

Humans can track but fail to predict accelerating objects

<https://doi.org/10.1523/ENEURO.0185-22.2022>

Cite as: eNeuro 2022; 10.1523/ENEURO.0185-22.2022

Received: 2 May 2022

Revised: 10 July 2022

Accepted: 27 July 2022

This Early Release article has been peer-reviewed and accepted, but has not been through the composition and copyediting processes. The final version may differ slightly in style or formatting and will contain links to any extended data.

Alerts: Sign up at www.eneuro.org/alerts to receive customized email alerts when the fully formatted version of this article is published.

Copyright © 2022 Kreyenmeier et al.

This is an open-access article distributed under the terms of the Creative Commons Attribution 4.0 International license, which permits unrestricted use, distribution and reproduction in any medium provided that the original work is properly attributed.

TRACKING AND PREDICTING ACCELERATING TARGETS

Title: Humans can track but fail to predict accelerating objects

Abbreviated Head: Tracking and predicting accelerating objects

Authors: Philipp Kreyenmeier^{1,2}, Luca Kämmer², Jolande Fooker^{2,4}, Miriam Spering^{1-3,5}

¹Graduate Program in Neuroscience, University of British Columbia, Vancouver, Canada

²Department of Ophthalmology and Visual Sciences, University of British Columbia, Vancouver, Canada

³Djavad Mowafaghian Centre for Brain Health, University of British Columbia, Vancouver, Canada

⁴Centre for Neuroscience Studies, Queen's University, Kingston, Canada

⁵Institute for Computing, Information, and Cognitive Systems, University of British Columbia, Vancouver, Canada

Author Contributions: PK, JF, & MS designed research, PK & LK performed research, PK analyzed data, PK wrote the paper, JF & MS provided critical revisions. All authors approved the final version of the manuscript.

Correspondence should be addressed to: philipp.kreyenmeier@alumni.ubc.ca
Koerner Pavilion, UBC Hospital
S257-211 Wesbrook Mall
Vancouver, BC, V6T 1Z3, Canada

Number of figures: 8

Number of words for Abstract: 246

Number of words for Significance Statement: 119

Number of words for Introduction: 722

Number of words for Discussion: 1590

Acknowledgements: The authors thank members of the Spering lab for comments on an earlier version of the manuscript.

Author Note: The study design and parts of the analysis were preregistered (<https://osf.io/adq9v>), all data and analyses are available on the Open Science Framework (<https://osf.io/4fv5m>). The model comparison was not included in the preregistration. Preliminary data were presented at the 2021 virtual meeting of the Vision Sciences Society (Kreyenmeier et al., 2021).

Conflict of interest: The authors report no conflict of interest.

Funding sources: This work was supported by a UBC International Doctoral Fellowship to PK, a Deutsche Forschungsgemeinschaft (DFG) Research Fellowships to JF (grant FO 1347/1-1), & an NSERC Discovery Grant and Accelerator Supplement to

Abstract

1 Objects in our visual environment often move unpredictably and can suddenly speed up
 2 or slow down. The ability to account for acceleration when interacting with moving
 3 objects can be critical for survival. Here, we investigate how human observers track an
 4 accelerating target with their eyes and predict its time of reappearance after a temporal
 5 occlusion by making an interceptive hand movement. Before occlusion, observers
 6 smoothly tracked the accelerating target with their eyes. At the time of occlusion,
 7 observers made a predictive saccade to the location where they subsequently
 8 intercepted the target with a quick pointing movement. We tested how observers
 9 integrated target motion information by comparing three alternative models that
 10 describe time-to-contact (TTC) based on the (1) final target velocity sample before
 11 occlusion, (2) average target velocity before occlusion, or (3) final target velocity and the
 12 rate of target acceleration. We show that observers were able to accurately track the
 13 accelerating target with visually-guided smooth pursuit eye movements. However, the
 14 timing of the predictive saccade and manual interception revealed inability to act on
 15 target acceleration when predicting TTC. Instead, interception timing was best
 16 described by the final velocity model that relies on extrapolating the last available target
 17 velocity sample before occlusion. Moreover, predictive saccades and manual
 18 interception showed similar insensitivity to target acceleration and were correlated on a
 19 trial-by-trial basis. These findings provide compelling evidence for the failure of
 20 integrating target acceleration into predictive models of target motion that drive both
 21 interceptive eye and hand movements.

22

TRACKING AND PREDICTING ACCELERATING TARGETS

- 23 **Keywords:** smooth pursuit, saccade, manual interception, eye-hand coordination,
24 prediction, acceleration

TRACKING AND PREDICTING ACCELERATING TARGETS

25

Significance Statement [119/120]

26

Acceleration is an essential feature of most moving objects in our environment, but the

27

human visual system is surprisingly insensitive to acceleration. We investigated

28

observers' ability to track an accelerating and disappearing target with their eyes and to

29

predict its time of reappearance by making an interceptive hand movement. Despite the

30

ability to accurately track the accelerating target with their eyes, observers failed to

31

consider acceleration when predicting target reappearance, resulting in systematic

32

interception errors. The magnitude of the error can be explained by a model that

33

describes interception timing based on extrapolation of the last available target velocity

34

signal. Observers fail to account for acceleration during target interception and instead

35

update target velocity while the target is visible.

36

Introduction

Seeing and perceiving object motion is a vital capability of the primate visual system. Animals hunting for prey or pedestrians crossing a street must be able to act upon a target's speed, direction, and sudden target accelerations or decelerations. Although acceleration is an important feature that describes the behavior of many moving objects, it is well established that the primate perceptual system is largely insensitive to it (Gottsdanker et al., 1961; Calderone & Kaiser, 1989; Werkhoven et al., 1992; Brouwer et al., 2002; Watamaniuk & Heinen, 2003; Benguigui et al., 2003; Mueller et al., 2017). How we incorporate visual acceleration signals into motor commands to interact with moving objects is still not fully understood. Here, we evaluate human observers' ability to track accelerating targets with their eyes and to predict accelerating target trajectories for manual target interception.

Tracking visual object motion with the eyes and predicting an object's motion path are two fundamental abilities that rely on decoding visual motion (Fiehler et al., 2019) and can inform interceptive hand movements (Mrotek & Soechting, 2007; Mrotek, 2013; Diaz et al., 2013; Cesqui et al., 2015; Fookien et al., 2016; 2021; de la Malla et al., 2017; Goettker et al., 2019; De Brouwer et al., 2021). Whereas tracking relies heavily on visual signals (e.g., Lisberger, 2015), predicting a trajectory also requires memory of previously seen motion (Orban de Xivry et al., 2013; Kowler et al., 2019; Rust & Palmer, 2021).

When tracking moving objects, humans rely on smooth pursuit eye movements—slow rotations of the eyes—to keep the object close to the fovea. Neurons in motion-sensitive extrastriate cortex (area MT) provide the sensory input that drives pursuit.

TRACKING AND PREDICTING ACCELERATING TARGETS

60 Neurophysiological studies in macaque monkeys found that single neurons in MT are
61 not tuned to a target's acceleration (Lisberger & Movshon, 1999); instead, acceleration
62 can be decoded indirectly from populations of speed-sensitive MT neurons (Lisberger &
63 Movshon, 1999; Price et al., 2005). These acceleration signals can drive pursuit eye
64 movements in monkeys (Krauzlis & Lisberger, 1994; Churchland & Lisberger, 2001).

65 Evidence for the use of acceleration signals for human pursuit comes from
66 studies investigating eye movements in response to small perturbations in target
67 velocity (Tavassoli & Ringach, 2010; Brostek et al., 2017) and those investigating eye
68 movements during temporary target occlusion (e.g., Bennett et al., 2007). When
69 tracking an accelerating target throughout a brief occlusion period, eye movements
70 (pursuit and saccades) scale with object acceleration in anticipation of target
71 reappearance (Bennett & Barnes, 2006; Bennett et al., 2007; Bennett & Benguigui,
72 2013). These findings indicate that the pursuit system can extract target acceleration
73 and use this signal to predictively drive continuous tracking eye movements.
74 Importantly, the ability to extract target acceleration signals improves with presentation
75 times (Bennett et al., 2007), indicating that the pursuit system requires a relatively long
76 initial exposure to target acceleration to form an acceleration-based prediction of target
77 motion. However, whether this ability translates to tasks, in which observers predict the
78 reappearance of accelerating objects, is unclear.

79 Tasks in which observers are asked to intercept accelerating objects with a quick
80 pointing movement, a projectile, or by pressing a button reveal systematic errors,
81 indicating inability to consider target acceleration for action-related motion prediction
82 (Bennett & Benguigui, 2010; Benguigui & Bennett, 2013; Benguigui et al., 2003;

TRACKING AND PREDICTING ACCELERATING TARGETS

Brenner & Smeets, 2015; Brenner et al., 2016; Port et al., 1997; Dubrowski & Carnahan, 2002). These errors were caused by observers' failure to adjust the timing or position of their hand movement to the target's acceleration, resulting in interceptions that are too early and ahead of the target when it decelerates, and interceptions that are too late and behind the target when it accelerates.

Whereas eye movements to accelerating targets appear to be responsive to acceleration, hand movements are prone to systematic errors that indicate inability to account for acceleration. Here, we directly compare eye movements and manual interception of accelerating targets in a track-intercept task. We varied the initial target presentation duration and the rates of target acceleration to test observers' sensitivity to track the accelerating target with their eyes and to predict its TTC for manual interception. We hypothesized that observers make systematic interception errors, indicating inability to account for target acceleration. Moreover, we predicted an improved ability to track target acceleration with longer presentation durations, which would also result in better adjustments of interception timing.

Materials and Methods

We report the results of one main experiment (Experiment 1) and one control experiment (Experiment 2). Apparatus, procedures, and analyses were identical between both experiments (unless otherwise stated). The critical difference between experiments was that all targets reached the occluder with the exact same final velocity in Experiment 1 (**Fig. 1B**), whereas in Experiment 2 all targets moved with the exact same average velocity but different final velocities (**Fig. 1C**). The study design and parts

TRACKING AND PREDICTING ACCELERATING TARGETS

106 of the analyses of Experiment 1 were preregistered (<https://osf.io/adq9v>)

107

108 **Observers**

109 **Experiment 1.** We tested 16 human adults (seven females; mean age 26.8 ± 5.1
110 years, range 19-37 years; including two authors) in this study. All participants had
111 normal or corrected-to-normal visual acuity and reported no history of neurological,
112 psychiatric, or eye disease. The study protocol was carried out in accordance with the
113 Declaration of Helsinki and was approved by the local Behavioural Research Ethics
114 Board. Participants gave written informed consent before participating and were
115 compensated at the rate of \$10/h.

116 **Experiment 2.** Ten healthy adults were recruited for participation in the control
117 experiments (6 females; mean age 28.7 ± 6.7 years, range 21-45 years; four of whom
118 also participated in Experiment 1; two authors). Experiment 2 was designed to replicate
119 the model comparison from Experiment 1. Specifically, based on Experiment 1, we
120 hypothesized that the final velocity model would produce smaller errors, compared to
121 the average velocity model. We used the effect size from Experiment 1 ($d = .86$) to
122 determine our sample size of $n = 10$ using an a priori power analysis in G*Power (Faul
123 et al., 2009; one-sided, paired t-test; power = .80; alpha = .05). Observers gave written
124 informed consent and were compensated at the rate of \$10/h.

