheta = 35°$
Gravitational acceleration[5]	$g = 9.81\ \text{m/s}^2$
Frequency of ball spin[4]	$f = 50\ \text{Hz}$
Empirical constant[6]	$\gamma = 1.2 \times 10^{-3}\ \text{kg}$
Initial *x*-*y* position[7]	$[\pm 14.1°, 0°]$
Initial absolute velocities[7]	24°, 29°, or 34°/s

Table 1. Conditions and constants used in the baseball trajectory simulation. *Notes*: [1] International Civil Aviation Organization, manual of the ICAO standard atmosphere; [2] Bahill, Baldwin, and Venkateswaran (2005); [3] NASA research; [4] Adair (2002); [5] International system of units; [6] Watts and Ferrer (1987); and [7] Experimental design.

We instructed observers to track the ball with their eyes and to continue to track it to the best of their abilities after it had disappeared. Observers then had to intercept the ball with their index finger in the hit zone as accurately as possible. Prior to each experimental block, observers completed a brief baseline pursuit block (27 trials) and nine practice interception trials, both with the entire trajectory visible. If interception occurred after the trajectory (including the visible and invisible part) had ended (trajectory durations 1.2, 1.4, and 1.6 s for fast, medium, and slow speed), observers received a "time out" message. However, trajectory durations were sufficiently long to complete the task without feeling rushed, and time outs only occurred during the first practice trials, but not during the experiment. Observers placed their hand on a table-fixed resting pad after each interception. At the end of each trial, observers received visual performance feedback: Interception location was shown as a red disk; true target position at time of interception was indicated by a black disk (Figure 1a). Each observer completed two blocks of 99 trials with each hand, resulting in a total of 198 trials per hand (11 trials per hand, per condition).

Eye and hand movement recordings and preprocessing

Monocular eye position signals were recorded with a video-based eye tracker (Figure 1b; Eyelink 1000 tower mount; SR Research Ltd., Ottawa, ON, Canada) and sampled at 1000 Hz. Eye movements were analyzed off-line using custom-made routines in Matlab. Eye velocity profiles were filtered using a low-pass, second-order Butterworth filter with cutoff frequencies of 15 Hz (position) and 30 Hz (velocity). Saccades were detected based on a combined velocity and acceleration criterion: Five consecutive frames had to exceed a fixed velocity criterion of 50°/s; saccade on- and offsets were then determined as acceleration minima and maxima, respectively, and saccades were excluded from pursuit analysis. Pursuit onset was detected in individual traces using a piecewise linear function fit to the filtered position trace. Each trial was manually inspected, and we excluded trials with blinks (0.85%) and those in which observers moved their hand before stimulus onset (0.2%).

Index finger position was recorded with a magnetic tracker (3D Guidance trakSTAR, Ascension Technology Corp., Shelburne, VT) at a sampling rate of 240 Hz; a lightweight sensor was attached to the observer's fingertip with a small Velcro strap. The 2D finger interception position was recorded in *x*- and *y*-screen-centered coordinates for each trial. Trials in which the point of interception was not detected were excluded (1.6% trials across all observers).

Eye and hand movement data analyses

Smooth pursuit in response to a moving target can be initiated reliably, even for targets which disappear after a brief presentation (Figure 2). Smooth pursuit is commonly separated into an initiation or open-loop phase (the first 140 ms after pursuit onset), where pursuit is usually driven by retinal image motion alone (Lisberger & Westbrook, 1985), and the maintenance or closed-loop phase (from 140 ms after pursuit onset to interception), where pursuit is driven by a combination of retinal image motion and feedback signals. Note that one implication of the limited stimulus duration in our study is that in some trials the target had already disappeared by the time pursuit was initiated. Hence, open-loop pursuit in our study must have been driven by a combination of retinal and velocity memory signals. We analyzed pursuit latency, initial pursuit peak velocity (0–140 ms after pursuit onset) and closed-loop velocity gain. We also analyzed the invisible tracking time, defined as the duration of continued smooth tracking after stimulus disappearance until the next catch-up saccade was made. Tracking error, defined as root mean square deviation of eye position relative to target position, was analyzed across the entire trial (from pursuit onset to interception). In 33% of all trials tracking was initiated with a saccade and no pursuit onset was detected prior to the first saccade. In those trials, tracking error was calculated for the time interval from first-saccade offset to interception. To assess the temporal evolution of tracking error in relation to interception performance, we also analyzed tracking error in separate 150-ms time bins aligned to interception. Finally, catch-up saccades

