

Rapid eye and hand responses in an interception task are differentially modulated by context-dependent predictability

Fooken, Jolande¹⁻², Balalaie, Parsa¹, Park, Kayne¹, Flanagan, J. Randall¹⁻², & Scott, Stephen H.^{1,3-4}

1. Centre for Neuroscience Studies, Queen's University, Kingston, Ontario, Canada
2. Department of Psychology, Queen's University, Kingston, Ontario, Canada
3. Department of Biomedical and Molecular Sciences, Queen's University, Kingston, Ontario, Canada
4. Department of Medicine, Queen's University, Kingston, ON, Canada

Credit authorship contribution statement

Conceptualization (JF, PB, KP, JRF, SHS), Methodology (JF, PB, KP, SHS), Software (PB, KP), Validation (PB, KP, SHS), Formal analysis (KP, JF, SHS), Resources (JRF, SHS), Data Curation (JF), Writing - Original Draft (JF, PB, KP), Writing - review & editing (JF, PB, KP, JRF, SHS), Visualization (JF), Supervision (JF, JRF, SHS), Funding acquisition (JF, JRF, SHS)

Declaration of Competing Interest

Stephen H. Scott is associated with Kinarm, which commercializes the robotic device used in the present study. The remaining authors declare no competing financial interests.

Acknowledgements

This work was supported by a Deutsche Forschungsgemeinschaft (DFG) Research Fellowship to JF (grant FO 1347/1-1), an NSERC Discovery grant to JRF, and an NSERC Discovery grant to SHS. The authors thank Elissa Robichaud and Nethmi Illamperuma for their help with data collection.

1 Abstract

2 Humans can quickly generate eye and hand responses to unpredictable changes in the
3 environment. Here, we investigated eye-hand coordination in a rapid interception task where
4 human participants used a virtual paddle to intercept a moving target. The target moved vertically
5 down a computer screen and could suddenly ‘jump’ to the left or right. In high-certainty blocks,
6 the target always jumped, and in low-certainty blocks, the target only jumped in a portion of trials.
7 Further, we manipulated response urgency by varying the time of target jumps, with early jumps
8 requiring less urgent and late jumps requiring more urgent responses. Our results highlighted
9 differential effects of certainty and urgency on eye-hand coordination. Participants initiated both
10 eye and hand responses earlier for high-certainty compared to low-certainty blocks. Hand reaction
11 times decreased and response vigor increased with increasing urgency levels. However, eye
12 reaction times were lowest for medium-urgency levels and eye vigor was unaffected by urgency.
13 Across all trials, we found a weak positive correlation between eye and hand responses. Taken
14 together, these results suggest that the limb and oculomotor systems use similar early
15 sensorimotor processing; however, rapid responses are modulated differentially to attain system-
16 specific sensorimotor goals.

17

18

19 Keywords: interception, eye-hand coordination, reaction time, vigor

20

21 Introduction

22 The ability to interact with moving objects in dynamic and unpredictable environments requires
23 complex coordination between the eyes and hands. In a game of table tennis, players track the
24 rapidly moving ball with their eyes and predict the ball's trajectory after it hits the table to
25 successfully intercept it. In such dynamic tasks, eye and hand movement control is shaped by
26 how certain the available sensory information is and how urgent the motor response has to be
27 executed. For example, there can be uncertainty in the direction the ball will travel following the
28 initial bounce on the table (i.e., if the opponent puts a spin on the ball). There can also be variability
29 in urgency as the opponent can hit the ball further or nearer to the player requiring less or more
30 urgent responses, respectively. Thus, goal-directed responses often require rapid updating of
31 visual and proprioceptive feedback to ensure successful motor actions.

32 In everyday action tasks, eye and hand movements have been shown to be coordinated
33 in stereotypical ways (Land, 2006). In stationary reaching, eye movements typically lead hand
34 movements, fixating on key landmarks and objects before they are manipulated (de Brouwer et
35 al., 2021; Johansson et al., 2001). This relationship is more complex when interacting with moving
36 targets. Intercepting a moving target involves predicting where the target will be at future states
37 (Bosco et al., 2015; Fooken et al., 2021; Zago et al., 2010). This prediction is crucial to overcome
38 the delays in our sensorimotor system (Brenner & Smeets, 2018; Todorov & Jordan, 2002; Zago
39 et al., 2009). During interception tasks, maintaining gaze on the moving target (via smooth pursuit
40 eye movements) allows continuous updating of the target's trajectory that can aid motion
41 prediction (Spering et al., 2011) and manual interception performance (Fooken et al., 2016;
42 Goettker et al., 2019; Kreyenmeier et al., 2022; Mrotek, 2013; Mrotek & Soechting, 2007).
43 However, eye movement behaviour is also affected by the predictability of the moving object's
44 path and visual certainty. In situations of high uncertainty, such as when the moving target
45 bounces or is occluded, observers shift their gaze away from the moving object to the anticipated
46 interception locations (de la Malla et al., 2019; Diaz et al., 2013; Fooken & Spering, 2019; Mann
47 et al., 2019). Thus, the coordination between eye and hand movements can be modulated by
48 visuomotor task demands.

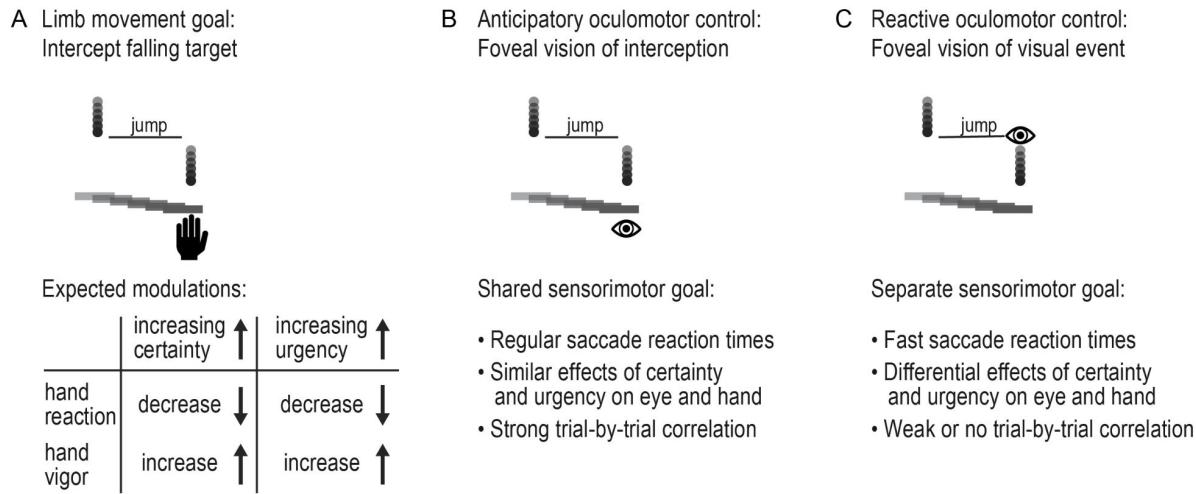
49 Whereas a close coordination between eye and hand movements has been observed in
50 action tasks, such as object manipulation or manual interception, the link between eye and hand
51 movement control in tasks requiring rapid visuomotor responses is less clear. Previous research
52 has shown that humans are able to elicit very rapid motor responses to sudden visual stimuli —a