125

126 **Apparatus**

127 Participants performed the task in a dimly lit laboratory, viewing the stimuli
128 binocularly at a distance of 44 cm. A PROPixx video-projector with a resolution of 1,280

TRACKING AND PREDICTING ACCELERATING TARGETS

129 × 1024 pixels and a refresh rate of 120 Hz (VPixx Technologies, Saint-Bruno, QC,
 130 Canada) was used to back-project the stimuli onto a 41.8 × 33.4 cm translucent screen.
 131 The position of participants' right eye was recorded using a video-based eye tracker
 132 (Eyelink 1000 Tower Mount, SR Research, Ottawa, ON, Canada) with a sampling rate
 133 of 1 kHz. A combined chin and forehead rest minimized head movements during the
 134 experiment. A small magnetic sensor was attached to the tip of participants' right index
 135 finger to record their 3D hand movements with a 3D Guidance trakSTAR (Ascension
 136 Technology, Shelburne, VT) at a sampling rate of 120 Hz. The experiment was
 137 programmed in Matlab (MathWorks, Natick, MA, USA), using the Psychophysics
 138 toolbox (version 3.0.16; Brainard, 1997; Pelli, 1997; Kleiner et al., 2007) and EyeLink
 139 toolbox (Cornelissen et al., 2002). Stimulus display and data collection were controlled
 140 by a PC (graphics card: NVIDIA GeForce GTX 1060).

141

142 **Stimuli and Procedure**

143 **Experiment 1.** Participants viewed and intercepted a small black disc (0.35° in
 144 diameter; 6.23 cd/m^2) that moved across a light grey background (229.8 cd/m^2) and
 145 then disappeared behind an occluder, a grey (181.3 cd/m^2) bar, that extended 13.4°
 146 from the horizontal midline into the right half of the screen. Each trial started with the
 147 disc shown on the left side of the screen. Participants had to fixate the target (400-800
 148 ms) and place their index finger on a designated start position on the table located 36
 149 cm below and 23 cm in front of the screen centre (**Fig. 2C**). Upon successful fixation,
 150 the target started moving to the right, either with a fixed velocity ($0^\circ/\text{s}^2$) or constantly
 151 accelerating at different rates ($-8, -4, 4, 8^\circ/\text{s}^2$). The target was shown for 200, 500, or

TRACKING AND PREDICTING ACCELERATING TARGETS

152 800 ms before occlusion. Participants were instructed to follow the disc closely with their
153 eyes during the initial presentation and to manually intercept the target at the time they
154 expected it to reappear behind the occluder. Target presentation ended either with the
155 time of interception, or 100 ms after target reappearance. Initial target position and
156 velocity were matched for each presentation time and acceleration so that all targets
157 reached the same position and velocity at the time of occlusion. The time of target
158 reappearance (equivalent to time-to-contact, TTC) depended on the target's
159 acceleration rate ($-8^\circ/\text{s}^2$: 797 ms, $-4^\circ/\text{s}^2$: 722 ms, $0^\circ/\text{s}^2$: 670 ms, $+4^\circ/\text{s}^2$: 630 ms, $+8^\circ/\text{s}^2$:
160 598 ms). Therefore, successful interception required adjusting the timing of manual
161 interception to target acceleration. Observers were instructed to intercept as closely to
162 the border of the occluder as possible at the time they expected the target to reappear.
163 Feedback about the interception performance was provided at the time of interception
164 by showing a red and a black dot, indicating the interception position and the actual
165 target location at the time of interception, respectively. The combination of acceleration
166 and presentation time resulted in 15 experimental conditions, presented in random
167 order within each block of trials. Each participant completed 40 trials per condition,
168 resulting in 600 trials total, presented in eight blocks of 75 trials each. The experiment
169 took approximately 90 minutes.

170 Although TTC typically refers to the time at which a moving object contacts a
171 secondary, stationary object, we use the term TTC to refer to the time of target
172 reappearance behind the occluder. Furthermore, we use the term TTC_{hand} to refer to
173 observers' estimate of target reappearance as indicated by the time of manual
174 interception.

175 **Experiment 2.** Stimuli and procedure were the same as in Experiment 1 with the
 176 following exceptions: (1) Only the 800 ms condition was tested in Experiment 2. (2) All
 177 targets moved with the same average velocity but reached the occluder with different
 178 final velocities (**Fig. 1C**), yielding occlusion times (TTC) of 1070, 797, 670, 588, and 529
 179 ms for the -8, -4, 0, +4, and +8°/s² acceleration conditions, respectively.

181 **Eye and Hand Movement Recordings and Analyses**

182 The data were pre-processed offline using custom-made routines in MATLAB.
 183 Eye velocity and acceleration were calculated as the first and second derivatives of the
 184 eye position signals over time. Position and velocity profiles were filtered using a low-
 185 pass, second-order Butterworth filter with cut-off frequencies of 15 Hz (position) and 30
 186 Hz (velocity). Saccades were detected when five consecutive frames exceeded a fixed
 187 velocity criterion of 30°/s; saccade on- and offsets were then determined as the nearest
 188 reversal in the sign of acceleration. For the analyses of the de-saccaded smooth pursuit
 189 eye movements, the identified saccades ± 25 ms were removed from pursuit velocity
 190 traces and replaced by linear extrapolation between the last velocity sample before
 191 saccade onset and the first velocity sample after saccade offset (de Brouwer et al.,
 192 2002). Pursuit onset in de-saccaded traces was detected within a 300-ms interval
 193 around stimulus motion onset (starting 150 ms before onset) in each individual trace.
 194 We first fitted each 2D position trace with a piecewise linear function, consisting of two
 195 linear segments and one breakpoint. The least-squares fitting error was then minimized
 196 iteratively (using the function `lsqnonlin` in MATLAB) to identify the best location of the
 197 breakpoint, defined as the time of pursuit onset.

TRACKING AND PREDICTING ACCELERATING TARGETS

198 The magnetic hand tracker recorded the 2D screen-centred interception position
199 as well as the participant's hand movement in 3D space. Hand position data were up-
200 sampled to 1 kHz by linear interpolation for precise temporal comparison with eye
201 movement data. Position data were filtered using a second-order Butterworth filter with
202 a cut-off frequency of 15 Hz. Hand latency was computed offline as the first sample that
203 exceeded 5 cm/s following stimulus onset. Hand movement offset was detected online
204 when the finger intercepted the screen (within 0.8 mm from the screen in the z-
205 dimension). If no offset was detected online, hand movement offset was detected offline
206 as the maximum hand position in the z-dimension.

207 All trials were manually inspected. We excluded trials with blinks during the task
208 and trials in which the eye tracker lost the signal (Experiment 1: 2.9% of trials across
209 participants; Experiment 2: 3.9%). Trials were also excluded when observers undershot
210 the right concluder's border by more than 3.5° or when no interception was detected
211 within 600 ms of target reappearance (Experiment 1: 1.5% of all trials, Experiment 2:
212 2.3%).

213

214 **Data Analyses**

215 The primary aim of the current study was to assess whether observers can track
216 and intercept accelerating targets. We assessed observers' ability to accurately track
217 accelerating targets with smooth pursuit eye movements during the initial target
218 presentation (visually-guided smooth pursuit). We calculated the average de-saccaded
219 pursuit velocity from stimulus or pursuit onset (whichever occurred earlier) and the
220 beginning of target occlusion. Pursuit gain was typically less than 1 and observers

TRACKING AND PREDICTING ACCELERATING TARGETS

221 showed anticipatory slowing in the pursuit before target occlusion. To account for these
222 general biases, we normalized pursuit velocity by subtracting the control condition
223 ($0^\circ/\text{s}^2$) from the experimental conditions (**Fig. 3B**). Following target occlusion, observers
224 typically stopped pursuing the target with smooth pursuit eye movements and used
225 predictive saccades to bring the eyes to the interception location. The primary predictive
226 saccade was determined as the saccade that brought the eye within 3.5° from the
227 occluder's right border (to allow for systematic undershooting of saccades). The landing
228 time of the eye was determined as the offset time of the predictive saccade. If additional
229 saccades were made to correct the undershooting (2.8% of trials), we used the offset
230 time of the last corrective saccade that was initiated from within the occluder. To assess
231 whether target acceleration was taken into account in manual interception, we
232 calculated the constant interception error as the difference between the time of
233 interception and the veridical time of target reappearance. To assess whether target
234 acceleration caused systematic biases in the timing of the interceptive hand
235 movements, we additionally analyzed the interception time (TTC_{hand}). Both saccade
236 landing time and TTC_{hand} were calculated relative to target occlusion onset.

237 **Model comparison.** To further analyze which target features were used to
238 estimate TTC for manual interception, we compared the biases in TTC_{hand} to three
239 different models on how observers might have predicted TTC. First, the final velocity
240 model postulates that observers continuously update target velocity and predict TTC
241 based on the last available velocity sample (**Fig. 7A**). Second, the average velocity
242 model assumes that observers base their TTC estimate on the average target velocity

TRACKING AND PREDICTING ACCELERATING TARGETS

243 (Fig. 7B). Finally, the acceleration model suggests that observers consider final target
 244 velocity and target acceleration for interception (Fig. 7C).

245 Because observers showed a general trend to hit the targets too late (Fig. 5A),
 246 we first normalized TTC_{hand} by subtracting the control condition ($0^\circ/s^2$) from the
 247 experimental conditions. We then calculated targets' TTC based on three models: For
 248 the final velocity model, TTC was calculated as $TTC(x) = d / v_{final}(x)$, for the average
 249 velocity model, TTC was calculated as $TTC(x) = d / v_{avg}(x)$, for the, and for the
 250 acceleration model as $TTC(x) = (-v_{final} + \sqrt{v_{final}^2 + 2ad}) / a$. Here, x indicates the 5
 251 different target trajectories, d the distance of the occluder, v_{avg} the average velocity of
 252 the target during the initial presentation duration, v_{final} the final target velocity at the time
 253 of occlusion onset, and a the rate of target acceleration. We then evaluated the fit of the
 254 different model predictions of TTC to our observed TTC_{hand} data by calculating the root-
 255 mean-square error (RMSE) for each observer.

256 To further analyse which target velocity sample best described each observer's
 257 TTC_{hand} bias, we modified the final velocity model to include target velocity as a free
 258 parameter, set to optimally predict observers' TTC_{hand} . To this end, we first calculated
 259 each observer's median TTC for each acceleration condition. Next, we predicted each
 260 observer's median TTC based on each timepoint along each target's velocity trajectory
 261 and determined the timepoint that produced the smallest RMSE. We coined this
 262 timepoint the hand prediction time. Note, for simplicity, we assumed that observers
 263 based their TTC estimate on a single velocity sample. Alternatively, observers might
 264 have averaged target velocity over a number of samples.