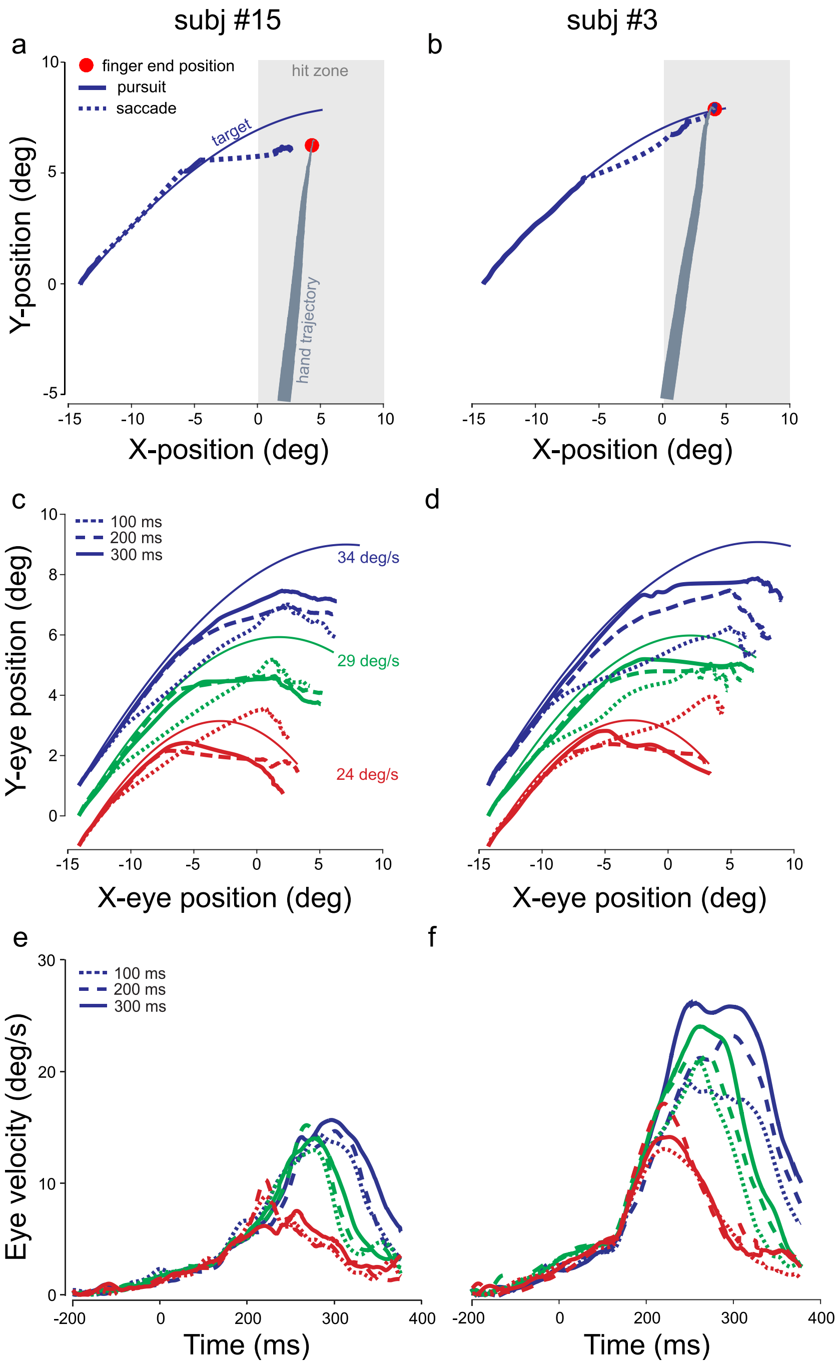

Figure 2. (A, B) 2D eye position (degree) and finger end position (red) from an individual trial of two representative observers in response to a target moving at 34°/s, shown for 300 ms. Pursuit portions of each position trace are denoted by a solid line, saccade portions by dotted line. Hand trajectories are plotted from when the hand reaches the bottom of the screen; line thickness denotes distance to screen. (C, D) 2D eye position (degree) for the same observers, averaged across all trials within each condition (speeds denoted by color, presentation durations denoted by line type). Saccades were replaced by linear interpolation. Target and eye starting positions are shifted along the vertical axis by ±1° for clarity for the 24°/s and 34°/s conditions. (E, F) Mean absolute eye velocity (°/s) over time for the same observers and conditions as shown in panels C, D. All traces were aligned to 200 ms before stimulus onset to show that anticipatory pursuit occurred frequently due to predictable target motion direction.

are an important and integral part of the pursuit response and occur when the eye falls behind the target (de Brouwer, Yüksel, Blohm, Missal, & Lefèvre, 2002; Ego, Orban de Xivry, Nassogne, Yüksel, & Lefèvre, 2013; Orban de Xivry & Lefèvre, 2007). We analyzed the amplitude of the first catch-up saccade and the cumulative catch-up saccade amplitude for the time interval from pursuit onset to interception.

Each observer completed the task with both left and right hand (two blocks of trials each), regardless of handedness. We analyzed finger latency, finger peak velocity, and interception accuracy, defined as interception error and calculated as the Euclidean distance between finger position and target position at time of interception. We found no difference in interception error between interception with the dominant hand and interception with the nondominant hand, $t(31) = 1.07$, $p = 0.29$; paired-sample, two-tailed t test, and averaged across data from right and left hand.

A standard score (*z* score) analysis was performed on all eye and finger measures across all trials and observers; individual observers' values that deviated from the respective measure's group mean by more than three standard deviations were flagged as outliers and excluded from further analysis (0.8%–3.5% per measure across all trials and observers); these were mostly due to small undetected saccades. To investigate the relation between eye movement error and interception error, we ran a multiple linear regression model with predictors: pursuit latency, open-loop peak velocity, initial saccade amplitude, overall peak velocity, velocity gain, eye position error, cumulative catch-up saccade sum, and invisible tracking time. We also included in the regression model the effect of feedback about the true position of the target and the point of interception (Figure 1a), calculated as the Euclidean distance between position of the feedback disk in the present trial and averaged feedback position across all previous trials per speed. We refer to this variable as feedback memory. Next, we conducted a feature selection to confirm the regression results using a random forest algorithm for classification and regression (Liaw & Wiener, 2002) on the same input variables as in the multiple linear regression model. The random forest algorithm is a simple machine learning model that constructs multiple decision trees using bootstrapping and then estimates the importance of each input attribute (between 0%–100%) by assessing how much the prediction error increases when the respective attribute is neglected. Selected parameter settings were mtry = 3 (number of variables randomly sampled as candidates in each split), and ntree = 500 (number of trees to grow).

To investigate interception timing we conducted a hazard analysis in Matlab to identify each observer's preferred interception time, i.e., the probability of intercepting at a particular point in time. The time interval from stimulus motion onset to offset was divided into 50-ms bins to achieve distinct hazard peaks (highest likelihood of interception) at high temporal accuracy; in every time bin the number of executed interceptions was counted across all trials for each observer. Next we computed the hazard level H_t, which is defined as the conditional probability of an interception occurring at time $\boldsymbol{t}$, given that it has not occurred before, as follows:

$$H_t = \frac{I_t}{N - \sum_{i=1}^{t-1} I_i}, \qquad (5)$$

where I_i is the number of interceptions counted within time interval i, N the total number of interceptions across all trials, and $\Sigma_{i=1}^{t-1} I_i$ the number of interceptions that occurred prior to time t; hazard levels close to 0 indicate a low probability of interception at time t, levels close to 1 indicate a high probability of interception. Hazard peaks across all observers were then analyzed with a k-means clustering algorithm to investigate if the data fell into distinct groups of observers intercepting at particular times.

A single-hidden-layer neural network (R CRAN package *caret*) was trained on trial-by-trial eye movement parameters (same as in the regression model defined above) of all 32 participants with respect to their interception groups. Subsequently, eye movement data of ten new participants were classified into early or late interception using the trained neural network. Neural network predictions were then compared to results from the hazard analysis.

Results

Eye movement quality and interception error

Figure 2 shows typical eye position traces for individual trials (Figure 2a, b), eye position traces averaged across trials within condition (Figure 2c, d), and averaged eye velocity (Figure 2e, f), for two representative observers. It is evident that there is a close relation between where subjects look and where they point to. Even though observers spent most of the trial fixating or tracking the target with pursuit eye movements (73% of total time per trial on average, $SD = 9.4$; solid lines in Figure 2a, b), considerable distance was covered by catch-up saccades (dotted lines in Figure 2a, b). Across all observers, the ability to accurately intercept a predicted target trajectory scaled with pursuit quality: A multiple linear regression model yielded a highly significant relationship between tracking error (2D eye position error calculated across the entire trial) and interception error, $R^2 = 0.24$, $F(9, 7814) = 281.1$, $p < 0.001$. Regression model results indicate that tracking error is the largest contributor to interception error (Table 2). This finding was confirmed by a random forest algorithm, which also selected tracking error as the most important contributor (68%, Figure 3a).

Predictor	Coefficient	*SE* coefficient	*T*	*P*
Pursuit latency	−0.0042	0.0003	−15.13	< 0.001
Open-loop peak velocity	0.0035	0.0018	1.87	0.06
Initial saccade amplitude	−0.051	0.0064	−8.01	< 0.001
Closed-loop gain	−0.042	0.061	−0.69	0.49
Eye peak velocity	0.0067	0.0017	4.04	< 0.001
Tracking error	0.82	0.02	38.56	< 0.001
Cumulative saccade amplitude	0.036	0.0045	7.96	< 0.001
Invisible tracking time	0.0018	0.0002	8.56	< 0.001
Feedback memory	0.10	0.0095	10.74	< 0.001

Table 2. Multiple linear regression model results. *Notes*: Shown are slope coefficients and their standard error, as well as *t* statistic and significance level for each predictor.