53 phenomenon referred to as express visuomotor responses or stimulus locked responses (Corneil
54 et al., 2008). Express visuomotor responses have been found in the generation of saccadic eye
55 movements (Dorris et al., 1997) as well as in the upper limb responses following visual target
56 appearance (Pruszynski et al., 2010). For upper limb responses, it has been shown that high
57 certainty about a forthcoming perturbation and temporal predictability of perturbation onset
58 evokes reliable and rapid muscle responses (Contemori et al., 2021; Kozak et al., 2020). Early
59 waves of upper limb muscle responses are also modulated by the level of response urgency, with
60 movement corrections occurring earlier relative to the moment of perturbation when the time
61 available to make a response is limited (Crévécoeur et al., 2013; Maurus et al., 2023; Poscente
62 et al., 2021). The response modulation by both jump certainty and urgency suggests an influence
63 of top-down control on express visuomotor responses, despite previous work highlighting their
64 reactive nature (Corneil & Munoz, 2014).

65 Here, we examined eye and hand responses to visual perturbations during a rapid
66 interception task. Participants used a virtual paddle to intercept a target moving down a vertically-
67 oriented computer screen. In the majority of trials, the moving target was visually perturbed
68 ('jumped'), suddenly shifting spatial location to the left or right and continuing moving down after
69 the jump. To examine the effect of jump certainty, we modified the frequency at which the target
70 jumped. In the high-certainty condition, the target jumped to the left or right of the midline in 100%
71 of trials. In the low-certainty condition, the target jumped in 60% of the trials and continued to
72 move straight down the midline in 40% of trials (no-jump trials). We further examined the effect of
73 response urgency, by varying the onset of jumps across all trials. Early jumps required a low level
74 of urgency (responses within 450 ms), middle jumps required a medium level of urgency
75 (responses within 350 ms), and late jumps required a high level of urgency (responses within 250
76 ms).

77 Using this paradigm, we had two expectations of how jump certainty and response
78 urgency would affect hand responses (Fig. 1A). First, we hypothesized that high-certainty blocks
79 would be associated with earlier (lower reaction time) and faster (higher vigor) hand responses
80 compared to low-certainty blocks. Second, we hypothesized that as the response urgency
81 increased, hand responses would be initiated earlier (lower reaction time) and with greater vigor.
82 However, the goal of the oculomotor system is less clear (Fig. 1B). An anticipatory saccade to the
83 location of interception could provide foveal vision to guide contact between the paddle and the
84 target (Fooken et al., 2021). In this case, we would predict 'regular' saccade latencies of ~200 ms
85 (Carpenter & Williams, 1995), and similar modulations of eye reaction times and vigor as

86 observed in hand responses for varying levels of certainty and urgency. Moreover, eye and hand
87 responses would be strongly correlated on a trial-by-trial basis (Fig. 1B). Alternatively, eye
88 responses in this task could be reactive. In this case, we would predict eye responses with similar
89 latencies to express saccades (Fischer & Ramsperger, 1984; Paré & Munoz, 1996). Moreover,
90 we would expect a differential modulation of eye and hand responses by jump certainty and
91 response urgency, and only a weak or no correlation between eye and hand responses (Fig. 1C).
92



93
94 **Figure 1.** Effects of jump certainty and response urgency on eye and hand responses. (A) Hand
95 movements generated to intercept a falling target are expected to be earlier and faster in high-certainty and
96 more urgent trials. (B) The oculomotor system may share the sensorimotor goal of the upper limb motor
97 system (anticipatory control for interception), in which case the effects of jump certainty and response
98 urgency will be similar. (C) Alternatively, the oculomotor system's goal may be to detect the visual event
99 (reactive control), in which case eye movements will be differentially affected by changes in jump certainty
100 and response urgency.
101

102 Methods

103 Participants

104 A total of 14 healthy individuals (12 right-handed; 11 females; mean age: 26.5 years; age range:
105 18-44 years) participated in the experiment. All participants had no self-reported neurological and
106 musculoskeletal impairments and normal or corrected-to-normal vision. The study was approved
107 by the Queen's University Health Sciences & Affiliated Teaching Hospitals Research Ethics Board

108 (TRAQ #: 6003707) and adheres with the Declaration of Helsinki. Participants gave written
109 informed consent and were compensated with a small honorarium (\$10 CAD).

110 Apparatus

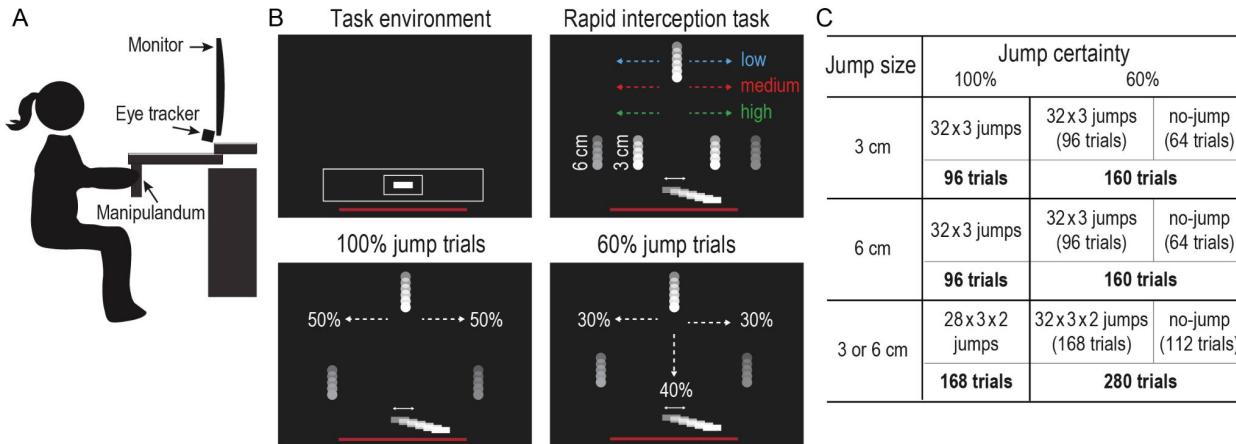
111 Experiments were conducted using the Kinarm Endpoint robot (Kinarm™, Kingston, ON,
112 Canada). Participants were seated in a chair supporting their backs, and used one hand to grasp
113 the handle of the robotic manipulandum, which allowed movement along the horizontal plane.
114 Movements made by the participant were tracked by the manipulandum and presented as a
115 cursor on a 32 *inch* vertical display placed 37 *cm* from the participant (Fig. 2A). The mapping
116 between the handle and cursor movement was the same as a standard computer mouse, such
117 that forward and backward movements of the handle moved the cursor up and down, and left and
118 right handle movements moved the cursor left and right. Movements of the handle were recorded
119 at a sampling rate of 1000 *Hz*. The inherent visual display delay was accounted for using the
120 latency reported by the graphics card in the robot computer and the calculated refreshing latency
121 (~50 *ms*). The position of the participants' right eye was recorded using a video-based eye tracker
122 (Eyelink, SR Research, Ltd., Kanata, ON, Canada) with a sampling rate of 500 *Hz*. A combined
123 chin and forehead rest minimized head movements during the experiment.