265

266 **Statistical Analyses**

267 All statistical analyses were performed in R (version 3.3.2; R Core Team) with an
 268 alpha level of .05. For all outcome variables, we calculated the condition median across
 269 trials for each individual observer. The median was used because it is more robust
 270 against outliers and skewed distributions. To assess differences in our experimental
 271 conditions, we compared the means across subjects using repeated-measures
 272 analyses of variance (rmANOVA) and post-hoc t-tests. Normal distribution of dependent
 273 variables for all ANOVAs was confirmed using the Shapiro-Wilk test (all $p > .14$).
 274 Violation of sphericity was assessed using the Mauchly's test and p -values were
 275 Greenhouse-Geisser corrected in case of significance. To correct the familywise error
 276 rate in multiway ANOVA, we applied a sequential Bonferroni procedure to all multiway
 277 ANOVA (Cramer et al., 2016). In case of significant interaction effects, we ran follow-up,
 278 one-way ANOVA with Bonferroni corrections. Bonferroni corrections were also applied
 279 to any pairwise post-hoc comparisons. To investigate whether saccade landing time
 280 predicted TTC_{hand} on a trial-by-trial basis, we ran a linear mixed model with random
 281 intercepts and slopes between saccade landing time (SLT) and TTC_{hand} per observer
 282 and *SLT*, *presentation duration*, and *acceleration* as fixed effects (using the functions
 283 *mixed* and *nice* of the R package *afex*; Singmann et al., 2021):

284
$$TTC_{hand} \sim SLT * presentation\ duration * acceleration + (1 + SLT \mid observer).$$

285

286 **Results**

287 Observers performed a track-intercept task in which they viewed a moving disc that
 288 disappeared behind an occluder after a presentation time of 200, 500, or 800 ms and

TRACKING AND PREDICTING ACCELERATING TARGETS

289 then reappeared for 100 ms (**Fig. 1A**). We instructed observers to intercept the target at
290 the estimated time of reappearance (equivalent to TTC) with a quick pointing movement
291 of their right index finger. In each trial, the target moved along a horizontal linear path
292 either at a constant velocity (no acceleration, $0^\circ/\text{s}^2$: control condition) or at a constant
293 rate of velocity change (deceleration: -8 or $-4^\circ/\text{s}^2$; acceleration: $+4$ or $+8^\circ/\text{s}^2$).

294 We analysed the eye and hand movement data in three parts: First, we
295 investigated visually-guided smooth pursuit and predictive eye movements in response
296 to accelerating targets. We asked whether target acceleration was reflected in the
297 visually-guided eye movement response during visible target presentation, and in the
298 timing of the predictive eye movement response during occlusion. Second, we
299 assessed the effect of target acceleration on the timing error of the interceptive hand
300 movement. These two analysis components are congruent with the preregistered
301 analysis plan for this study. Third, we compared the performance of three models
302 predicting TTC based on different target signals to observers' hand movement data.
303 This exploratory model comparison was confirmed in a control experiment, in which all
304 targets moved with the same average velocity, but with different final velocities
305 (Experiment 2). We restricted the exploratory model comparison to the 800 ms
306 conditions, because it yielded the most reliable biases in both eye and hand movements
307 and allowed for the longest integration of the changing target velocities over time.

308

309 **Target Presentation Duration Affects Ability to Track but not to Predict**

310 **Accelerating Targets**

TRACKING AND PREDICTING ACCELERATING TARGETS

311 Observers tracked the target with a combination of smooth pursuit and saccadic
312 eye movements during the initial period, in which the target was visible. Two example
313 trials, in which the target either accelerated (**Fig. 2A**) or decelerated (**Fig. 2B**) show
314 typical eye movement position and velocity during the task: After pursuit initiation, an
315 initial catch-up saccade aligned the eyes with the target and was typically followed by a
316 period of closed-loop smooth pursuit, during which eye velocity matched the
317 continuously changing target velocity. In some trials, smooth pursuit was supported by
318 additional catch-up saccades (**Fig. 2B**). Around the time of target occlusion, observers
319 stopped smoothly tracking the target and pursuit velocity decreased to 0°/s. Observers
320 then made a distinctly identifiable predictive saccade of relatively large amplitude to the
321 right border of the occluder, where they then intercepted the target with a pointing
322 movement of their right index finger (see 3D hand trajectory from a single trial in **Fig.**
323 **2C**). To investigate how finely-tuned these different eye movement responses are to
324 target acceleration, we analysed the effect of presentation duration on the ability to
325 smoothly track the visible, accelerating target and to predict its time of reappearance
326 (TTC) with a predictive saccade.

327 Observers' ability to accurately and smoothly track the accelerating target
328 increased with increasing presentation duration, here taken as a direct measure of the
329 availability of target motion signals (**Fig. 3A-B**). Whereas no difference in average
330 pursuit velocity was observed in the shortest presentation duration (200 ms), average
331 pursuit velocity sensitively reflected different target velocities for both longer
332 presentation durations (500, 800 ms; **Fig. 3A**). This observation was confirmed by a 5
333 (*acceleration*) x 3 (*presentation duration*) rmANOVA on average pursuit velocity,

TRACKING AND PREDICTING ACCELERATING TARGETS

334 yielding a significant *acceleration* \times *presentation duration* interaction ($F(8,120) = 18.52$;
 335 $p < .001$; $\eta_p^2 = .55$). Both main effects of *presentation duration* ($F(2,30) = 184.76$; $p <$
 336 $.001$; $\eta_p^2 = .92$) and target *acceleration* ($F(4,60) = 40.75$; $p < .001$; $\eta_p^2 = .73$) reached
 337 significance. We performed follow-up, one-way rmANOVA with factor *acceleration* for
 338 each presentation duration and found a significant main effect of *acceleration* in both
 339 the 500 and 800 ms conditions ($F(4,60) = 8.31$; $p < .001$; $\eta_p^2 = .36$ and $F(4,60) = 50.08$;
 340 $p < .001$; $\eta_p^2 = .77$, respectively), but not in the 200 ms condition ($F(4,60) = 1.05$; $p = 1$;
 341 $\eta_p^2 = .07$).

342 We next asked, whether observers continuously tracked the changing target
 343 velocity over time. To this end we normalized pursuit velocity traces in the acceleration
 344 conditions relative to the control condition ($0^\circ/\text{s}^2$) for each observer. This additional
 345 analysis accounts for imperfect pursuit velocity gain and individual differences.
 346 The normalized pursuit velocity over time revealed how closely observers' pursuit
 347 velocity matched the continuously changing target velocity for the two longer
 348 presentation durations (**Fig. 3B**): After the first catch-up saccade, the eye continuously
 349 accelerated in response to accelerating targets and decelerated in response to
 350 decelerating targets. These findings show that visually-guided pursuit closely matches
 351 the continuously changing target velocity, and that these effects are amplified with
 352 longer presentation duration where differences in target velocities were more
 353 pronounced. In contrast, pursuit velocity was similar across target accelerations in the
 354 200 ms condition. This similarity might have been due to the small differences in the
 355 velocity of a target shown only very briefly.

TRACKING AND PREDICTING ACCELERATING TARGETS

356 Next, we asked whether the ability to accurately track the accelerating targets
357 with increased presentation duration also affected the ability to predict its reappearance
358 (TTC) with a predictive saccade. Predictive saccades are typically made several
359 hundred milliseconds before target reappearance or interception. Because their timing
360 is tuned to expectations of target motion (Diaz et al., 2013) and reflect decision
361 outcomes in manual interception (Fookien & Spering, 2020), they can provide a
362 sensitive indicator of target motion prediction. Although observers were not instructed to
363 make such a predictive saccade, it was clearly identifiable in virtually every trial (>99%
364 of all trials). These saccades were initiated on average 137 ms (± 71 ms; mean ± 1 std
365 across observers; **Fig. 3A**) after occlusion onset and landed clustered around the right
366 border of the occluder (**Fig. 3C**) approximately 262 ms (± 70 ms) after occlusion onset.
367 In most trials, observers made one large predictive saccade with an average amplitude
368 of 12.1° ($\pm 0.8^\circ$) across observers and trials, and this average amplitude was similar
369 across acceleration conditions. On average, saccades were initiated 1.2° ($\pm 0.8^\circ$) from
370 within the occluder and landed close to the occluder's right border at 13.2° ($\pm 0.3^\circ$; see
371 upper panels in **Fig. 2 A-B** and **Fig. 3C**). In trials where a second predictive saccade
372 was made to correct for undershooting, initiation and landing time of the first predictive
373 saccade were substantially later (319 ms \pm 94 ms and 414 ms \pm 93 ms, respectively)
374 than in trials with only one predictive saccade.

375 Interestingly, the landing time of predictive saccades did not scale with target
376 acceleration, i.e., the eye did not land earlier at the border of the occluder for
377 accelerating targets and did not land later for decelerating targets. Instead, the saccade
378 landing time showed a consistent bias in the opposite direction, i.e., later for

TRACKING AND PREDICTING ACCELERATING TARGETS

379 accelerating targets and earlier for decelerating targets. This observation was confirmed
 380 by a main effect of target acceleration ($F(4,60) = 8.17$; $p = .008$; $\eta_p^2 = .35$; **Fig. 3D**) in a
 381 5 (*acceleration*) \times 3 (*presentation duration*) rmANOVA. Note that this small bias was
 382 also present in the predictive saccade initiation time (**Fig. 3A**) and was neither caused
 383 by differences in saccade duration nor in amplitude across acceleration conditions. We
 384 also found a main effect of presentation duration on predictive saccade landing time of
 385 the predictive saccades ($F(2,30) = 12.54$; $p = .003$; $\eta_p^2 = .46$). Saccades landed later in
 386 the 200 ms condition, compared to the other presentation durations (**Fig. 3D**). Despite
 387 the short presentation duration of 200 ms, observers typically made one early catch-up
 388 saccade followed by a predictive saccade (see upper panel in **Fig. 3A**). This often
 389 delayed the onset of the predictive saccade and observers tracked the target until
 390 shortly after target occlusion onset. In addition, in a subset of trials (22.7%) in the 200
 391 ms condition, observers only made one saccade. These saccades had slightly larger
 392 amplitudes, which might have contributed to the later saccade landing times in the 200
 393 ms condition. There was no significant interaction between target *acceleration* and
 394 *presentation duration* ($F(8,120) = 1.31$; $p = .284$; $\eta_p^2 = .08$). To further analyze which
 395 acceleration conditions were significantly different from one another, we performed
 396 pairwise comparisons after averaging saccade landing times across presentation
 397 durations. Post hoc t-tests revealed significant differences between the $-8^\circ/\text{s}^2$ and the
 398 $+4^\circ/\text{s}^2$ as well as the $+8^\circ/\text{s}^2$ conditions ($t(15) = -4.04$; $p = .01$ and $t(15) = -3.35$; $p = .044$,
 399 respectively), between the $-4^\circ/\text{s}^2$ and $+4^\circ/\text{s}^2$ ($t(15) = -3.90$; $p = .001$), and between the
 400 $0^\circ/\text{s}^2$ and $+4^\circ/\text{s}^2$ ($t(15) = -3.29$; $p = .050$) acceleration conditions. All other comparisons
 401 did not reach significance (all $p > .10$).