Note that for the regression model analysis, tracking error was averaged across the entire trial from pursuit onset to interception (or, if no pursuit onset was found, from offset of the first saccade to interception) and includes the part of the trial where the ball was invisible. The second most important parameter according to this model is cumulative saccade amplitude (Figure 3a). Catch-up saccades likely have a strong influence on tracking error as well. To control for the effect of the first saccade, we recalculated tracking error from offset of the first saccade to interception for all trials, but the model results for this version of tracking error were almost identical (coefficient $= 0.74$, $T = 38.18$, $p < 0.001$; compare with tracking error in Table 2) and the order of predictors in the random-forest analysis was unchanged. It is interesting that open-loop pursuit parameters, the eyes' immediate response to visual target motion, were least predictive of interception performance, possibly due to strong anticipatory pursuit (Figure 2e, f).

Figure 3b through e shows the temporal development of the relation between tracking error (calculated in 150-ms time bins, aligned with time of interception) and interception error from hand movement onset (mean movement duration: 588 ± 12.4 ms) to interception. Regardless of speed and presentation durations (variations not shown), the eye-hand link increased over time, reaching a maximum close to the time of interception (Figure 3e). Congruently, the Euclidean distance between eye and finger at time of interception is relatively small, 1.36° ($SD = 0.44$), indicating that observers intercept close to their current eye position (see also Figure 2a, b). These findings extend the close relation between saccades and hand movements in manual interception tasks to smooth pursuit and show temporally linked behavior, relying on common trajectory estimation and planning mechanisms. Moreover, eye tracking error initially increases but then decreases (data points are shifted to the left along the *x* axis), from an average of 2.9° ($SD = 1.32$) at 600–450 ms before interception (Figure 3b) to 2.5° (*SD*

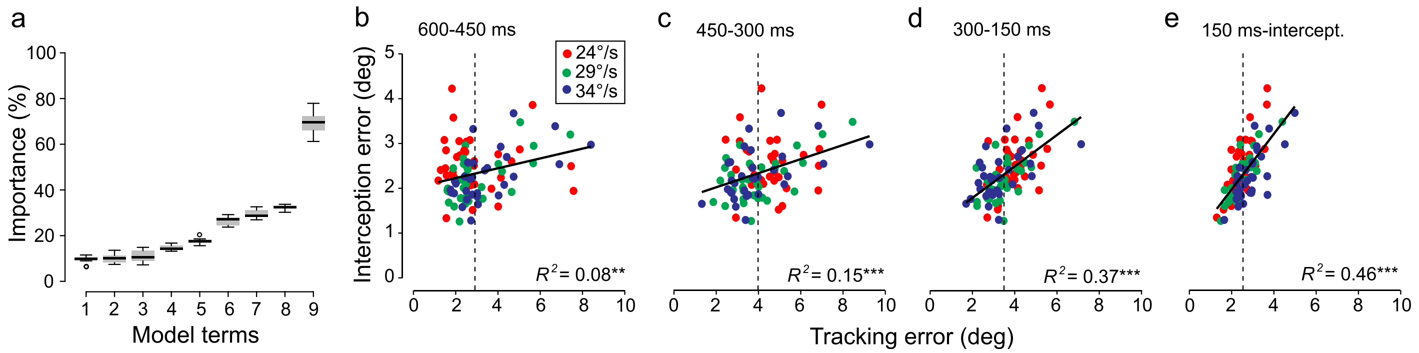

Figure 3. Relation between eye position (tracking error) and interception error. (A) Random-forest regression results as boxplot of median importance for each variable (1: open-loop peak velocity, 2: initial saccade amplitude, 3: invisible tracking time, 4: overall peak velocity, 5: velocity gain, 6: latency, 7: feedback memory, 8: cumulative catch-up saccade sum, 9: tracking error); error bars denote the range, circles are outliers. The model identified tracking error as the most important contributor. (B) Temporal evolution of the relationship between tracking and interception error relative to time of interception, averaged across the time interval 600–450 ms before interception, (C) 450–300 ms before interception, (D) 300–150 ms before interception, (E) 150 ms until interception. Plots are exemplary for 200 ms presentation duration; target speeds are indicated by color. Solid lines are best fit linear regressions; significance of adjusted R^2 is ** $p < 0.01$, *** $p < 0.001$. Dashed vertical lines denote mean tracking error for each time interval.

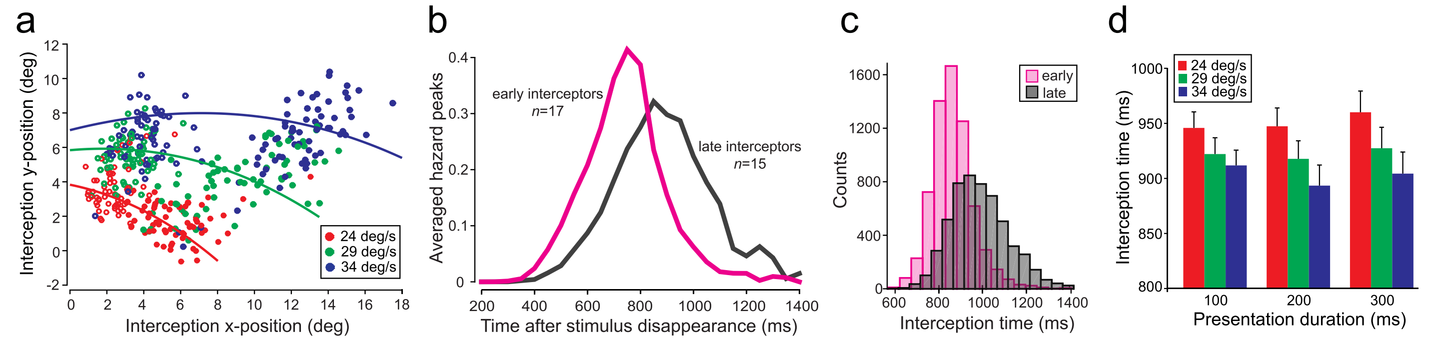

Figure 4. Interception timing. (A) 2D interception positions for two representative observers for the 200-ms presentation duration and all three speeds (denoted by colors). Curves correspond to the (invisible) trajectory of the ball for each speed. Observer #9 tended to intercept early regardless of speed; observer #18 intercepted late. (B) Average probability to intercept at a given point in time (hazard peaks) per group for early (magenta) versus late interceptors (gray). (C) Interception time peak histogram for early versus late. (D) Effects of presentation duration and speed on interception time (ms). Error bars are standard errors of the mean.

$= 0.53$) close to interception (Figure 3e; mean tracking errors denoted by dashed vertical lines in each panel). This improvement close to the time of interception happens despite increasing duration of target invisibility over time, and hence might be linked to the engagement of the hand.

Eye movement quality and interception strategy

Humans can continue to track a moving object that has disappeared based on internal target velocity memory (Orban de Xivry, Coppe, Blohm, & Lefèvre, 2013; Orban de Xivry, Missal, & Lefèvre, 2008), but this memory signal decays over time. Thus, the longer the ball is invisible the greater the uncertainty about its current position. Given this constraint, it seems that intercepting as soon as the ball enters the strike zone would be the most effective strategy. Note that we did not provide a "go" signal; observers were free to intercept the ball at any time while it was in the hit zone. We observed different but stable interception timing strategies: Some participants tended to always intercept early in the hit zone; others intercepted late.