124 Experimental Protocol

125 We modified a previously established interception task to assess the coordination between eye
126 and hand responses (Park et al., 2023). Figure 2B illustrates the rapid interception task, in which
127 participants intercepted a target moving down a vertical screen with a virtual paddle (white
128 rectangle 2 × 0.5 *cm* or 3 × 0.8 *deg*) representing the position of the hand. At the beginning of
129 each trial, participants were shown the task environment, which consisted of the workspace
130 represented by a white box (Workspace, 28 × 3.5 *cm* or 37.1 × 5.4 *deg*) indicating the allowed
131 area of movement. A smaller box (Starting Area, 3.5 × 2 *cm* or 5.4 × 3.1 *deg*) indicated the area
132 that participants had to move their paddle into to begin a trial. A red line representing the bottom
133 limit for intercepting the moving target was displayed to deter individuals from moving below the
134 workspace. After holding the paddle in the starting area for 200 *ms*, the task environment
135 disappeared, and a target (white circle with a radius 0.5 *cm* or 0.8 *deg*) appeared at the top of the
136 screen (22 *cm* or 30.7 *deg* from the centre of the starting area). The target then immediately
137 started to move down the screen at a speed of 25 *cm/s* or 34 *deg/s*. The target either continued
138 to move straight down or could be visually perturbed to the left or right by a same probability. The

139 onset of perturbation was randomized at three different distances from the centre of the starting
140 area (11.25 cm or 16.9 deg , 8.75 cm or 13.3 deg , or 6.25 cm or 9.6 deg). After the perturbation,
141 the target continued to move straight down. Participants had to intercept the target before it
142 reached the bottom of the workspace. They were able to intercept the target with any part of the
143 paddle and in any direction. In case participants left the workspace that was shown at the
144 beginning of the trial (the large white box), the robot applied a step force in the opposite direction
145 of their hand movement in order to push their hand back into the box. On successful interceptions,
146 haptic feedback was applied to the participant's hand via the robotic manipulandum to indicate
147 success. Subsequent trials began 500 ms after the target was intercepted or missed.

148 To investigate the relationship between eye and hand movements, we manipulated jump
149 certainty and response urgency. We examined certainty by having two groups of blocks of either
150 high-certainty conditions (target jumped in 100% of the trials) or low-certainty (target jumped in
151 60%). We probed response urgency by varying the onset of visual perturbation. The target was
152 perturbed at three different locations from the top of the workspace, requiring more urgent
153 responses for later target jumps. The highest jump position was 11.25 cm (16.9 deg) above the
154 Starting Area (low-urgency; $\sim 450\text{ ms}$ to respond), the middle jump position was 8.75 cm (13.3 deg)
155 above the Starting Area (medium-urgency; $\sim 350\text{ ms}$ to respond), and the lowest jump
156 position was 6.25 cm (9.6 deg) away (high-urgency; $\sim 250\text{ ms}$ to respond). Response urgency
157 (i.e., jump onset position) was randomized at equal probability across all trials. Further, we
158 examined the magnitude of motor responses by varying the size of the jump (3 cm or 4.6 deg , 6 cm or
159 9.2 deg , or both 3 and 6 cm with equal probability). The size of the jump was varied in three
160 separate blocks and for each jump size, we tested both high and low-certainty, resulting in six
161 total blocks (Fig. 2C). Within each certainty condition, the order of blocks with different jump sizes
162 was randomized. Participants completed either three high-certainty blocks, then three low-
163 certainty blocks, or three low-certainty blocks and three high-certainty blocks. There were 960
164 trials in total, which took participants ~ 1 hour to complete, including the breaks.



165

166 **Figure 2.** Experimental setup and conditions. (A) Participants moved the handle of a robotic manipulandum
167 in the horizontal plane to intercept moving targets viewed on a vertical screen. (B) Each trial started by
168 showing the task environment (top left). The response urgency was manipulated by changing the position
169 at which the target jumped (top right). The target could jump 3 cm, 6 cm, or both within a block. In the high-
170 certainty condition (100% jump trials; lower left), the target moved down the midline before it randomly
171 jumped to the left or right side (lower left). In the low-certainty condition, the target could continue to move
172 down the midline (no-jump) in 40% of the trials (lower right). (C) Participants performed 32 or 28
173 interceptions for each urgency level in different blocks of jump certainty and jump size combinations.

174

175 Eye and Hand movement analysis

176 Eye and hand movement data were analyzed offline using custom-made codes in MATLAB
177 R2021a (Mathworks Inc. Natick MA, USA). The x and y positions of the center of the robotic
178 handle were used for hand movement analysis. The position of the handle was filtered using a
179 third order, zero-phase lag, 20 Hz Butterworth filter. We analyzed horizontal and vertical
180 interception position, defined as the x and y position of the robotic handle at the time the target
181 first contacted any part of the paddle. We further analyzed hand movement reaction time and
182 vigor. Hand movement reaction time was defined as the difference from the time the visual target
183 jumped to the time of hand movement onset, with hand movement onset being the first moment
184 in time at which the hand velocity was greater than 8% of the peak hand velocity in the current
185 reach. Hand movement vigor was calculated similar to movement vigor previously reported in the
186 literature (Reppert et al., 2015). In each trial, we defined the hand movement amplitude as the
187 absolute furthest distance the hand travelled between the time of target movement onset and the
188 time of target interception, or the time the target left the interception zone in target-miss trials. We

189 then fitted a hyperbolic function for each participant n to capture the relationship between
190 movement peak velocity v_n and amplitude x

191

$$v_n = \alpha_n \left(1 - \frac{1}{1 + \beta_n x}\right) \quad (1).$$

192 This fit yielded participant-specific parameters of α_n and β_n that were used to calculate the
193 expected movement velocity v_{fit} given each observed movement amplitude. Vigor was defined
194 as a within-participant measure by comparing the actual movement velocity with the expected
195 movement velocity v_n/v_{fit} . Thus, a vigor value > 1 indicates that a given movement was faster
196 than expected, and a value < 1 indicates that the movement was slower than the average
197 movement for this amplitude.