TRACKING AND PREDICTING ACCELERATING TARGETS

402 Taken together, these findings show that predictive saccades appear to follow a
403 bias in the opposite direction to what we would expect if target acceleration was used to
404 estimate TTC. Moreover, the landing time of predictive saccades was relatively less
405 affected by the presentation duration of the target than what was observed for visually-
406 guided pursuit. Next, we asked whether observers considered target acceleration in
407 order to time their interceptive hand movement.

408

409 **Target Acceleration Causes Systematic Manual Interception Errors**

410 To intercept the target on the screen, observers moved their hand from the
411 designated start position on the table to the screen (**Fig. 2C**). On average, hand
412 movement paths did not differ between the different target acceleration conditions (**Fig.**
413 **4A**). Due to the long occlusion times, hand movements were largely executed during
414 the occlusion and were thus not systematically corrected mid-flight. As instructed,
415 observers intercepted the target close to the occluder's right border (mean distance 1.7°
416 $\pm 1.1^\circ$; **Fig. 4B**). Distributions of horizontal interception positions largely overlapped
417 across target acceleration conditions (**Fig. 4C**). Yet, there was a small tendency to hit
418 further to the right for accelerating targets (main effect of *acceleration* on horizontal
419 interception position: $F(4,60) = 9.21$; $p = .006$; $\eta_p^2 = .38$). This effect was primarily driven
420 by the $+8^\circ/\text{s}^2$ condition because targets often reappeared before interception in this
421 condition (see green data points in **Fig. 5B**). In these trials, observers tended to adjust
422 the interception position, resulting in a more skewed distribution for the $+8^\circ/\text{s}^2$ condition
423 (bottom panel in **Fig. 4C**).

TRACKING AND PREDICTING ACCELERATING TARGETS

424 In parallel to investigating effects of acceleration on the predictive saccade, we
 425 next analyzed the effect of target acceleration on the timing of the interceptive hand
 426 movement (TTC_{hand}). If observers accounted for target acceleration when timing their
 427 hand movement, we would expect them to intercept earlier for accelerating targets and
 428 later for decelerating targets, relative to the zero-acceleration (control) condition. In
 429 contrast to this hypothesis, we found that observers intercepted later in response to
 430 target acceleration and earlier for deceleration (main effect of *acceleration*: $F(4,60) =$
 431 10.80 ; $p = .002$; $\eta_p^2 = .42$; **Fig. 5A**). This effect was more pronounced in the 500 and
 432 800 ms presentation duration conditions, confirmed by a significant *acceleration* \times
 433 *presentation duration* interaction ($F(8,120) = 3.15$; $p = .037$; $\eta_p^2 = .17$). Accordingly,
 434 main effects of acceleration were found for both the 500 ms (follow-up, one-way
 435 rmANOVA: $F(4,60) = 10.61$; $p < .001$; $\eta_p^2 = .41$) and 800 ms conditions ($F(4,60) = 5.94$;
 436 $p = .048$; $\eta_p^2 = .28$), but not for the 200 ms condition ($F(4,60) = 2.62$; $p = .13$; $\eta_p^2 = .15$).

437 Observers also tended to hit the targets later in the 200 ms condition compared
 438 to the 500 and 800 ms conditions, as indicated by a main effect of *presentation duration*
 439 ($F(2,30) = 16.21$; $p < .001$; $\eta_p^2 = .52$).

440 The failure to take acceleration into account to time the interceptive hand
 441 movement resulted in systematic temporal constant interception errors: Relative to
 442 target reappearance, observers intercepted too late (i.e., the target had already
 443 reappeared) for accelerating targets and too early for decelerating targets (i.e., the
 444 target had not yet reappeared). The main effect of target *acceleration* on the constant
 445 interception error was significant ($F(4,60) = 492.61$; $p < .001$; $\eta_p^2 = .97$; **Fig. 5B**). We
 446 also observed a main effect of *presentation duration* ($F(2,30) = 16.47$; $p < .001$; $\eta_p^2 =$

TRACKING AND PREDICTING ACCELERATING TARGETS

.52), which was caused by a general tendency to intercept targets later in the 200 ms condition (see also **Fig. 5A**). Although, there was a significant *acceleration* × *presentation duration* interaction term ($F(8,120) = 3.28$; $p = .032$; $\eta_p^2 = .18$), follow-up, one-way rmANOVA showed main effects of target acceleration on the constant interception error for all three presentation durations (all $p < .001$).

Overall, observers were not able to accurately adjust the timing of their interceptive hand movement (TTC_{hand}) to target acceleration, causing systematic temporal constant interception timing errors. Notably, the observed opposite bias in interception time is similar as the bias found for predictive saccades (**Fig. 3D**): the eye lands later and the finger intercepts later for accelerating targets, and both eye and hand intercept earlier for decelerating targets.

We found that interception time (TTC_{hand}) and saccade landing time followed strikingly similar biases opposite to what we would expect if observers accounted for target acceleration. Given that the eye landed at the location of subsequent target reappearance several hundred milliseconds before the hand, we next asked whether saccade landing time was a predictor of TTC_{hand} on a trial-by-trial basis. Trial-by-trial correlations imply a similarity in the trial-based variability between eye and hand movements and are interpreted as evidence for common information sources in the signals that drive eye and hand movements (Sailer et al., 2000). Using a linear mixed model, we found that saccade landing time indeed significantly predicted TTC_{hand} on a trial-by-trial basis ($b = .351$; $F(1,15.73) = 66.96$; $p < .001$). Note, however, that the relation between saccade landing time and TTC_{hand} varied substantially across

TRACKING AND PREDICTING ACCELERATING TARGETS

469 observers, indicated by individual trial-by-trial Person's correlations ranging from $r = .20$
470 to $r = .57$ (**Fig. 6A-C**).

471 Our findings of similar biases in predictive saccades and prediction-based
472 interceptive hand movements and of a medium trial-by-trial correlation between
473 saccade and hand movement timing suggest that both systems relied on similar motion
474 prediction. Notably, despite the ability to closely track accelerating objects with visually-
475 guided pursuit, predictive eye and hand movements appear to be insensitive to target
476 acceleration, raising the question which target features were used to predict TTC for
477 manual interception.

478

479 Which Target Features Determine TTC Predictions?

480 The observed constant interception errors and the systematic biases in TTC_{hand}
481 (later interception for accelerating targets and earlier interception for decelerating
482 targets) suggest that observers were not able to correctly adjust their interception timing
483 according to target acceleration. We next asked which target features observers used
484 instead to estimate TTC for manual interception. We compared three competing
485 models, describing which target motion signals observers might have used to estimate
486 TTC of accelerating targets (Bennett et al., 2007; Heinen, 2007; **Fig. 7A-C**).

487 As one possibility, observers could continuously update target velocity and
488 estimate TTC based on the last available target velocity sample before occlusion (final
489 velocity model; **Fig. 7A**). Alternatively, observers might use the average velocity during
490 the visible period to estimate target reappearance (average velocity model; **Fig. 7B**).
491 Finally, if observers indeed considered target acceleration, we would predict accurate

TRACKING AND PREDICTING ACCELERATING TARGETS

492 scaling of the estimated TTC with target acceleration (acceleration model; **Fig. 7C**). We
 493 compared the TTC predictions of the different models to the observed biases in TTC_{hand}
 494 (**Fig. 7D**) and quantified the performance of each model by calculating the root-mean-
 495 square error (RMSE) for each observer.

496 Using the acceleration model to predict TTC data in eye and hand interception
 497 confirms that interception does not utilize acceleration (**Fig. 7D**; bright grey line).
 498 Although the average velocity model captures the small, reversed trend we observed in
 499 TTC_{hand} (**Fig. 7D**; dark grey line), this model performs poorly at predicting the measured
 500 TTC_{hand} . The final velocity model produced the lowest RMSEs (**Fig. 7D**; black line).
 501 These observations were confirmed statistically by a main effect of *model* on RMSEs in
 502 a one-way rmANOVA ($F(2,30) = 18.00$; $p < .001$; $\eta_p^2 = .55$) and post-hoc pairwise
 503 comparisons. These showed that the final velocity model produced significantly lower
 504 RMSEs compared to the acceleration ($t(15) = 9.64$; $p < .001$; $d = 2.41$) and average
 505 velocity models ($t(15) = 3.46$; $p = .011$; $d = .86$; **Fig. 7E**).

506 The final velocity model predicts that observers rely on the last available velocity
 507 sample. To pinpoint the approximate time sample observers relied on when estimating
 508 TTC, we determined the timepoint along each target's velocity trajectory that best
 509 accounted for each observer's bias in TTC_{hand} . We termed this the hand prediction time.
 510 A negative value indicates that the observer based the TTC prediction on a velocity
 511 sample before occlusion, whereas a positive value would indicate that the TTC
 512 prediction was based on a partial extrapolation of the veridical target trajectory during
 513 occlusion. We found an average hand prediction time of -96.4 ms (**Fig. 7F**), which
 514 captures the small opposite bias we observed in TTC_{hand} (dashed in line in **Fig. 7D**).

TRACKING AND PREDICTING ACCELERATING TARGETS

515

516 **Final Velocity Model Prediction Generalizes to Different Target Configurations**

517 Our model comparison indicates that observers continuously updated their
518 prediction of target velocity until shortly before occlusion. One possible shortcoming of
519 our experimental design was that the target moved at the same final velocity in all
520 acceleration conditions. This might have induced a bias to always hit the target at the
521 same time, favouring the final velocity model. Moreover, our data also showed a small
522 bias toward the average velocity model. We conducted a control experiment to address
523 whether the predictions of the final velocity model hold true when targets moved with
524 different final velocities. In the control experiment, all targets moved with the same
525 average velocities and different final velocities (**Fig. 1C**). Importantly, these target
526 configurations predict the same difference in RMSEs between the average and final
527 velocity models as in Experiment 1, allowing us to directly compare the model fits
528 between the two experiments. Note that in contrast to Experiment 1 the average velocity
529 model here predicts no TTC adjustments, whereas the final velocity model predicts
530 earlier TTC for accelerating targets and later TTC for decelerating targets (**Fig. 8A-B**).

531 In line with the prediction of the final velocity model, we found that observers
532 intercepted accelerating targets earlier (negative TTC values in **Fig. 8C**) and
533 decelerating targets later (positive TTC values in **Fig. 8C**). This observation was
534 supported by a significant one-sided paired t-test, testing whether the final velocity
535 model produced significantly lower RMSEs compared to the average velocity model
536 ($t(9) = 2.12$; $p = .031$; $d = .67$; **Fig. 8D**). We also estimated the target velocity sample
537 that best predicted observers' TTC bias. We found a mean hand prediction time of 65.8

TRACKING AND PREDICTING ACCELERATING TARGETS

ms before occlusion onset, which was similar but slightly smaller than the hand prediction time in Experiment 1. Together, these results replicate our findings from Experiment 1 and confirm the use of the final target velocity to predict TTC.