Figure 4a shows 2D interception positions for two representative observers and illustrates that across all levels of stimulus speed one observer intercepts early, and the other observer intercepts late. To quantitatively investigate observers' preferred interception strategy, we conducted a Hazard analysis based on each individual observer's interception times. Splitting our data into two groups using a k-means cluster analysis of individual Hazard peaks (Figure 4b) reduced within-group variability (within-cluster sum of squares) of interception times by 80% and 86% for the two groups; increasing the cluster number to three or beyond led to only marginal further reductions in variability. We thus compared performance between two clusters: a group of "early" interceptors ($n = 17$; mean interception time 865 ± 79 ms) and a group of "late" interceptors ($n = 15$), who hit the target on average 129 ms later (994 ± 93 ms; $t = -14.23$, $p < 0.001$; see Figure 4c). We conducted this analysis across presentation durations and speeds. Although both factors significantly affect interception time [main effect of presentation duration: $F(2, 60) = 4.02$, $p = 0.02$; speed: $F(2, 60) = 23.88$, $p = 0.001$; Presentation Duration × Speed interaction: $F(2, 60) = 3.41$, $p = 0.01$; see Figure 4d], there were no differential effects of duration or speed on the two groups [Duration × Group: $F < 1$; Speed × Group: $F(2, 60) = 1.73$, $p = 0.19$].

Even though late interceptions followed a longer period of invisible ball flight, thus creating larger spatio-temporal uncertainty, spatial interception performance was similar between early versus late interceptors. These results are reflected in a repeated-measures ANOVA for interception error with within-subjects factors presentation duration and speed and between-subjects factor group; ANOVA results can be visualized using Figure 5a, which shows interception position within the strike zone for all early versus late interceptors. The ANOVA showed expected significant main effects of presentation duration, $F(2, 60) = 131.71$, $p < 0.001$; (compare symbol types in Figure 5a) and speed, $F(2, 60) = 12.07$, $p < 0.001$, but no main effect of group, $F(1, 30) = 0.99$, $p = 0.34$; (compare open vs. closed symbols in Figure 5a), indicating similar magnitude of interception error across groups. We next computed interception error in separate time bins, aligned with time of interception (Figure 5b). Results reveal similar interception errors for early and late interceptors across time; however, there is a trend for late interceptors to hit more accurately if their interception occurs in the last time bin, relative to early interceptors: two-sample *t test*, $t(89.9) = 1.87$, $p = 0.06$. The finding that late interceptors are at least as accurate as early interceptors indicates an actual performance advantage in late interceptors, as we

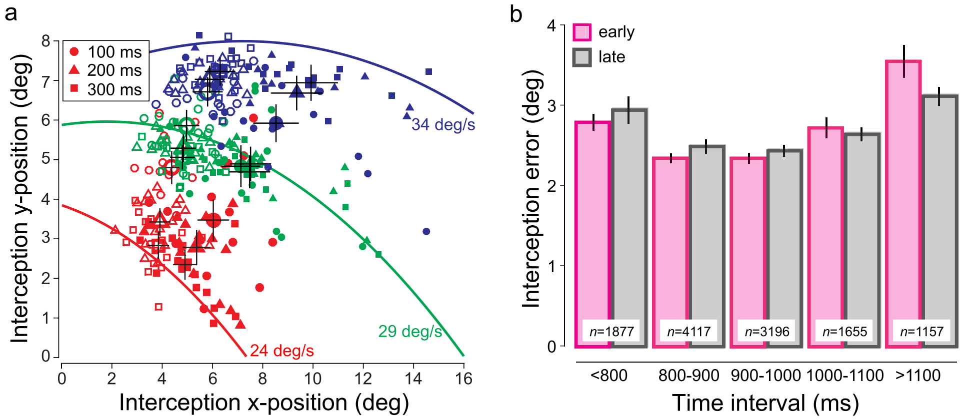

Figure 5. (A) Interception positions in early versus late interceptors within the strike zone. Each symbol is the average per condition for one individual subject. Color denotes speed, symbol types denote presentation duration; open symbols are for early interceptors, filled symbols for late interceptors. Larger symbols with 2D error bars are group means. (B) Interception error (degree) for early versus late interceptors across time intervals, for interceptions earlier than 800 ms, 800–900, 900–1000, 1000–1100, and later than 1100 ms. Number of trials included in each interval are indicated in the Figure. Error bars are standard errors of the mean.

expect higher errors with uncertainty accumulating over time.

Figure 5a also reveals an interesting tendency to intercept close to the medium-speed trajectory, thus remaining inside the range of space covered by the three possible trajectories: Interception locations for the slowest speed showed positive-sign vertical position errors ($M = 1.16$, $SD = 0.72$); interception locations for the fastest speed showed negative-sign vertical position errors ($M = -0.92$, $SD = 0.52$). This spatial averaging effect scaled with presentation duration: Averaging was strongest for the shortest presentation duration. This finding is reflected in a highly significant Speed × Presentation Duration interaction on vertical position error, $F(4, 120) = 119.44$, $p < 0.001$, regardless of group (no three-way interaction with group, $F < 1$).

Notwithstanding between-group similarities in interception error, the two groups differ in the type of information used, as well as in their eye movement quality, hand movement dynamics, hand movement path, and speed. We evaluated differences between early and late interceptors by fitting multiple linear regressions to eye and hand movement data determining which parameters best predict early versus late interception error. We included finger latency and peak velocity in this model to investigate the extent to which hand movement speed affects accuracy in early versus late. Interception error in both groups is best predicted by tracking error (early: coefficient = 0.86, $t = 27.8$, $p < 0.001$; late: coefficient = 0.86, $t = 28.0$, $p < 0.001$), and this result was confirmed with a random forest model run separately for each group (early: 43%, late: 64%). However, the second most important variable in the early group is memorized position of the interception feedback from previous trials within the same speed condition (coefficient = 0.18, $t = 12.6$, $p < 0.001$; random forest 30%). By contrast, feedback memory does not play a major role in predicting late interceptors' performance (coefficient = 0.03, $t = 2.30$, $p = 0.02$; random forest: 16%). In accordance with the model, early interceptors hit significantly closer to the memorized feedback position across previous trials within the same speed condition, mean distance 2.5° ± 1.6°, than late interceptors, mean distance 3.2° ± 1.9°, significant main effect of group, $F(1, 30) = 17.25$, $p < 0.001$.

These results indicate that the two groups of observers use different tactics to intercept accurately: early interceptors rely on a combination of accurate eye movements and cognitive heuristics, whereas late interceptors rely on accurate eye movements only. In line with these regression results, we found superior pursuit quality in late versus early interceptors. Figure 6a shows mean eye velocity traces for each group (early vs. late interceptors) for the fastest speed and all presentation durations, revealing faster pursuit (13% increase in overall peak velocity across all conditions) in late as compared to early interceptors. These group differences can also be seen in individual observer's velocity profiles (representative early interceptor in Figure 2e; representative late interceptor in Figure 2f). A significant main effect of group on peak velocity, $F(1, 30) = 4.29$, $p = 0.04$) supports this observation. Late interceptors also initiated pursuit earlier than late interceptors with a 30% decrease in latency. Late interceptors' initial saccade amplitude was smaller ($M = 6.4$, $SD = 1.0$) than in early interceptors ($M = 6.8$, $SD = 1.3$). However, these differences in latency and initial saccade were nonsignificant ($F < 1$, *ns*).