198 The x and y eye positions of the right eye were sampled in screen-centred coordinates,
199 and position signals were filtered using a second-order 15 Hz Butterworth low pass filter. We
200 analyzed vertical and horizontal eye positions at selected times throughout the task (time of target
201 movement onset, at the time of target jump, and 250 ms after target jump). We further analyzed
202 eye movement accuracy, reaction time, and vigor of the first saccade that occurred at least 50 ms
203 following the target jump. Akin to hand movement measures, reaction time was defined as the
204 difference from the time the visual target jumped to the time of saccade onset. Eye movements
205 were labelled as saccades when five consecutive samples of the filtered eye velocity exceeded a
206 fixed velocity criterion of 30 cm/s. Saccade on- and offsets were labelled as the time that the sign
207 of the acceleration signal reversed either before eye velocity exceeded (saccade onset) or
208 succeeded (saccade offset) the velocity threshold. To determine eye movement vigor, we
209 followed the same procedure as outlined for hand movement vigor. Saccade accuracy was
210 defined as the x and y distance between eye and target position at the time of saccade offset.

211 Statistical Analysis

212 To evaluate the effects of jump certainty and response urgency on hand and eye movement
213 measures, we calculated the median value for each condition and participant. We then used
214 repeated-measures ANOVAs with an alpha level of 0.05. Post hoc comparisons were done using
215 two-sided, paired *t*-tests with Bonferroni correction. Because we did not have an a priori
216 hypothesis of how jump size (3 or 6 cm) would affect selected eye and hand measures, we
217 averaged across jump size unless stated otherwise in the manuscript. Statistical tests were
218 conducted using R (R Core Team, 2022; www.r-project.org).

219 Data exclusion
220 One participant was excluded due to a high number of eye data loss, affecting 47% of their trials.
221 Across the remaining participants' trials, 2034 out of 13440 (15%) were flagged. Trials were
222 flagged if the eye signal was lost (e.g., due to blinks) in the time window from target movement
223 onset to the time of interception (6.5%) or if the participant would move pre-emptively (8.5%). We
224 labelled hand movements as pre-emptive if the participant's reaction time was lower than 120 ms
225 after the target jumped or if they moved to the opposite side of the jump direction.
226

227 Results

228 The goal of this experiment was to investigate the coordination of eye and hand responses when
229 intercepting a rapidly moving target that could jump at a variable time to the left or right. In a given
230 block, the target either jumped with high-certainty (100% jump trials) or low-certainty (60% jump
231 trials). In no-jump trials (40% of all trials in the low-certainty condition), the target continued to
232 travel down the midline, and participants were required to keep the paddle at the centre of the
233 screen to intercept the target successfully. We manipulated response urgency by changing the
234 time at which the target jumped (see Fig. 2B).

235 Patterns of eye and hand movements are similar in jump and no-jump trials

236 The rapid interception task elicited a combination of tracking and saccadic eye movements. The
237 upper panels in Figure 3 show the eye, hand, and target position of a representative high-certainty
238 trial in a screen-centred reference frame (Fig. 3A) and across time (Fig. 3B). Eye, hand, and target
239 velocity of the same trial are also shown across time (Fig. 3C). In this trial, the participant looked
240 at the centre of the screen and 'waited' for the target to move down the midline. The participant
241 briefly tracked the target with smooth pursuit eye movements before initiating a reactive saccade
242 towards the target after it jumped to the right.

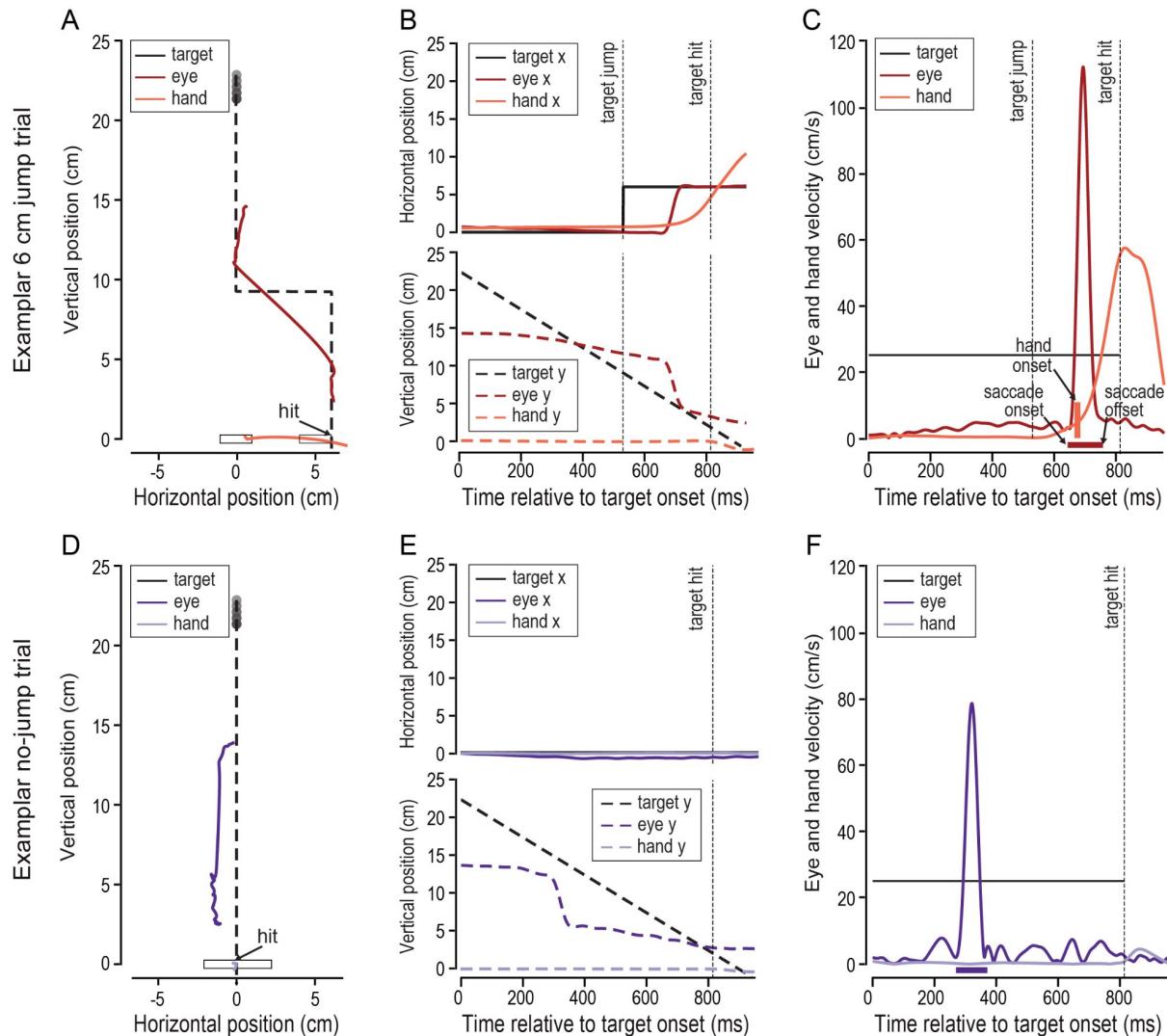
243 The lower panels in Figure 3 show the eye, hand, and target position of a representative
244 low-certainty trial—in which the target did not jump—in a screen-centred reference frame (Fig.
245 3D) and across time (Fig. 3E). Eye, hand, and the target velocity of the same trial are also shown
246 across time (Fig. 3F). Similar to the perturbation trial, the participant looked at the centre of the
247 screen at the beginning of the trial. The participant tracked the target with smooth pursuit and a
248 catch-up saccade until it was intercepted by keeping the paddle on the midline.