541

542

Discussion

The aim of the current study was to investigate how humans integrate visual motion information to track and predict accelerating objects for manual interception. Our task required observers to track an accelerating target before a temporary occlusion, and to predict the time of target reappearance by making an interceptive hand movement. This hand movement was naturally accompanied by a predictive saccade to the interception position, even though no explicit instruction to make such a saccade was given. Our results show that observers were insensitive to target acceleration when predicting future target motion. Neither the timing of the predictive saccade nor the interceptive hand movement (TTC_{hand}) scaled with acceleration, resulting in systematic constant interception errors. Inability to account for target acceleration was observed irrespective of target presentation duration and of whether observers were able to accurately track the accelerating target before the occlusion. TTC estimates were best described by a model that relied on the final velocity of the target just before occlusion, indicating that observers based their prediction on the memory of the last available velocity signal (first-order motion; Benguigui et al., 2003; Benguigui & Bennett, 2010).

558

Different Acceleration Sensitivity for Tracking and Predicting?

TRACKING AND PREDICTING ACCELERATING TARGETS

560 To successfully interact with a moving object, we must continuously monitor its
561 dynamically-changing motion trajectory. Due to sensorimotor delays, we need to quickly
562 form a prediction of current and future object motion. This form of prediction is also
563 important when we lose sight of an object, or when it is temporarily occluded. Naturally-
564 moving objects do not necessarily move at constant velocity but can suddenly
565 accelerate or decelerate. Forming a prediction that can capture dynamically-changing
566 object motion is therefore an integral part of everyday actions (e.g., Fiehler et al., 2019;
567 Zhao & Warren, 2015).

568 The abilities to track and predict the motion trajectory of objects that move at
569 constant velocity are often closely linked (Makin & Poliakoff, 2011). Accurate tracking of
570 a moving object with smooth pursuit eye movements can enhance temporal (Bennett et
571 al., 2010) and spatial (Spering et al., 2011) predictions of target trajectories. Yet, our
572 results suggest that tracking an accelerating target does not necessarily extend to
573 predicting accelerating objects when aiming to intercept them. Specifically, we show
574 that observers' eye movements closely matched the velocity profile of accelerating
575 targets for target presentations of longer than 200 ms. However, irrespective of how
576 long observers had time to track and potentially integrate acceleration signals, they did
577 not consider target acceleration when timing their manual interception and predictive
578 saccade.

579 One explanation for the apparent discrepancy between tracking and predicting
580 accelerating targets could be that visually-guided tracking can rely on detecting and
581 updating the changing target velocity over time and might thus not require a direct
582 consideration of the acceleration signal. Conversely, to intercept accelerating targets,

TRACKING AND PREDICTING ACCELERATING TARGETS

583 observers would need to consider an explicit readout of target acceleration to form a
584 prediction of target motion to overcome sensorimotor delays or a temporary occlusion of
585 the moving object. The finding that acceleration is not used during manual interception
586 suggests that observers continuously update their judgment of target velocity but cannot
587 integrate acceleration signals to inform their prediction. Instead, they predicted TTC
588 based on a velocity sample ~100 ms before target occlusion, suggesting the use of
589 velocity memory when predicting future target motion (Soechting et al., 2009; Benguigui
590 & Bennett, 2010; Rust & Palmer, 2021). Continuously tracking the changing target
591 velocity with smooth pursuit eye movements might have thus supported manual
592 interception by continuously updating observers' prediction of target velocity.

593 Alternatively, tracking and predicting might exhibit different sensitivity to
594 acceleration signals. A possible dissociation in integrating acceleration signals between
595 tracking and interception is congruent with two sets of literature that have typically
596 tested both behaviors—tracking and interception—separately. First, the smooth pursuit
597 system can be sensitive to acceleration signals when probing it with velocity
598 perturbations (Brostek et al., 2017; Tavassoli & Ringach 2010). Moreover, predictive
599 pursuit during a target's occlusion period scales with the target's acceleration (Bennett
600 & Barnes, 2006; Bennett et al., 2007; Bennett & Benguigui, 2013). These findings
601 suggest that the oculomotor system can extract acceleration signals even to predictively
602 drive pursuit. Second, interceptive hand movements are comparatively unresponsive to
603 visual acceleration, reflected in systematic errors when intercepting accelerating targets
604 (Benguigui et al., 2003; Brenner & Smeets, 2015; Brenner et al., 2016; Dubrowski &
605 Carnahan, 2002; Port et al., 1997). These systematic interception errors can be

TRACKING AND PREDICTING ACCELERATING TARGETS

606 explained by a failure to predict accelerating target motion to overcome sensorimotor
607 delays (Brenner & Smeets, 2015) or temporary target occlusion, in line with our results
608 (see also Reid & Dessing, 2018). Moreover, we showed that systematic interception
609 errors can be described by a model that relied on target velocity just before target
610 occlusion (first-order motion; Benguigui et al., 2003; Benguigui & Bennett, 2010).
611 Together, our results are congruent with the idea that target velocity estimates are
612 continuously updated for both visually-guided pursuit and prediction-guided interception.

613

614 **Extending the Eye-Hand Link to Prediction-Based Actions**

615 We observed trial-by-trial correlations between the timing of the predictive
616 saccade and TTC_{hand} , extending the known close coupling of eye and hand movements
617 during visually-guided actions (Hayhoe, 2017; De Brouwer et al., 2021) to predictive
618 actions (Binaee & Diaz, 2019). During visually-guided reaching, observers commonly
619 shift their eyes to the reach target prior to hand movement execution (Ballard et al.,
620 1992; Johansson et al. 2001; Neggers & Bekkering, 2000; Horstmann & Hoffmann,
621 2005; Barany et al., 2020; Land & Hayhoe, 2001). When intercepting moving targets,
622 observers naturally track the target with their eyes, even when no explicit instruction to
623 do so is given (Mrotek & Soechting, 2007). In interception tasks, eye and hand
624 movement endpoints are also correlated (Kreyenmeier et al., 2017; Li et al., 2018;
625 Fookien et al., 2021). Our results extend these findings in two ways. First, correlations of
626 predictive eye movements and interceptive hand movements reveal that the
627 coordinated control of eye and hand movements also applies to memory-based actions.
628 Second, correlations of temporally-based estimations show that eye and hand

TRACKING AND PREDICTING ACCELERATING TARGETS

629 movements can be correlated not just in the spatial, but also in the temporal domain.
630 Similarly, previous studies showed that the timing of predictive saccades is finely tuned
631 to stimulus properties (ball speed and elasticity; Diaz et al., 2013) and is a sensitive
632 indicator of decision outcomes in manual interception tasks (Fookien & Spering, 2020).
633 Although the eyes reach the interception location several hundred milliseconds before
634 the hand in our task, the timing of predictive saccades and interceptive hand
635 movements showed strikingly similar biases and were correlated on a trial-by-trial basis.
636 A strong eye-hand link is expected when intercepting targets that move unpredictably
637 and are partially occluded from view (Fookien et al., 2021). If acceleration is indeed not
638 considered in a predictive model of target motion, the extrapolation of accelerating
639 target motion becomes highly inaccurate and observers rely on their eye movements to
640 continuously update their prediction of the target motion (Brenner & Smeets, 2018; de la
641 Malla et al., 2019).

642

643 **Assessing Model Predictions of Accelerating Motion Integration**

644 Given the limited perceptual sensitivity to acceleration, and the lack of
645 acceleration tuning in key motion-sensitive cortical areas (Lisberger & Movshon, 1999;
646 Price et al., 2005) the question arises what information observers rely on when
647 interacting with accelerating objects in everyday life. It is well known that humans use
648 physical laws of motion, such as gravity, which are learned throughout the lifespan, as
649 an implicit prior when interacting with real-world objects (Zago & Lacquaniti, 2005;
650 Jörges & López-Moliner, 2017). For instance, observers are more accurate when
651 tracking and predicting simulated fly balls that move with natural gravity compared to

TRACKING AND PREDICTING ACCELERATING TARGETS

652 balls that do not (0g), or that are unnaturally impacted by gravity (2g; Russo et al., 2017;
653 Bosco et al., 2012). Although naturalistic priors influence ocular and perceptual motion
654 prediction (Delle Monache et al., 2019), other studies have also found that observers
655 assume that targets move with constant velocity when predicting object motion (Jörges
656 et al., 2021).

657 When intercepting targets that are impacted by arbitrary acceleration, we found
658 that observers make systematic interception errors (Benguigui et al., 2003; Port et al.,
659 1997; Dubrowski & Carnahan, 2002). In situations where the target is not occluded from
660 view and remains visible throughout, observers can minimize these interception errors
661 by continuously adjusting their interceptive hand movement online (Brenner & Smeets,
662 1997; Reid & Dessing, 2018). Nonetheless, even when intercepting visible accelerating
663 targets, systematic interception errors occur due to sensorimotor delays (Brenner &
664 Smeets, 2015; Brenner et al., 2016). One possibility to compensate for the inability to
665 extrapolate accelerating motion, is to quickly adapt movements, given that sufficient trial
666 repetitions are available (Ruttle et al., 2021). For example, improvements in the ability to
667 manually intercept (Brenner et al., 2016) and predictively pursue (Bennett & Barnes,
668 2006) accelerating targets after a few (eight to twelve) repetitions of the same
669 acceleration rate have been reported. These findings suggest that observers might be
670 able to form short-term and long-term (naturalistic) priors to counteract the lack of
671 acceleration signal integration.

672 In conclusion, our study shows that observers failed to use an acceleration-based
673 prediction of the target's motion to inform manual interception. Instead, the timing of
674 manual interception was best predicted by an extrapolation of target velocity shortly

TRACKING AND PREDICTING ACCELERATING TARGETS

675 before target occlusion. Systematic interception errors occurred irrespective of the
676 target presentation duration and how well observer's visually-guided eye movements
677 matched the different target velocity profiles. Interestingly, the timing of both predictive
678 eye and interceptive hand movements showed strikingly similar biases and were
679 correlated on a trial-by-trial basis, indicating a strong coupling between both effectors
680 during prediction-guided interception tasks.

Citation Diversity Statement

Recent work in several fields of science has identified a bias in citation practices such that papers from women and other minority scholars are under-cited relative to the number of such papers in the field (Zurn et al., 2020). Here we sought to proactively choose references that reflect the diversity of the field in thought, form of contribution, gender, race, ethnicity, and other factors. First, we obtained the predicted gender of the first and last author of each reference by using databases that store the probability of a first name being carried by a woman (Dworkin et al., 2020; Zhou et al., 2020). By this measure (and excluding self-citations to the first and last authors of our current paper), our references contain 12.9% woman(first)/woman(last), 12.26% man/woman, 22.58% woman/man, and 52.25% man/man. This method is limited in that a) names, pronouns, and social media profiles used to construct the databases may not, in every case, be indicative of gender identity and b) it cannot account for intersex, non-binary, or transgender people. Second, we obtained predicted racial/ethnic category of the first and last author of each reference by databases that store the probability of a first and last name being carried by an author of color (Ambekar et al., 2009; Sood & Laohaprapnon, 2018). By this measure (and excluding self-citations), our references contain 9.24% author of color (first)/author of color(last), 19.02% white author/author of color, 16.68% author of color/white author, and 55.06% white author/white author. This method is limited in that a) names and Florida Voter Data to make the predictions may not be indicative of racial/ethnic identity, and b) it cannot account for Indigenous and mixed-race authors, or those who may face differential biases due to the ambiguous

TRACKING AND PREDICTING ACCELERATING TARGETS

- 703 racialization or ethnicization of their names. We look forward to future work that could
- 704 help us to better understand how to support equitable practices in science.