Hand movements (finger latency and peak velocity) were less predictive of interception error in either group (<15% in either random forest model), but early and late interceptors show different hand movement strat-

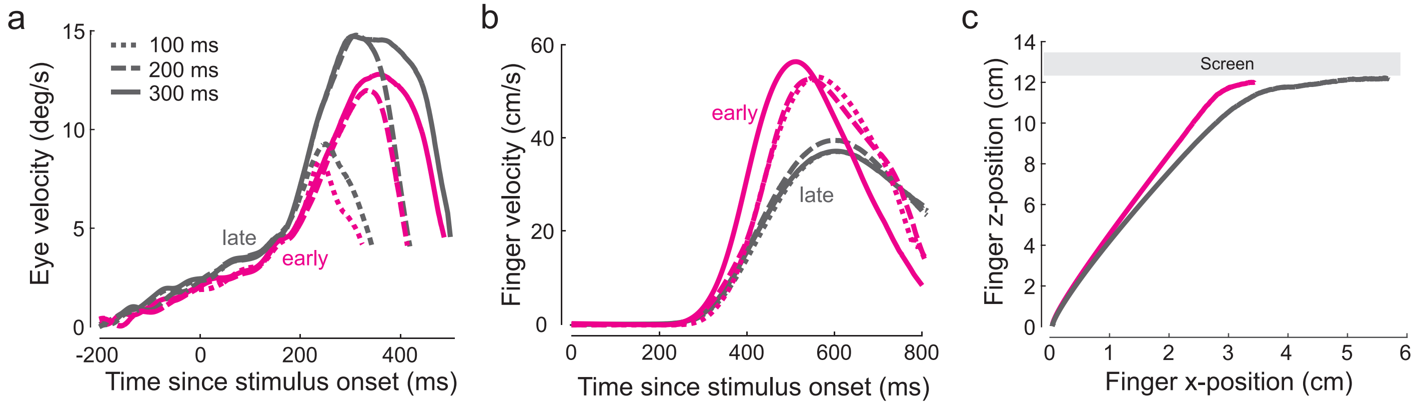

Figure 6. Vectorial eye and finger velocity traces across all observers for early (magenta) versus late interceptors (gray) for the fastest speed (34°/s) and all presentation durations (indicated by line type). Saccades were replaced by linear interpolation. (A) Eye velocity (°/s) aligned to 200 ms before stimulus motion onset. (B) Finger velocity (cm/s) in 3D aligned to stimulus onset. (C) Bird's eye view of interception hand path (finger position in cm) aligned to stimulus motion onset, averaged across presentation durations.

egies (Figure 6b, c). Early interceptors start moving their hand earlier (12% lower finger latency across all conditions), confirmed by a main effect of group on finger latency, $F(1, 30) = 3.8$, $p = 0.05$, and they move their hand faster (10% increase in peak velocity; $F(1, 30) = 4.76$, $p = 0.03$, and in a more direct path (see Figure 6c). By contrast, late interceptors move more slowly and seem to perform online corrections to the target position until late in the trajectory. Similar to eye movement data, finger peak velocity also shows expected significant main effects of speed, $F(2, 60) = 180.96$, $p < 0.001$, but was unaffected by presentation duration, ($F < 1$, *ns*).

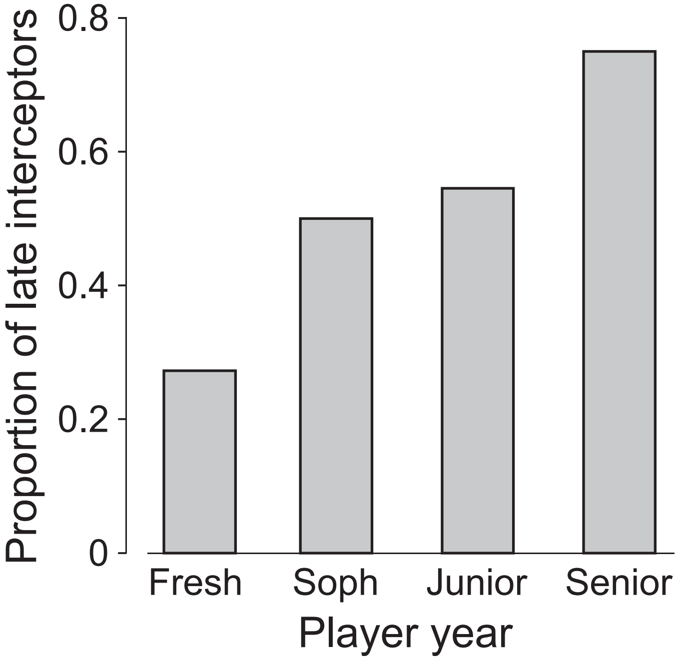

Figure 7. Proportion of late interceptors out of 32 observers who were freshmen, sophomore, junior, or senior. All were members of the UBC varsity baseball team.

In sum, these findings reveal striking differences between early and late interceptors' eye and hand movements. Interception strategy is intricately linked to eye movement quality: Hand movements are initiated when uncertainty increases and tracking quality declines; this limit may be reached earlier in early interceptors due to lower eye movement quality, whereas late interceptors can afford to track invisible balls longer. This strategy allows more time to extract important ball trajectory information, thus enabling late interceptors to remain temporally and spatially accurate for late interceptions (Figure 5b). Remarkably, our data reveal a close relation between early versus late interception strategy and level of experience in our cohort of varsity baseball players. A larger proportion of senior players chose to intercept late (Figure 7), indicating a strong link between experience and interception strategy.

Next, trial-by-trial eye movement data of all observers were used to train a neural network with respect to interception strategy. We then used the model to classify 10 new observers into early versus late interceptors based on only their eye movement quality (the same parameters as in multiple linear regressions, Table 2). The model classified nine out of 10 observers correctly, i.e., in accordance with a hazard analysis of the respective hand movement data, solely based on their eye movement quality. Only one late interceptor was falsely assigned to the early group. When the neural net was trained with a single parameter, tracking error, we were still able to classify seven out of 10 observers correctly. These classification results emphasize the importance of smooth pursuit eye movements for manual interception; however, they are not proof of causality between eye movements and interception error. They indicate that attributes of smooth pursuit eye movements may be sufficient to predict, with up to 90% accuracy, the preferred interception strategy.