249 Across all trials and participants, and in both certainty conditions (including jump and no-
250 jump trials), we found a consistent pattern of eye movements. In the time window from target
251 movement onset to the time of target jump or target interception for no-jump trials, participants
252 made no saccades in 42% of the trials, made a single saccade in 47% of the trials, and elicited
253 more than one saccade in 11% of the trials. Eye velocity in the same time window was on average
254 $7.58 \pm 0.97 \text{ cm/s}$ (mean eye velocity and standard error across participants), which was much
255 lower than the target velocity of 25 cm/s , indicating that participants did not smoothly pursue the
256 moving target prior to target jump. Following a target jump (in the jump trials), participants initiated
257 a reactive saccade in 93% of all trials. Of note, in a majority of these trials (96%) participants did
258 not make another saccade before they intercepted the moving target. The described eye
259 movement patterns show that whereas eye movements prior to target jump were quite variable
260 (short periods of pursuit, catch-up saccades, or fixation), a single reactive saccade was elicited
261 following target jump in almost every trial.

262

263 Eye movement position is modulated by the response urgency

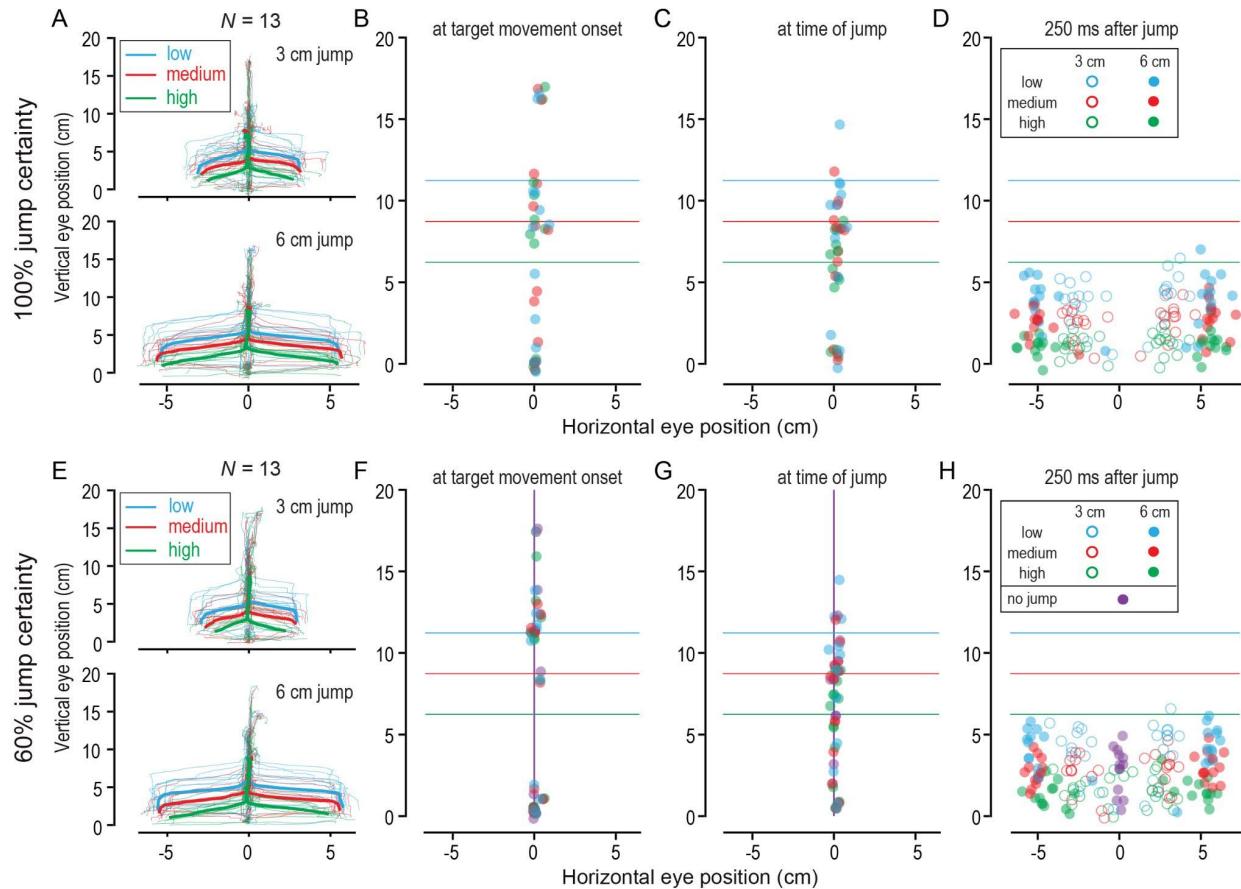
264 Figure 4 illustrates the overall gaze pattern observed in our experiment. Figure 4A shows the
265 gaze position (from target movement onset to target interception) of all participants (thin lines) in
266 screen-centred coordinates averaged across high-certainty 3 cm (top) and 6 cm (bottom) jump
267 trials, respectively. The gaze position averaged across participants at different urgency levels is
268 indicated by thick blue (low-urgency), red (medium-urgency), and green (high-urgency) lines.
269 Figure 4E shows the corresponding screen-centred gaze position in low-certainty trials. To further
270 describe the observed gaze pattern, we compared participants' eye position at three distinct time
271 points: (1) at the time of target movement onset (Fig. 4B, F), (2) at the time of target jump (Fig.
272 4C, G), and (3) 250 ms after the time of jump (Fig. 4D, H). We chose 250 ms to allow sufficient
273 time for saccades to land following the target jump.



274

275 **Figure 3.** Eye and hand movement responses in the rapid interception task. (A) Eye (dark red), hand (light
276 red), and target (black) position in screen-centred coordinates in a representative jump trial. (B) Horizontal
277 eye, hand, and target position (top panel) and vertical eye, hand, and target position (bottom panel) across
278 time. The time of target jump and target interception are indicated by dashed vertical lines. (C) Eye, hand,
279 and target velocity across time. Saccade onset and offset of the targeting saccade following the target jump
280 are indicated by arrows and the thick horizontal bar. Hand movement onset is indicated by the thick vertical
281 bar. (D) Eye (dark purple), hand (light purple), and target (black) position in screen-centred coordinates in
282 a representative no-jump trial. (E) Horizontal eye, hand, and target position (top panel) and vertical eye,
283 hand, and target position (bottom panel) across time. The time of the target interception is indicated by the
284 dashed vertical line. (F) Eye, hand, and target velocity across time.