References

- 705
- 706 Ambekar A, Ward C, Mohammed J, Male S, Skiena S (2009) Name-ethnicity
 707 classification from open sources. *Proceedings of the 15th ACM SIGKDD*
 708 *international conference on Knowledge Discovery and Data Mining*: 49-58.
- 709 Ballard DH, Hayhoe MM, Li F, Whitehead SD (1992) Hand-eye coordination during
 710 sequential tasks. *Philos Trans R Soc Lond B Biol Sci* 337(1281):331-339.
- 711 Barany DA, Gómez-Granados A, Schroyer M, Cutts SA, Singh T (2020) Perceptual
 712 decisions about object shape bias visuomotor coordination during rapid
 713 interception movements. *J Neurophysiol* 123(6):2235-2248.
- 714 Benguigui N, Bennett SJ (2010) Ocular pursuit and the estimation of time-to-contact
 715 with accelerating objects in prediction motion are controlled independently based
 716 on first-order estimates. *Exp Brain Res* 202(2): 327-339.
- 717 Benguigui N, Ripoll H, Broderick M (2003) Time-to-contact estimation of accelerating
 718 stimuli is based on first-order Information. *J Exp Psychol: Hum Percept Perform*
 719 29(6): 1083-1101.
- 720 Bennett SJ, Barnes GR (2006) Smooth ocular pursuit during the transient
 721 disappearance of an accelerating visual target: The role of reflexive and voluntary
 722 control. *Exp Brain Res* 175(1):1-10.
- 723 Bennett SJ, Baures R, Hecht H, Benguigui N (2010) Eye movements influence
 724 estimation of time-to-contact in prediction motion. *Exp Brain Res* 206(4): 399-407.
- 725 Bennett SJ, Benguigui N (2013) Is Acceleration used for ocular pursuit and spatial
 726 estimation during prediction motion? *PLoS One* 8(5):e63382.
- 727 Bennett SJ, De Xivry JJO, Barnes GR, Lefèvre P (2007) Target acceleration can be
 728 extracted and represented within the predictive drive to ocular pursuit. *J*
 729 *Neurophysiol* 98(3):1405-1414.
- 730 Binaee K, Diaz G (2019) Movements of the eyes and hands are coordinated by a
 731 common predictive strategy. *J Vis* 19(12):1–16.
- 732 Bosco G, Delle Monache S, Lacquaniti F (2012) Catching what we can't see: Manual
 733 interception of occluded fly-ball trajectories. *PLoS One* 7(11):e49381.
- 734 Brainard DH (1997) The Psychophysics Toolbox. *Spat Vis* 10:433-436.
- 735 Brenner E, Smeets JBJ (2018) Continuously updating one's predictions underlies
 736 successful interception. *J Neurophysiol* 120(6):3257-3274.

TRACKING AND PREDICTING ACCELERATING TARGETS

- 737 Brenner E, Smeets JBJ (1997) Fast responses of the human hand to changes in target
738 position. *J Motor Behav* 29(4):297-310.
- 739 Brenner E, Smeets JBJ (2015) How people achieve their amazing temporal precision in
740 interception. *J Vis* 15(3):1-21.
- 741 Brenner E, Rodriguez IA, Muñoz VE, Schootemeijer S, Mahieu Y, Veerkamp K, et al.
742 (2016) How can people be so good at intercepting accelerating objects if they are
743 so poor at visually judging acceleration? *Iperception* 7(1):1-13.
- 744 Brostek L, Eggert T, Glasauer S (2017) Gain control in predictive smooth pursuit eye
745 movements: Evidence for an acceleration-based predictive mechanism. *eNeuro*
746 4(3):1-13.
- 747 Brouwer AM, Brenner E, Smeets JBJ (2002) Perception of acceleration with short
748 presentation times: Can acceleration be used in interception? *Percept*
749 *Psychophys* 64(7):1160-1168.
- 750 Calderone JB, Kaiser MK (1989) Visual acceleration detection: Effect of sign and motion
751 orientation. *Percept Psychophys* 45(4): 391-394.
- 752 Cesqui B, Mezzetti M, Lacquaniti F, D'Avella A (2015) Gaze behavior in one-handed
753 catching and its relation with interceptive performance: What the eyes can't tell.
754 *PLoS One* 10(3): e0119445.
- 755 Churchland MM, Lisberger SG (2001) Experimental and computational analysis of
756 monkey smooth pursuit eye movements. *J Neurophysiol* 86(2):741-759.
- 757 Cornelissen FW, Peters EM, Palmer J (2002) The Eyelink toolbox: eye tracking with
758 MATLAB and the Psychophysics toolbox. *Behav Res Method Instrum Comput*
759 34(4):613-617.
- 760 Cramer AOJ, van Ravenzwaaij D, Matzke D, Steingroever J, Wetzels R, Grasman
761 RPPP, Waldorp LJ, Wagenmakers JE (2016) Hidden multiplicity in exploratory
762 multiway ANOVA: Prevalence and remedies. *Psychon Bull Rev* 23:640-647.
- 763 De Brouwer AJ, Flanagan JR, Spering M (2021) Functional use of eye movements for
764 an acting system. *Trends Cog Sci* 25(3):252-263.
- 765 De Brouwer S, Missal M, Barnes G, Lefèvre P (2002) Quantitative analysis of catch-up
766 saccades during sustained pursuit. *J Neurophysiol* 87:1772–1780.
- 767 De la Malla C, Rushton SK, Clark K, Smeets JBJ, Brenner E (2019) The predictability of
768 a target's motion influences gaze, head, and hand movements when trying to
769 intercept it. *J Neurophysiol* 121(6):2416–2427.

TRACKING AND PREDICTING ACCELERATING TARGETS

- 770 De la Malla C, Smeets JBJ, Brenner E (2017) Potential Systematic Interception Errors
771 are Avoided When Tracking the Target with One's Eyes. *Sci Rep* 7(1):10793.
- 772 Delle Monache S, Lacquaniti F, Bosco G (2019) Ocular tracking of occluded ballistic
773 trajectories: Effects of visual context and of target law of motion. *J Vis* 19(4):1-21.
- 774 Diaz GJ, Cooper J, Rothkopf C, Hayhoe M (2013) Saccades to future ball location
775 reveal memory-based prediction in a virtual-reality interception task. *J Vis*
776 13(1):1–14.
- 777 Dubrowski A, Carnahan H (2002) Action-perception dissociation in response to target
778 acceleration. *Vision Res* 42(11):1465-1473.
- 779 Dworkin JD, Linn KA, Teich EG, Zurn P, Shinohara RT, Bassett DS (2020) The extent
780 and drivers of gender imbalance in neuroscience reference lists. *Nat Neurosci*
781 23:918-926.
- 782 Faul F, Erdfelder E, Buchner A, Lang AG (2009) Statistical power analyses using
783 G*Power 3.1: Tests for correlation and regression analyses. *Behav Res Methods*
784 41(4):1149–1160.
- 785 Fiehler K, Brenner E, Spering M (2019) Prediction in goal-directed action. *J Vis* 19(9):1-
786 21.
- 787 Fookien J, Kreyenmeier P, Spering M (2021) The role of eye movements in manual
788 interception: A mini-review. *Vision Res* 183:81-90.
- 789 Fookien J, Spering M (2020) Eye movements as a readout of sensorimotor decision
790 processes. *J Neurophysiol* 123(4):1439-1447.
- 791 Fookien J, Yeo SH, Pai DK, Spering M (2016) Eye movement accuracy determines
792 natural interception strategies. *J Vis* 16(14):1-15.
- 793 Goettker A, Brenner E, Gegenfurtner KR, de la Malla C (2019) Corrective saccades
794 influence velocity judgments and interception. *Sci Rep* 9(1):1–12.
- 795 Gottsdanker R, Frick JW, Lockard RB (1961) Identifying target acceleration of visual
796 targets. *Br J Physiol* 52(1):31-42.
- 797 Hayhoe MM (2017) Vision and Action. *Annu Rev Vis Sci* 3:389–413.
- 798 Heinen SJ (2007) Oculomotor hide and seek: pursuing an accelerating target behind an
799 occluder. Focus on "Target acceleration can be extracted and represented within
800 the predictive drive to ocular pursuit." *J Neurophysiol* 98:1073-1074.

TRACKING AND PREDICTING ACCELERATING TARGETS

- 801 Horstmann A, Hoffmann KP (2005) Target selection in eye–hand coordination: Do we
802 reach to where we look or do we look to where we reach? *Exp Brain Res*
803 167(2):187-195.
- 804 Johansson RS, Westling G, Bäckström A, Flanagan JR (2001) Eye-hand coordination in
805 object manipulation. *J Neurosci* 21(17):6917-6932.
- 806 Jörges B, La Scaleia B, López-Moliner J, Lacquaniti F, Zago M (2021) Perceptual
807 judgements of duration of parabolic motions. *Sci Rep* 11(1):7108.
- 808 Jörges B, López-Moliner J (2017) Gravity as a strong prior: Implications for perception
809 and action. *Front Hum Neurosci* 11:1-16.
- 810 Kleiner M, Brainard D, Pelli D, Ingling A, Murray R, Broussard C (2007) What's new in
811 Psychtoolbox-3. *Percept* 36(14):1-16.
- 812 Kowler E, Rubinstein JF, Santos EM, Wang J (2019) Predictive smooth pursuit eye
813 movements. *Annu Rev Vis Sci* 5:223-246.
- 814 Krauzlis RJ, Lisberger SG (1994) Temporal properties of visual motion signals for the
815 initiation of smooth pursuit eye movements in monkeys. *J Neurophysiol*
816 72(1):150-162.
- 817 Kreyenmeier P, Fookien J, Spering M (2017) Context effects on smooth pursuit and
818 manual interception of a disappearing target. *J Neurophysiol* 118(1):404-415.
- 819 Land MF, Hayhoe MM (2001) In what ways do eye movements contribute to everyday
820 activities? *Vision Res* 41(25–26):3559-3565.
- 821 Lisberger SG (2015) Visual guidance of smooth pursuit eye movements. *Annu Rev Vis*
822 *Sci* 1(1):447-468.
- 823 Lisberger SG, Movshon AJ (1999) Visual motion analysis for pursuit eye movements in
824 area MT of macaque monkeys. *J Neurosci* 19:2224-2246.
- 825 Li Y, Wang Y, Cui H (2018) Eye-hand coordination during flexible manual interception of
826 an abruptly appearing, moving target. *J Neurophysiol* 119(1):221–234.
- 827 Makin ADJ, Poliakoff E (2011) Do common systems control eye movements and motion
828 extrapolation? *Q J Exp Psychol* 64(7):1327-1343.
- 829 Mrotek LA (2013) Following and intercepting scribbles: Interactions between eye and
830 hand control. *Exp Brain Res* 227(2):161–174.
- 831 Mrotek LA, Soechting JF (2007) Target interception: Hand-eye coordination and
832 strategies. *J Neurosci* 27(27):7297-7309.