Discussion

Eye and hand movements are closely linked in space and time in visually guided reaching, grasping, pointing, or interception tasks. Most behavioral and neurophysiological studies on the relation between eye and hand movements have focused on saccades to stationary or moving objects. Knowledge about the role of smooth pursuit for the control of hand movements is sparse. Because of the known advantages of pursuit for motion prediction (Bennett et al., 2010; Spering et al., 2011) and the importance of prediction for manual interception (Flanagan, Bowman, & Johansson, 2006; Soechting, Juveli, & Rao, 2009), we assume that accurate pursuit is critical for the ability to predictively intercept a moving visual object. Here we used a novel naturalistic task to directly test this assumption and report the following key findings:

First, a position-dependent variable, 2D eye position error (tracking error calculated across the entire trial), is the most important predictor of interception error. This finding might be due to the overall low quality of smooth tracking in a task that included only brief periods of target visibility; keeping the target close to the fovea by any means possible determines the ability to intercept. The close relation between tracking error and interception error increases over time: Eye movement quality is most informative for hand movement control just before the hand intercepts the target, and interception occurs close to the location of the eye (within <1.4°; see Figure 2a, b, and Figure 3e). This temporal evolution of the link between pursuit and interception error extends earlier findings that the eye guides the hand (Ballard et al., 1992; Johansson et al., 2001; Land, 2006; Sailer et al., 2005; Smeets et al., 1996). Previous studies focused on patterns of fixations and saccades, ballistic eye movements of short duration, which arrive at the target long (up to 1 s) before the hand, indicating that gaze supports hand movement planning. We assessed a continuous eye-movement response and show that the link between smooth pursuit and hand movement is closest at the time of interception, indicating joint mechanisms of trajectory prediction and movement planning. Indeed, common prediction has been shown to be useful in synthesizing eye and hand movements in a computational model of interception (Yeo, Lesmana, Neog, & Pai, 2012).

The temporal evolution of the eye-hand link (Figure 3b through e) also reveals that eye tracking error is smallest at the time of interception. This is noteworthy, given that the target has long disappeared at the time of interception. These findings indicate that an ongoing hand movement may boost eye movement accuracy, as has previously been shown for saccades (Dean, Martí, Tsui, Rinzel, & Pesaran, 2011; Epelboim et al., 1997; Lünenburger, Kutz, & Hoffmann, 2000; Snyder, Calton, Dickinson, & Lawrence, 2002) and smooth pursuit during manual tracking (Niehorster, Siu, & Li, 2015) or when visual target motion is controlled by observers' own finger movements (Chen, Valsecchi, & Gegenfurtner, 2016).

Second, our task involves a considerable amount of uncertainty, given that the target always disappears after its initial launch. We found that observers tend to intercept close to the spatial average of all potential target trajectories, i.e., the trajectory of the target moving at medium speed. The extent to which observers intercept close to the spatial average increased for shorter target presentation (i.e., with larger uncertainty). These findings indicate that observers learn the statistics of the trajectory to increase the likelihood of an interception within the range of target motion. Such use of a Bayesian prior, in combination with sensory information, has been shown with tasks involving uncertainty due to low stimulus contrast (Stocker & Simoncelli, 2006) or ambiguous motion information (Weiss, Simoncelli, & Adelson, 2002).

Third, we found that eye movement quality predicts observers' preference to intercept early versus late with greater than 90% accuracy. Interception error in the early group was best predicted by a combination of accurate smooth pursuit eye movements (tracking error) and cognitive heuristics, whereas late interceptors' hitting error was best predicted by accurate pursuit only. In line with these results, obtained from a random-forest regression model, late interceptors have better pursuit, move their hand more slowly, and continuously correct their hand movement near the point of interception. Remarkably, group membership was closely linked to experience in a real-world task, baseball. More senior varsity athletes had a higher probability of intercepting late. In baseball, hitters have to extract visual trajectory information about the ball in limited time. Late interceptions allow more time for information accrual and decision making. Different strategies used by the two groups of early versus late interceptors could thus point to different capabilities in motion perception, and to differences in how motion information is used in an internal model for trajectory estimation. As an alternative, later interception, indicating better trajectory estimation, could be a direct consequence of better pursuit. To investigate the direct effect of pursuit on trajectory estimation, we developed an experimental paradigm in which observers had to judge whether a linearly moving target (the "ball") would hit or miss a stationary vertical line segment (the "goal"). Ball and goal were shown only briefly and disappeared before the perceptual judgment was prompted. Prediction performance was significantly enhanced when observers tracked the ball with smooth pursuit, versus when they fixated on the goal (Spering et al., 2011). In conjunction with the finding of better pursuit in late interceptors these findings indicate that longer and more accurate ball tracking (Bahill, Baldwin, & Venkateswaran, 2005; Bahill & LaRitz, 1984) and hence better trajectory estimation (Spering et al., 2011) may lead to better hitting.

Our findings advance previous studies demonstrating links between smooth pursuit and hand movements which either did not directly link pursuit quality with hand movement performance (Brenner & Smeets, 2011; Mrotek & Soechting, 2007; Soechting & Flanders, 2008; van Donkelaar et al., 1994) or reported that pursuit quality and catching a ball were unrelated (Cesqui et al., 2015). By contrast, we found a strong relation between pursuit quality and interception error. We also identified an additional factor that might influence performance, at least in some observers: the memorized position of the ball at time of interception (feedback memory) across previous trials. Even though this cognitive heuristic is specific to our laboratory task, memory of ball position (e.g., relative to bat or racquet) has been shown to play a role in other manual tasks (Bosco, Delle Monache, & Lacquaniti, 2012; Brenner, Canal-Bruland, & van Beers, 2013) and could be equally important in the field, where hitters often rely on simple heuristics.

It is important to note that some aspects of our experimental design, task and stimulus, are unnatural. In a natural environment, a ball moving towards a hitter would be tracked with a combination of eye and head movements (Land & McLeod, 2000; Mann, Spratford, & Abernethy, 2013). In our paradigm, the head was constrained by using a chin- and forehead rest. The observer's viewpoint was orthogonal to the ball trajectory, which moved in the fronto-parallel plane only, requiring pursuit and saccades, but not vergence eye movements. The ball was occluded for the majority of its flight to mimic the amount of visual information available to a hitter in baseball (Adair, 2002). This design choice largely prevents the use of online interception strategies (Zhao & Warren, 2015). Even though we tested a range of different ball trajectories by varying ball speed, natural ball trajectories are much more variable. However, our paradigm allows us to manipulate all aspects of the trajectory, and future studies could target the role of visual ball features in determining interception performance. The limited range of trajectory types also mimics the kind of environment batters would encounter when practicing with a ball launching machine. Critically, despite these limitations in the naturalness of our paradigm, we found a strong relation between interception strategy and baseball experience, indicating that the requirements of our task might be relevant to real-world performance. It is possible that more experienced players applied the strategies used in the field to our laboratory task. Many features of our task resemble the requirements of baseball hitting: limited time for information accrual, the necessity to extrapolate trajectories, and—to some degree—the uncertainty about the upcoming ball trajectory. Moreover, our findings are important for understanding the effect of eye movements on interception performance, prerequisite for the development of experiments involving more natural 3D stimuli or conducted in situ.

The results reported here are most consistent with a view of oculomotor and hand movement control as interdependent, cooperative processes. The importance of pursuit for interception movements and the effect of interception movements on pursuit indicate a co-optimization of both behaviors, potentially mediated through parietal cortical circuits implicated in eye-hand coordination. A growing body of literature has revealed similarities in how visual information is processed, selected and transformed for the control of eye movements—mostly—saccades—hand movements—mostly reaching—in areas such as the parietal reach region (Batista, Buneo, Snyder, & Andersen, 1999; Hwang, Hauschild, Wilke, & Andersen, 2014; Snyder, Batista, & Andersen, 2000), lateral intraparietal area (Balan & Gottlieb, 2009; Crawford, Henriques, & Medendorp, 2011; Yttri, Liu, & Snyder, 2013), and superior colliculus (Carello & Krauzlis, 2004; McPeek & Keller, 2004; Nummela & Krauzlis, 2010; Song, Rafal, & McPeek, 2011). What remains to be shown is whether these neurophysiological findings extend to smooth pursuit eye movements. Our findings suggest that accurate smooth pursuit is critical for manual interception of moving objects and may lead to tangible performance improvements in real-world tasks such as baseball. The close link between smooth pursuit accuracy and interception strategy—whether to intercept early versus late—indicates a common spatiotemporal framework for the control of smooth pursuit and hand movements.