285



286

287 **Figure 4. Eye responses in rapid interception task.** (A) Gaze position in 100% certainty trials averaged
288 across low (blue), medium (red), and high (green) urgency trials of each participant (thin lines) and
289 averaged across the group (thick lines) separately plotted for the 3 cm (top) and 6 cm (bottom) target jump
290 size conditions. (B-D) The average 2D eye position is shown for each participant and each urgency level
291 at the time of the target movement onset (B), the time of the target jump (C), and 250 ms after the target
292 jump (D). (E-H) Corresponding plots for the 60% jump certainty condition. Eye positions in no-jump trials
293 are indicated in purple.

294

295 We first compared the effect of certainty (high vs. low) and urgency (low, medium, high)
296 on vertical eye position at the three selected time points using a repeated-measures 2x3 ANOVA.
297 We found no effect of certainty, urgency, and no interaction on vertical eye position at the time of
298 target movement onset ($F < 1.7$; $p > 0.2$; $\eta^2 < 0.13$). We also found no effect of certainty and no
299 interaction on vertical eye position at the time of the target jump ($F < 0.7$; $p > 0.5$; $\eta^2 < 0.06$). We
300 found an effect of urgency on vertical eye position at the time of target jump ($F_{2,24} = 20.72$; $p <$
301 0.001 ; $\eta^2 = 0.63$). Finally, we did not find an effect of jump certainty ($F < 1.5$; $p > 0.2$; $\eta^2 < 0.12$) on
302 vertical eye position 250 ms after target jump, but a significant effect of urgency ($F_{2,24} = 91.82$; p

303 < 0.001; $\eta = 0.88$) and a significant interaction between jump certainty and response urgency
304 ($F_{2,24} = 6.52$; $p = 0.005$; $\eta = 0.35$). Taken together, these results indicate that vertical eye position
305 was significantly affected by target jump times with vertical eye position being lower as the
306 urgency level increased. Vertical eye position was not affected by jump certainty. As illustrated
307 by each participant's gaze position (Figs. 4A, E), the between-participants variability was high at
308 target movement onset (~6 cm), but participants converged to similar vertical gaze positions
309 following the target jump.

310 Horizontal gaze positions were near the midline until after the target jumped (Figs. 4 B-C,
311 F-G), and horizontal gaze remained at the midline during trials where the target did not jump
312 (purple dots in Figs. 4 F-H). Following the target jump, the horizontal eye position scaled with the
313 size of the target jump, landing on average 2.65 ± 0.16 cm away from the midline in 3 cm jump
314 trials and 5.29 ± 0.09 cm away from the midline in 6 cm jump trials.

315 Finally, we investigated the accuracy of the first saccade that occurred after target jump.
316 Whereas horizontal saccade accuracy was unaffected by jump certainty and response urgency,
317 vertical saccade accuracy was affected by jump certainty ($F_{1,12} = 4.85$; $p = 0.048$; $\eta = 0.29$) and
318 response urgency ($F_{2,24} = 123.92$; $p < 0.001$; $\eta = 0.91$). Post hoc comparison showed that
319 participants were on average very accurate in high-certainty blocks (vertical saccade error: -
320 0.08 ± 0.32 cm), but tended to land above, or behind, the actual target position in low-certainty
321 blocks (vertical saccade error: 0.27 ± 0.32 cm). Moreover, saccades were most accurate in
322 medium-urgency trials (vertical saccade error: 0.05 ± 0.19 cm). In low-urgency trials, saccades
323 tended to land below, or ahead, of the moving target position (vertical saccade error: -0.94 ± 0.26
324 cm), and in high-urgency trials saccades tended to land above, or behind, the moving target
325 position (vertical saccade error: 1.19 ± 0.16 cm).

326 Interception accuracy decreases with uncertainty and increasing urgency
327 Figure 5 illustrates the overall hand movements observed in our experiment. Figures 5A and B
328 show the horizontal hand position (upper panels) and absolute hand velocity (lower panels) during
329 high-certainty 6 cm jump trials for an exemplar participant and the average of all participants,
330 respectively. The corresponding plots of the horizontal hand position and velocity during 6 cm
331 low-certainty trials are shown in Figures 5 D and E. In these plots, hand movements are averaged
332 across different levels of urgency as indicated by colour. Because the moving target could be
333 intercepted with any part of the paddle, there is a 4 cm wide region and a limited time window to
334 intercept the falling target successfully (see grey-shaded regions and horizontal, coloured lines in

335 panels of Fig. 5A-B, D-E). We found that the onset of participants' hand responses scaled with
336 response urgency.