TRACKING AND PREDICTING ACCELERATING TARGETS

- 833 Mueller AS, González EG, McNorgan C, Steinbach MJ, Timney B (2017) Aperture
834 extent and stimulus speed affect the perception of visual acceleration. *Exp Brain*
835 *Res* 235(3):743-752.
- 836 Neggers S, Bekkering H (2000) Ocular gaze is anchored to the target of an ongoing
837 pointing movement. *J Neurophysiol* 83(2):639-651.
- 838 Orban de Xivry JJ, Coppe S, Blohm G, Lefèvre P (2013) Kalman filtering naturally
839 accounts for visually guided and predictive pursuit dynamics. *J Neurosci*
840 584(1):11-23.
- 841 Pelli DG (1997) The VideoToolbox software for visual psychophysics: Transforming
842 numbers into movies. *Spat Vis* 10: 437-442
- 843 Port NL, Lee D, Dassonville P, Georgopoulos AP (1997) Manual interception of moving
844 targets. I. Performance and movement initiation. *Exp Brain Res* 116(3):406-420.
- 845 Price NSC, Ono S, Mustari MJ, Ibbotson MR (2005) Comparing acceleration and speed
846 tuning in macaque MT: Physiology and modeling. *J Neurophysiol* 94(5):3451-
847 3464.
- 848 Reid SA, Dessing JC (2018) Spatial biases in motion extrapolation for manual
849 interception. *J Exp Psych Hum Percept Perform* 44(1):38-52.
- 850 Rust NC, Palmer SE (2021) Remembering the Past to See the Future. *Annu Rev Vis*
851 *Sci* 7:349-365.
- 852 Russo M, Cesqui B, La Scaleia B, Ceccarelli F, Maselli A, Moscatelli A, Zago M,
853 Lacquaniti F (2017) Intercepting virtual balls approaching under different gravity
854 conditions: evidence for spatial prediction. *J Neurophysiol* 118(4):2421-2434.
- 855 Ruttle JE, Hart BM 't, Henriques DYP (2021) Implicit motor learning within three trials.
856 *Sci Rep* 11(1):1-11.
- 857 Sailer U, Eggert T, Ditterich J, Straube A (2000) Spatial and temporal aspects of eye-
858 hand coordination across different tasks. *Exp Brain Res* 134(2):163-173.
- 859 Singmann H, Bolker B, Westfall J, Aust F, Mattan BS (2021) afex: Analysis of Factorial
860 Experiments. R package Version 1.0-1. [https://CRAN.R-](https://CRAN.R-project.org/package=afex)
861 [project.org/package=afex](https://CRAN.R-project.org/package=afex).
- 862 Soechting JF, Juveli JZ, Rao HM (2009) Models for the extrapolation of target motion for
863 manual interception. *J Neurophysiol* 102(3):1491-1502.
- 864 Sood G, Laohaprapanon S (2018) Predicting race and ethnicity from the sequence of
865 characters in a name. *arXiv*:1805.02109.

TRACKING AND PREDICTING ACCELERATING TARGETS

- 866 Spering M, Schütz AC, Braun DI, Gegenfurtner KR (2011) Keep your eyes on the ball:
 867 Smooth pursuit eye movements enhance prediction of visual motion. *J*
 868 *Neurophysiol* 105(4):1756-1767.
- 869 Tavassoli A, Ringach DL (2010) When your eyes see more than you do. *Curr Biol*
 870 20(3):93-94.
- 871 Watamaniuk SNJ, Heinen SJ (2003) Perceptual and oculomotor evidence of limitations
 872 on processing accelerating motion. *J Vis* 3(11):698-709.
- 873 Werkhoven P, Snippe HP, Toet A (1992) Visual processing of optic acceleration. *Vision*
 874 *Res* 32(12):2313-2329.
- 875 Zago M, Lacquaniti F (2005) Visual perception and interception of falling objects: a
 876 review of evidence for an internal model of gravity. *J Neural Eng* 2:S198-S208.
- 877 Zhao H, Warren WH (2015) On-line and model-based approaches to the visual control
 878 of action. *Vision Res* 110:190-202.
- 879 Zhou D, Bertolero MA, Stiso J, Cornblath EJ, Teich EG, Blevins AS, Virtualmario, Camp
 880 C, Dworkin JD, Bassett DS (2020) Gender diversity statement and code notebook
 881 v1.1.
- 882 Zurn P, Bassett DS, Rust NC (2020) The Citation Diversity Statement: A Practice of
 883 Transparency, A Way of Life. *Trends Cog Sci* 24(9):669-672.
 884

Figure Legends

885

886 **Figure 1. (A)** Task procedure. A black disc moved across a grey monitor background
 887 from left to right at a constant rate of acceleration. After an initial period during which the
 888 target was visible, it moved behind an occluder of a fixed width (13.4°) and then
 889 reappeared. Observers had to estimate the time of reappearance (equivalent to time-to-
 890 contact; TTC) and intercept the target with a rapid pointing movement of their right index
 891 finger (red dot). **(B)** Target parameters in Experiment 1. Targets moved with a variable
 892 initial velocity (v_{init}) and accelerated or decelerated at a constant rate. The initial and
 893 average velocities (v_{avg}) of the targets were related in such a way with acceleration rate
 894 that all targets reached the occluder with the same velocity (v_{final}) of $20^\circ/\text{s}$. **(C)** Target
 895 parameters in Experiment 2. Initial and final target velocities were related in such a way
 896 with acceleration rate that all targets had the same v_{avg} of $20^\circ/\text{s}$.
 897

898 **Figure 2.** Single trial eye and hand movements from one representative observer. **(A)**
 899 and **(B)** show two trials with a $+8^\circ/\text{s}^2$ accelerating target **(A)** or $-8^\circ/\text{s}^2$ decelerating target
 900 **(B)**. Light blue traces indicate smooth pursuit components, dark blue traces represent
 901 saccades. Upper panels show the horizontal position of the eye (blue) and target (black)
 902 locked to target motion onset. The red 'x' represents the interception position and time.
 903 Lower panels show horizontal velocity of the eyes and target over time. Grey area
 904 represents the time of target occlusion. **(C)** shows the 3D-hand position trace (green)
 905 from the same trial as in **(A)**. The 2D interception position on the screen is indicated by
 906 the red 'x' and the target position at the time of interception is represented by the black
 907 disc. The grey area illustrates the position of the occluder on the screen. Dotted lines in
 908 the x-y plane illustrate the upper and bottom edges of the screen.
 909

910 **Figure 3.** Effect of presentation duration on smooth pursuit and predictive saccades. **(A)**
 911 Average de-saccaded smooth pursuit velocities. Squares and errorbars at the top show
 912 the mean ± 1 standard error of the mean (SEM) of the first catch-up saccade (left) and
 913 predictive saccade (right) onsets. Shaded areas indicate occlusion period and dashed
 914 lines represent target velocities. **(B)** Normalized pursuit velocity during target
 915 presentation. **(C)** Distribution of 2D saccade landing positions. The black line represents
 916 the location of target reappearance (i.e., right border of the occluder). **(D)** Saccade
 917 landing times. Dots and errorbars represent the mean across observers ± 1 SEM.
 918

919 **Figure 4.** Hand movement paths and interception position. **(A)** Top view of the hand
 920 movement paths in the x-z plane. The grey bar illustrates the x-position of the occluder
 921 on the screen. Hand movement paths were shifted along the z-axis for better visibility.
 922 **(B)** Distribution of 2D interception positions. Histogram shows the distribution of
 923 horizontal interception positions. **(C)** Kernel density plots of horizontal interception
 924 positions for the different target acceleration condition.
 925

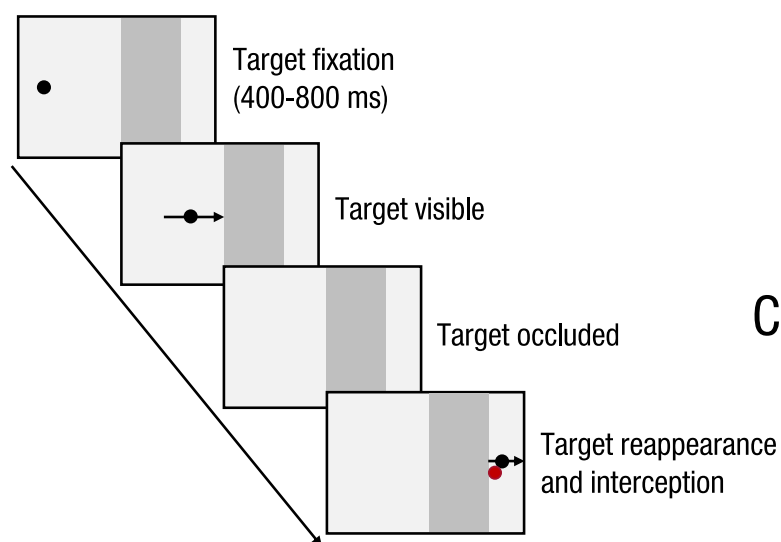
Figure 5. Manual interception time. **(A)** Mean TTC_{hand} (interception time relative to occlusion onset). **(B)** Mean and individual observers' constant interception errors. Semi-transparent dots represent individual observers' median performance. Negative values indicate interceptions that occurred before the target reached the end of the occluder (too early), and positive values indicate interceptions occurring after the target reached the end of the occluder (too late). Errorbars represent ± 1 SEM.

Figure 6. Trial-by-trial correlation across acceleration conditions and presentation durations between saccade landing time and TTC_{hand} . **(A)** Distribution of individual correlation coefficients. **(B, C)** Scatterplot and trend lines of the trial-by-trial correlation for an observer with a strong **(B)** and for an observer with a weak **(C)** correlation between saccade landing time and TTC_{hand} . Dots represent individual trials. Thin lines represent trend lines for the different acceleration conditions, thick line shows the trend across conditions.

Figure 7. Model comparison. **(A-C)** Three competing models of how observers might predict TTC for predictive eye and interceptive hand movements: **(A)** The final velocity model postulates that observers predict TTC based on v_{final} (identical for all targets in our design, hence predicting a fixed TTC). **(B)** The average velocity model predicts interception timing based on the average target velocity before occlusion, yielding a negative correlation between veridical and measured TTC. **(C)** The acceleration model suggests that observers use target acceleration for interception and predicts the veridical TTC. **(D)** Comparison of model predictions and measured TTC_{hand} data. Dashed line shows the TTC prediction based on the mean hand prediction times. **(E)** Root mean squared errors for the competing models on TTC_{hand} . **(F)** Individual and mean hand prediction times.

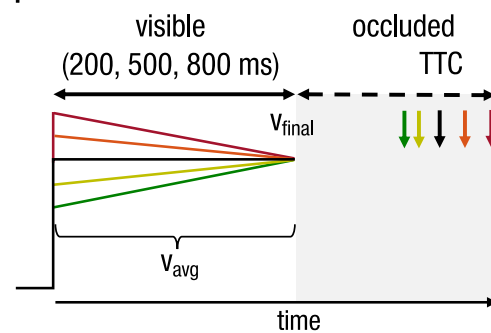
Figure 8. Results from Experiment 2. **(A-B)** The model predictions of the final **(A)** and average velocity **(B)** models in Experiment 2. **(C)** Comparison of TTC_{hand} to the model predictions. **(E)** Comparison of model fits.