Conclusions

Our results verify a strong relationship between eye movements and hand movements and show, for the first time, which aspects of smooth pursuit eye movement quality determine interception accuracy and strategy. Interception strategy is optimally adapted to the constraints of the eye movement system: Good pursuit enables later interceptions, thus extending the

time interval available for sensory information accrual and decision making. We directly link this novel finding to experience, revealing a stronger tendency for senior varsity baseball players to be late interceptors. In addition to obvious advantages in sports, late interception may have conferred an evolutionary advantage to predators deciding to strike at their prey or their prey deciding on an evasive maneuver.

Keywords: eye movements, smooth pursuit, saccades, motion prediction, interception, eye-hand coordination, timing

Acknowledgments

This work was supported by NSERC Discovery Grants to MS (RGPIN 418493) and DKP (RGPIN 153236) and Canada Foundation for Innovation (CFI) John R. Evans Leaders Fund to MS, and CFI Leading Edge Fund to DKP. The authors thank Cole Shin for technical support, UBC baseball coach Terry McKaig for help with recruitment, and members of the Spering lab for helpful comments on the manuscript. Data were presented in preliminary form at the 2014 Society for Neuroscience meeting in Washington, DC (Fooken, Yeo, Pai, & Spering, 2014).

Commercial relationships: none.
Corresponding author: Jolande Fooken.
Email: fooken@cs.ubc.ca.
Address: Department of Ophthalmology & Visual Sciences, Blusson Spinal Cord Research Centre, University of British Columbia, Vancouver, Canada.

References

Adair, R. K. (2002). *The physics of baseball* (3rd ed.). New York, NY: Harper Collins.

Bahill, A. T., Baldwin, D., & Venkateswaran, J. (2005). Predicting a baseball's path. *American Scientist*, *93*, 218–225.

Bahill, A. T., & LaRitz, T. (1984). Why can't batters keep their eyes on the ball? *American Scientist*, *72*, 249–253.

Balan, P. F., & Gottlieb, J. (2009). Functional significance of nonspatial information in monkey lateral intraparietal area. *Journal of Neuroscience*, *29*, 8166–8176.

Ballard, D. H., Hayhoe, M. M., Li, F., & Whitehead, S. D. (1992). Hand-eye coordination during sequential tasks. *Philosophical Transactions of the Royal Society B*, *337*, 331–338.

Batista, A. P., Buneo, C. A., Snyder, L. H., & Andersen, R. A. (1999). Reach plans in eye-centered coordinates. *Science*, *285*, 257–260.

Becker, W., & Fuchs, A. F. (1985). Prediction in the oculomotor system: Smooth pursuit during transient disappearance of a visual target. *Experimental Brain Research*, *57*, 562–575.

Belardinelli, A., Stepper, M. Y., & Butz, M. V. (2016). It's in the eyes: Planning precise manual actions before execution. *Journal of Vision*, *16*(1):18, 1–18, doi:10.1167/16.1.18. [PubMed] [Article]

Bennett, S. J., & Barnes, G. R. (2005). Combined smooth and saccadic ocular pursuit during the transient occlusion of a moving visual object. *Experimental Brain Research*, *168*, 313–321.

Bennett, S. J., Baures, R., Hecht, H., & Benguigui, N. (2010). Eye movements influence estimation of time-to-contact in prediction motion. *Experimental Brain Research*, *206*, 399–407.

Bennett, S. J., Orban de Xivry, J. J., Barnes, G. R., & Lefèvre, P. (2007). Target acceleration can be extracted and represented within the predictive drive to ocular pursuit. *Journal of Neurophysiology*, *98*, 1405–1414.

Bosco, G., Delle Monache, S., & Lacquaniti, F. (2012). Catching what we can't see: Manual interception of occluded fly-ball trajectories. *PLoS One*, *7*(11), e49381.

Brenner, E., Canal-Bruland, R., & van Beers, R. J. (2013). How the required precision influences the way we intercept a moving object. *Experimental Brain Research*, *230*, 207–218.

Brenner, E., & Smeets, J. B. J. (2011). Continuous visual control of interception. *Human Movement Science*, *30*, 475–494.

Brenner, E., & Smeets, J. B. J. (2015). How people achieve their amazing temporal precision in interception. *Journal of Vision*, *15*(3):8, 1–21, doi:10.1167/15.3.8. [PubMed] [Article]

Carello, C. D., & Krauzlis, R. J. (2004). Manipulating intent: Evidence for a causal role of the superior colliculus in target selection. *Neuron*, *43*, 575–583.

Cesqui, B., Mezzetti, M., Lacquaniti, F., & d'Avella, A. (2015). Gaze behavior in one-handed catching and its relation with interceptive performance: What the eyes can't tell. *PLoS One*, *10*(3), e0119445.

Chen, J., Valsecchi, M., & Gegenfurtner, K. R. (2016). LRP predicts smooth pursuit eye movement onset during the ocular tracking of self-generated movements. *Journal of Neurophysiology*, *116*, 18–29.

Crawford, J. D., Henriques, D. Y. P., & Medendorp, W. P. (2011). Three-dimensional transformations for goal-directed action. *Annual Review of Neuroscience*, *34*, 309–331.

Dean, H. L., Martí, D., Tsui, E., Rinzel, J., & Pesaran, B. (2011). Reaction time correlations during eye-hand coordination: Behavior and modeling. *Journal of Neuroscience*, *31*, 2399–2412.

de Brouwer, S., Yüksel, D., Blohm, G., Missal, M., & Lefèvre, P. (2002). .What triggers catch-up saccades during visual tracking? *Journal of Neurophysiology*, *87*, 1646–1650.

Diaz, G., Cooper, J., Rothkopf, C., & Hayhoe, M. (2013). Saccades to future ball location reveal memory-based prediction in a virtual-reality interception task. *Journal of Vision, 13*(10):20*,* 1–14, doi: 10.1167/13.1.20. [PubMed] [Article]

Ego, C., Orban de Xivry, J. J., Nassogne, M. C., Yüksel, D., & Lefèvre, P. (2013). The saccadic system does not compensate for the immaturity of the smooth pursuit system during visual tracking in children. *Journal of Neurophysiology*, *110*, 358–367.

Epelboim, J., Steinman, R. M., Kowler, E., Pizlo, Z., Erkelens, C. J., & Collewijn, H. (1997). Gaze-shift dynamics in two kinds of sequential looking tasks. *Vision Research*, *18*, 2597–2607.

Flanagan, J. R., Bowman, M. C., & Johansson, R. S. (2006). Control strategies in object manipulation tasks. *Current Opinion in Neurobiology*, *16*, 650–659.

Fooken, J., Yeo, S.-H., Pai, D.K., & Spering, M. (2014). Accurate smooth pursuit eye movements improve hand movements in a manual interception task. *Program No. 533.12/HH2. 2014 Neuroscience Meeting Planner*, Washington, D.C.: Society for Neuroscience, 2014. Online.