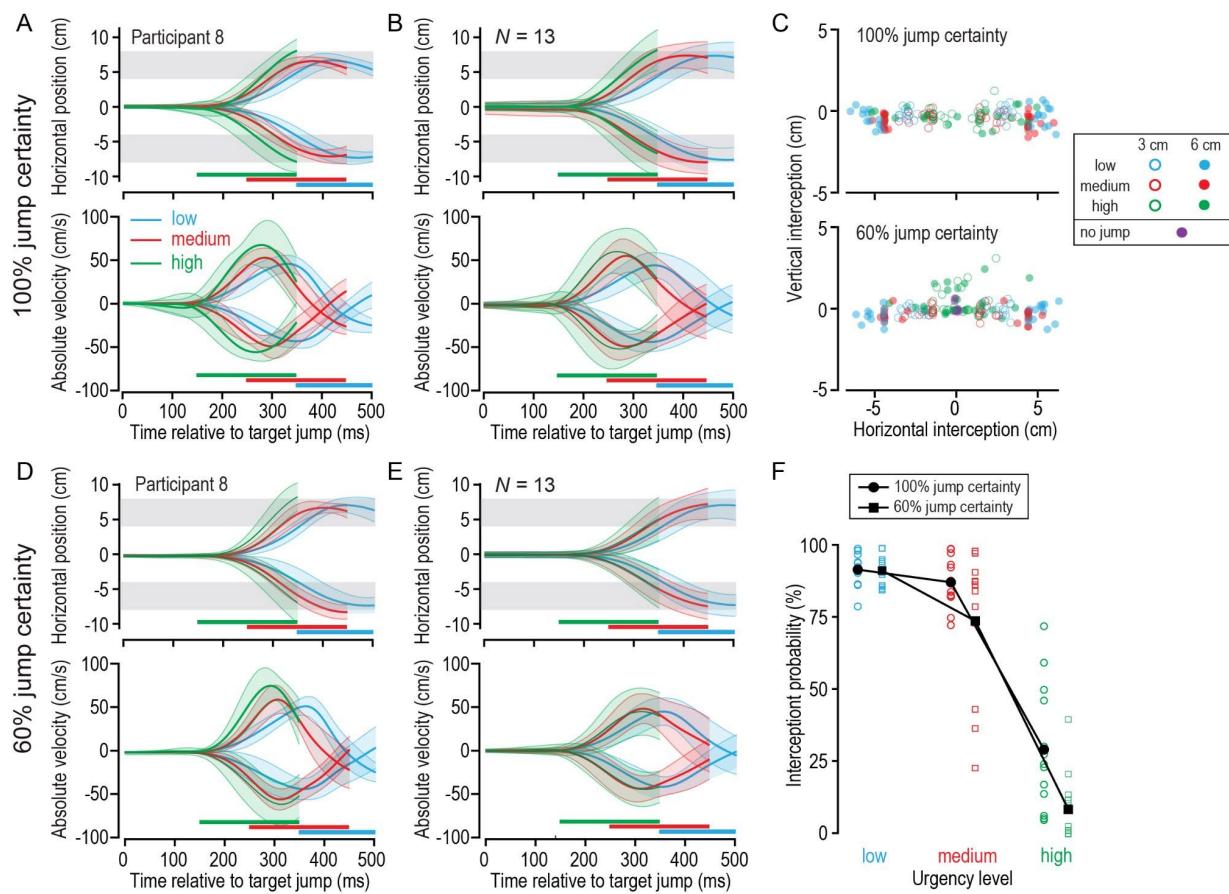
337 To compare performance across conditions, we analyzed hand position at the time of the
338 target interception and the probability of successfully intercepting the falling target across
339 conditions. Figure 5C shows for each certainty condition, urgency level, and jump size, the
340 average screen-centred hand position at the time of the target interception or when the missed
341 target left the screen. Overall, hand movement scaled with the size of the jump, and participants
342 intercepted the target on average 2.02 ± 0.10 cm away from the midline in 3 cm jump trials and
343 3.95 ± 0.15 cm away from the midline in 6 cm jump trials. The fact that participants undershot the
344 actual target position indicates that they tended to contact the falling target with the outer side of
345 the paddle.

346 We used a repeated-measures 2x3 ANOVA to quantify the effect of certainty and urgency
347 on horizontal interception position. We found an effect of jump certainty ($F_{1,12} = 30.55$; $p < 0.001$;
348 $\eta^2 = 0.72$), response urgency ($F_{2,24} = 193.09$; $p < 0.001$; $\eta^2 = 0.94$), and a significant interaction ($F_{2,24}$
349 = 4.18; $p = 0.028$; $\eta^2 = 0.26$). The strong effect of response urgency on horizontal interception
350 position reflects the shorter time available for intercepting the perturbed target (see Figs. 5 A-B,
351 D-E). Participants intercepted the target with the centre of the paddle in low-urgency trials, but
352 intercepted the target with the outer edge of the paddle in medium and high-urgency trials. On
353 average, participants tended to move the paddle slightly downwards to intercept the falling object
354 (vertical interception position: -0.27 ± 0.06 cm). Interestingly, we observed that in the low-certainty
355 and high-urgency conditions, participants tended to move the paddle upwards (vertical
356 interception position: 0.34 ± 0.22 cm), as if they expected the target to stay in the middle (see green
357 dots above the centre in the lower panel of Fig. 5C).

358 Figure 5F shows the averaged probability of intercepting the falling target across task
359 conditions. Individual colour-coded symbols represent the median response value of each
360 participant, and larger black-coloured symbols (connected by black lines) represent the group
361 means. We found an effect of jump certainty ($F_{1,12} = 24.27$; $p < 0.001$; $\eta^2 = 0.67$), response urgency
362 ($F_{2,24} = 194.12$; $p < 0.001$; $\eta^2 = 0.94$), and a significant interaction effect ($F_{2,24} = 5.73$; $p = 0.009$; η^2
363 = 0.32). Whereas participants successfully intercepted a majority of targets in low-urgency trials
364 (high-certainty: $91.7 \pm 1.5\%$; low-certainty: $91.4 \pm 1.4\%$) and medium-urgency trials (high-certainty:
365 $87.3 \pm 2.4\%$; low-certainty: $73.9 \pm 6.7\%$), they only intercepted about a third of targets in high-

366 certainty, high-urgency trials ($29.2 \pm 6.0\%$) and only a few targets in low-certainty, high-urgency
367 trials ($8.5 \pm 3.2\%$).

368



369

370 **Figure 5.** Hand responses in the rapid interception task. (A) Horizontal hand position (top) and velocity
371 (bottom) across time for low (blue), medium (red), and high (green) urgency trials shown for an exemplar
372 participant in the high-certainty condition. The grey-shaded areas represent the region in which the
373 paddle could intercept the target. The horizontal coloured bars indicate the time period in which the target
374 had to be intercepted for each urgency level. (B) Corresponding plots averaged across all participants in
375 the high-certainty condition. (C) Hand position at the time of interception or when the missed target left
376 the screen in the high-certainty (top) and low-certainty (bottom) conditions. Open circles indicate 3 cm
377 jump trials and filled circles indicate 6 cm jump trials. Colour denotes urgency level, and purple indicates
378 trials in which the target did not jump. (D-E) Plots of horizontal hand position and velocity across time for
379 an exemplary participant (D) and averaged across all participants (E) in the low-certainty condition. (F)
380 Probability of intercepting the moving target following a target jump in the high-certainty (circles) and low-
381 certainty (squares) jump conditions and across urgency levels.

382 Differential effects of certainty and urgency on eye and hand responses

383 Figure 6 shows the eye and hand reaction times, vigor, and trial-by-trial correlation between eye
384 and hand responses for the two certainty conditions and three urgency levels. To directly compare
385 eye and hand responses, only trials in which a saccade was made (93% of all trials) were included
386 in this analysis. To test the effect of jump certainty and response urgency on eye and hand
387 responses, we used four separate repeated-measures 2x3 ANOVA. Hand responses were on
388 average initiated 188.5 ± 3.4 ms after the target jump. We found an effect of jump certainty ($F_{1,12} = 27.04$; $p < 0.001$; $\eta^2 = 0.69$) and response urgency ($F_{2,24} = 13.86$; $p < 0.001$; $\eta^2 = 0.54$) on hand
389 reaction time, and no significant interaction (Fig. 6A). A post hoc comparison of the two certainty
390 conditions confirmed that participants on average initiated their hand responses 14 ms earlier in
391 the high-certainty blocks compared to the low-certainty blocks ($t(38) = 6.8$; $p_{\text{adjust}} < 0.001$; $d = 1.1$).
392 Compared to low-urgency trials, hand responses were initiated 18 ms earlier in medium-urgency
393 trials ($t(25) = 7.4$; $p_{\text{adjust}} < 0.001$; $d = 1.4$) and 19 ms earlier in high-urgency trials ($t(25) = 4.3$; $p_{\text{adjust}} < 0.001$; $d = 0.8$).
395