A



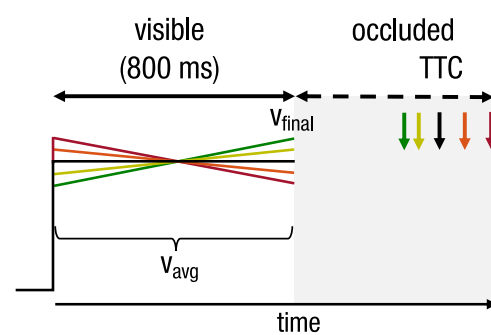
B

Experiment 1

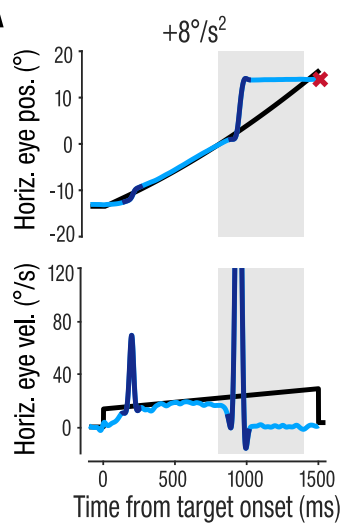


C

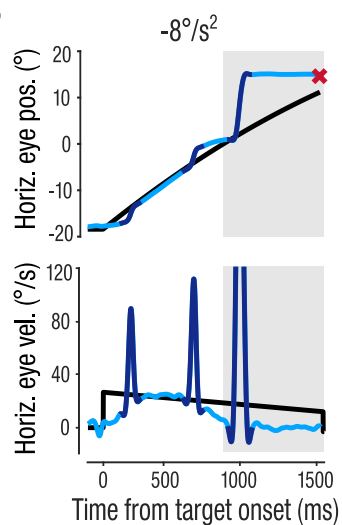
Experiment 2



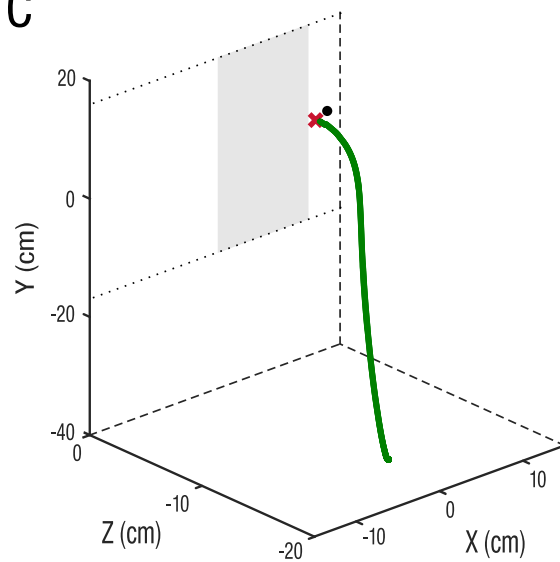
A

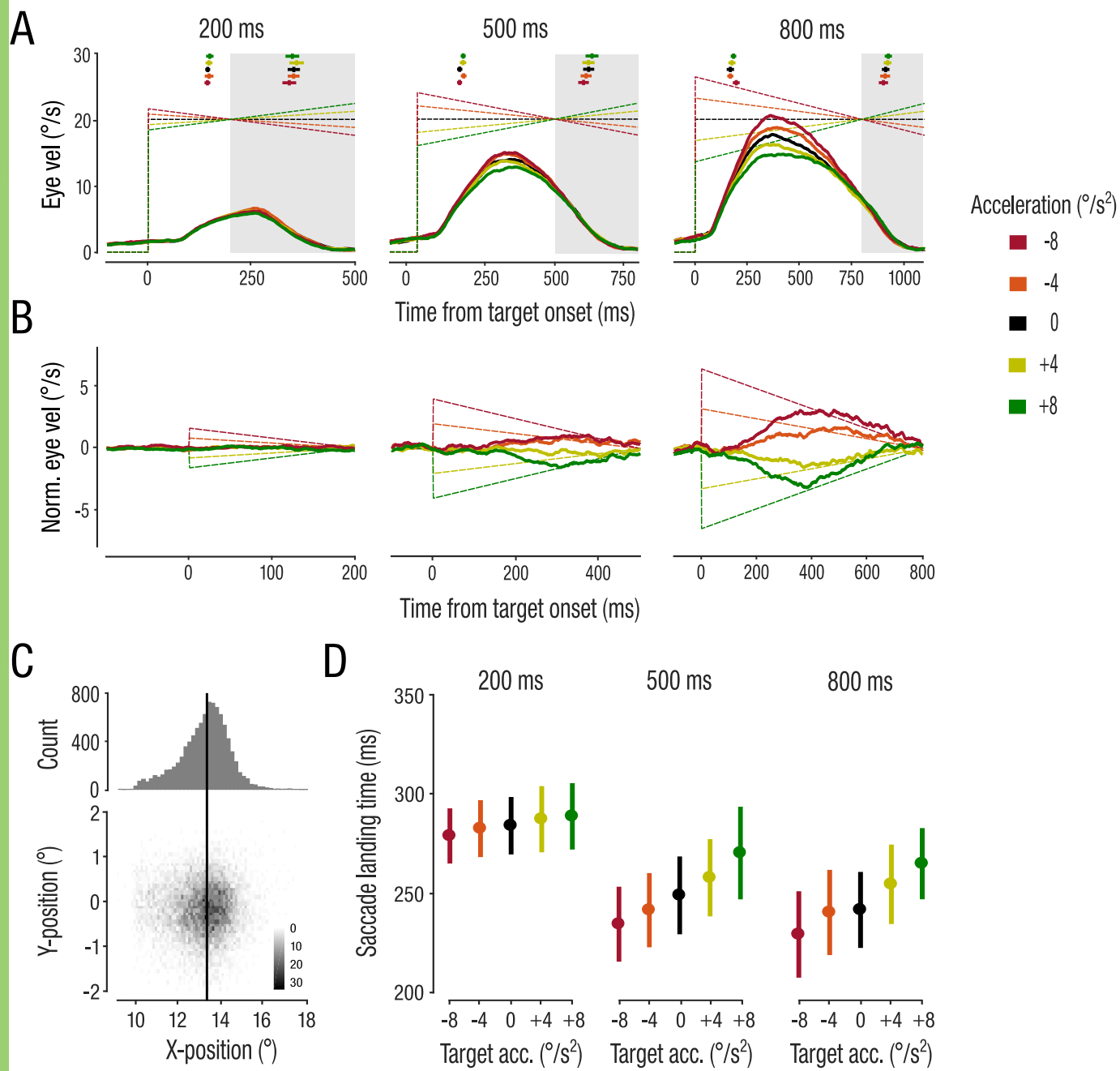


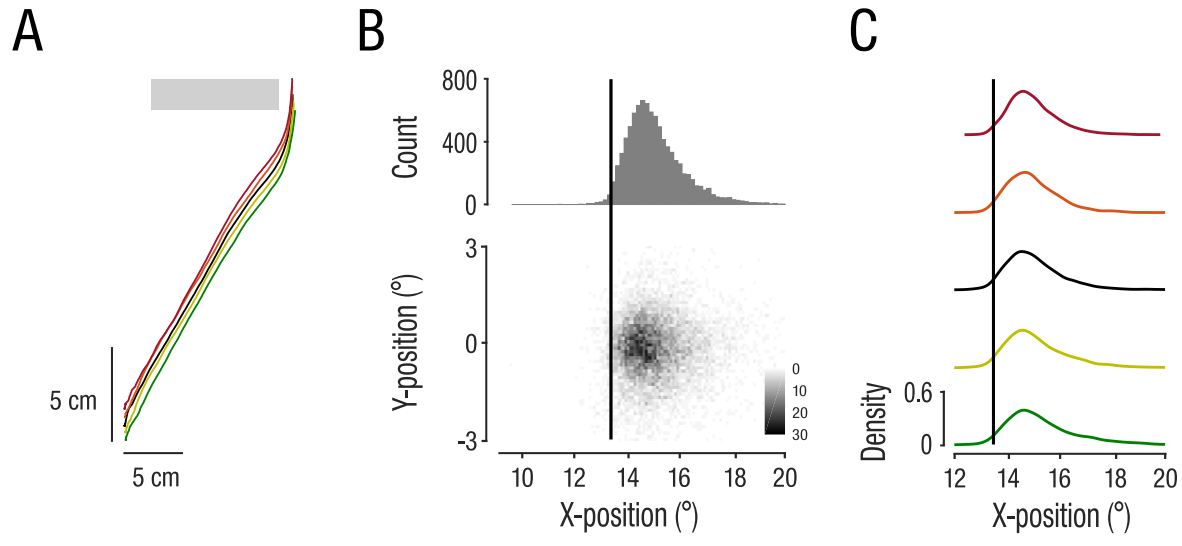
B



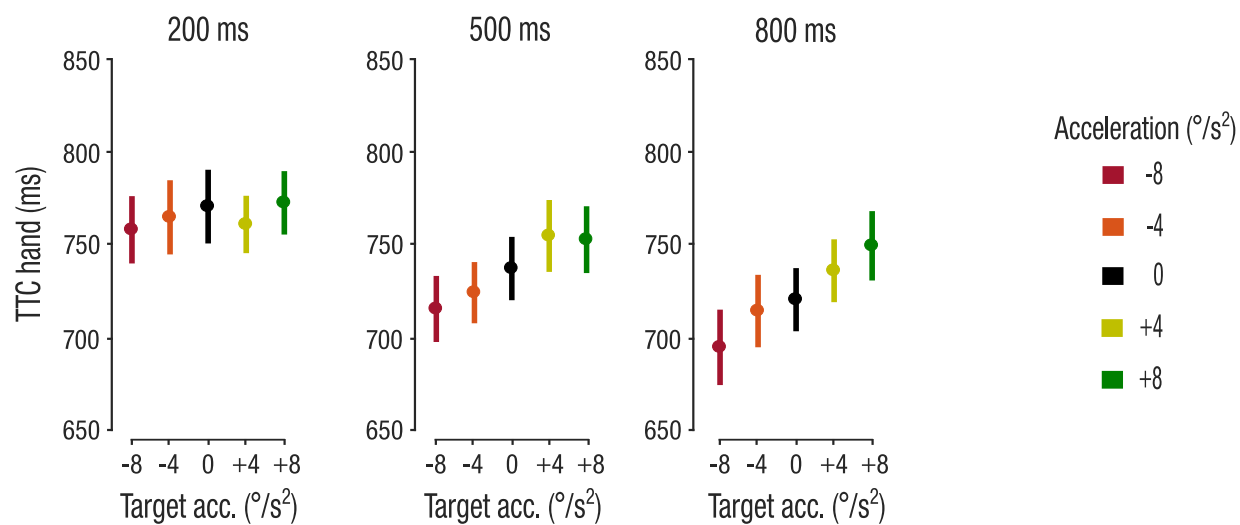
C







A



B