Gribble, P. L., Everling, S., Ford, K., & Mattar, A. (2002). Hand-eye coordination for rapid pointing movements. *Experimental Brain Research*, *145*, 372–382.

Hayhoe, M. M., & Ballard, D. (2005). Eye movements in natural behavior. *Trends in Cognitive Science*, *9*, 188–194.

Hayhoe, M. M., McKinney, T., Chajka, K., & Pelz, J. B. (2012). Predictive eye movements in natural vision. *Experimental Brain Research*, *217*, 125–136.

Hwang, E. J., Hauschild, M., Wilke, M., & Andersen, R. A. (2014). Spatial and temporal eye-hand coordination relies on the parietal reach region. *Journal of Neuroscience*, *34*, 12884–12892.

Johansson, R. S., Westling, G., Bäckström, A., & Flanagan, J. R. (2001). Eye-hand coordination in object manipulation. *Journal of Neuroscience*, *21*, 6917–6932.

Kowler, E. (2011). Eye movements: The past 25 years. *Vision Research*, *51*, 1457–1483.

Land, M. F. (2006). Eye movements and the control of actions in everyday life. *Progress in Retinal and Eye Research*, *25*, 296–324.

Land, M. F., & Furneaux, S. (1997). The knowledge base of the oculomotor system. *Philosophical Transactions of the Royal Society B*, *352*, 1231–1239.

Land, M. F., & McLeod, P. (2000). From eye movements to actions: How batsmen hit the ball. *Nature Neuroscience*, *3*, 1340–1345.

Liaw, A., & Wiener, M. (2002). Classification and regression by random forest. *R News*, *2*, 18–22.

Lisberger, S. G. (2015). Visual guidance of smooth pursuit eye movements. *Annual Review of Vision Science*, *1*, 447–468.

Lisberger, S. G., & Westbrook, L. E. (1985). Properties of visual inputs that initiate horizontal smooth pursuit eye movements in monkeys. *Journal of Neuroscience*, *5*(6), 1662–1673.

Lünenburger, L., Kutz, D. F., & Hoffmann, K. P. (2000). Influence of arm movements on saccades in humans. *European Journal of Neuroscience*, *12*, 4107–4116.

Mann, D., L. W. Spratford & B. Abernethy, (2013). The head tracks and gaze predicts: How the world's best batters hit a ball. *PLoS One*, *8*(3), e58289.

McPeek, R. M., & Keller, E. L. (2004). Deficits in saccade target selection after inactivation of superior colliculus. *Nature Neuroscience*, *7*, 757–763.

Mrotek, L. A., & Soechting, J. F. (2007). Target interception: Hand-eye coordination and strategies. *Journal of Neuroscience*, *27*, 7297–7309.

Neggers, S. F. W., & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology*, *83*, 639–651.

Niehorster, D. C., Siu, W. W., & Li, L. (2015). Manual tracking enhances smooth pursuit eye movements. *Journal of Vision*, *15*(15):11, 1–14, doi:10.1167/15.15.11. [PubMed] [Article]

Nummela, S. U., & Krauzlis, R. J. (2010). Inactivation of primate superior colliculus biases target choice for smooth pursuit, saccades, and button press responses. *Journal of Neurophysiology*, *104*, 1538–1548.

Orban de Xivry, J. J., Coppe, S., Blohm, G., & Lefèvre, P. (2013). Kalman filtering naturally accounts for visually guided and predictive smooth pursuit dynamics. *Journal of Neuroscience*, *33*, 17301–17313.

Orban de Xivry, J. J., & Lefèvre, P. (2007). Saccades and pursuit: Two outcomes of a single sensorimotor process. *Journal of Physiology*, *548*, 11–23.

Orban de Xivry, J. J., Missal, M., & Lefèvre, P. (2008). A dynamic representation of target motion drives predictive smooth pursuit during target blanking. *Journal of Vision*, *8*(15):6, 1–13, doi:10.1167/8.15.6. [PubMed] [Article]

Ripoll, H., Bard, C., & Paillard, J. (1986). Stabilization of head and eyes on target as a factor in successful basketball shooting. *Human Movement Science*, *5*, 47–58.

Sailer, U., Flanagan, J. R., & Johansson, R. S. (2005). Eye-hand coordination during learning of a novel visuomotor task. *Journal of Neuroscience*, *25*, 8833–8842.

Smeets, J. B., Hayhoe, M. M., & Ballard, D. H. (1996). Goal-directed arm movements change eye-head coordination. *Experimental Brain Research*, *109*, 434–440.

Snyder, L. H., Batista, A. P., & Andersen, R. A. (2000). Saccade-related activity in the parietal reach region. *Journal of Neurophysiology*, *83*, 1099–1102.

Snyder, L. H., Calton, J. L., Dickinson, A. R., & Lawrence, B. M. (2002). Eye-hand coordination: Saccades are faster when accompanied by a coordinated arm movement. *Journal of Neurophysiology*, *87*, 2279–2286.

Soechting, J. F., & Flanders, M. (2008). Extrapolation of visual motion for manual interception. *Journal of Neurophysiology*, *99*, 2956–2967.

Soechting, J. F., Juveli, J. Z., & Rao, H. M. (2009). Models for the extrapolation of target motion for manual interception. *Journal of Neurophysiology*, *102*, 1491–1502.

Song, J.-H., Rafal, R. D., & McPeek, R. M. (2011). Deficits in reach target selection during inactivation of the midbrain superior colliculus. *Proceedings of the National Academy of Sciences, USA, 108*, 1433–1440.

Spering, M., & Carrasco, M. (2015). Acting without seeing: Eye movements reveal visual processing without awareness. *Trends in Neuroscience*, *38*, 247–258.

Spering, M., & Montagnini, A. (2011). Do we track what we see? Common versus independent processing for motion perception and smooth pursuit eye movements: A review. *Vision Research*, *51*, 836–852.

Spering, M., Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2011). Keep your eyes on the ball: Smooth pursuit eye movements enhance prediction of visual motion. *Journal of Neurophysiology*, *105*, 1756–1767.

Stocker, A. A., & Simoncelli, E. P. (2006). Noise characteristics and prior expectations in human visual speed perception. *Nature Neuroscience*, *9*, 578–585.

van Donkelaar, P., Lee, R. G., & Gellman, R. S. (1994). The contribution of retinal and extraretinal signals to manual tracking movements. *Experimental Brain Research*, *99*, 155–163.

Watts, R. G., & Ferrer, R. (1987). The lateral force on a spinning sphere: Aerodynamics of a curveball. *American Journal of Physiology*, *55*, 40–44.

Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience*, *5*, 598–604.

Yeo, S.-H., Lesmana, M., Neog, D. R., & Pai, D. K. (2012). Eyecatch: Simulating visuomotor coordination for object interception. *ACM Transactions on Graphics*, *31*(4), 42.

Yttri, E. A., Liu, Y., & Snyder, L. H. (2013). Lesions of cortical area LIP affect reach onset only when the reach is accompanied by a saccade, revealing an active eye-hand coordination circuit. *Proceedings of the National Academy of Sciences, USA, 110*, 2371–2376.

Zhao, H., & Warren, W. H. (2015). On-line and model-based approaches to the visual control of action. *Vision Research*, *110*, 190–202.