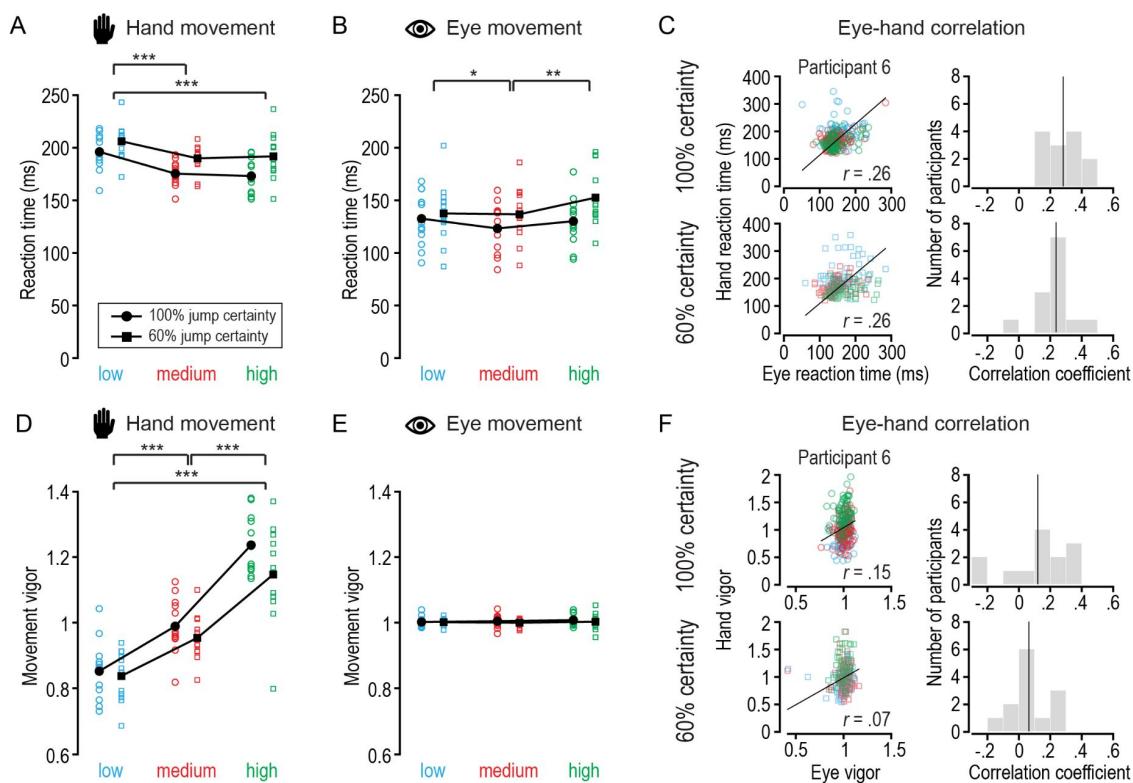
396 Eye movements preceded hand movements by ~50 ms and were on average initiated
397 135.4 ± 6.3 ms after the target jump. We found an effect of jump certainty ($F_{1,12} = 11.72$; $p = 0.005$;
398 $\eta^2 = 0.49$) and response urgency ($F_{2,24} = 5.27$; $p = 0.01$; $\eta^2 = 0.31$) on eye reaction time, and a
399 significant interaction ($F_{2,24} = 13.48$; $p < 0.001$; $\eta^2 = 0.53$; Fig. 6B). Posthoc comparison of the two
400 certainty conditions confirmed that participants on average initiated their eye movements 14 ms
401 earlier in the high-certainty blocks compared to low-certainty blocks ($t(38) = 5.0$; $p_{\text{adjust}} < 0.001$; $d = 0.8$). Compared to medium-urgency trials, eye responses were initiated 5 ms later in low-
402 urgency trials ($t(25) = 2.8$; $p_{\text{adjust}} = 0.03$; $d = 0.6$) and 11 ms later in high-urgency trials ($t(25) = 4.1$;
403 $p = 0.001$; $d = 0.8$). Thus, whereas hand reaction times were systematically faster for high-urgency
404 levels, eye reaction times were differentially affected. On a trial-by-trial level, eye and hand
405 reaction times were on average weakly correlated with a mean correlation of $r = 0.28$ in high-
406 certainty trials and $r = 0.24$ in low-certainty trials (Fig. 6C).
407

408 We found an effect of response urgency ($F_{2,24} = 68.71$; $p < 0.001$; $\eta^2 = 0.85$) on hand vigor
409 and a significant interaction between jump certainty and response urgency ($F_{2,24} = 3.42$; $p = 0.049$;
410 $\eta^2 = 0.22$). However, jump certainty did not systematically affect hand vigor ($F_{1,12} < 2.2$; $p > 0.1$; $\eta^2 < 0.2$; Fig. 6D). Post hoc comparison of different urgency levels confirmed that participants
411 responded more vigorously with increasing urgency. Specifically, hand vigor was greater in
412 medium ($t(25) = 8.7$; $p_{\text{adjust}} < 0.001$; $d = 1.7$) and high-urgency trials compared to low-urgency
413

414 trials ($t(25) = 11.3$; $p_{adjust} < 0.001$; $d = 2.2$), and hand vigor was also greater in high compared to
415 medium-urgency trials ($t(25) = 9.4$; $p_{adjust} < 0.001$; $d = 1.9$).

416 Finally, we found no effect of jump certainty or response urgency on eye vigor (all $F < 5.2$;
417 $p > 0.5$; $\eta^2 < 0.05$; Fig. 6E). On a trial-by-trial level, eye and hand vigor were on average very
418 weakly correlated, with a mean correlation of $r = 0.12$ in high-certainty jump trials and $r = 0.06$ in
419 low-certainty jump trials (Fig. 6F). Thus, whereas hand movements became more vigorous as the
420 urgency level increased, eye vigor was unaffected and not related to the hand response.

421



422
423 **Figure 6.** Eye and hand responses across task conditions. (A) Hand movement reaction times for different
424 task conditions. Single symbols indicate median reaction times for each participant for high-certainty jumps
425 (circles) and low-certainty jumps (squares), and separate for low (blue), medium (red), and high (green)
426 urgency trials. (B) Corresponding eye reaction times. (C) Trial-by-trial correlation between eye and hand
427 responses for high-certainty (top left panel) and low-certainty (bottom left panel) trials for a representative
428 single participant, and histograms of the correlation coefficients of all participants in the high-certainty (top
429 right panel) and low-certainty (bottom right panel) condition. (D-F) Corresponding results for hand and eye
430 vigor.

431 Jump size differentially modulates eye and hand movement reaction times

432 We additionally investigated the effect of block type (constant jump size or mixed jump size) and
433 jump size (3 or 6 cm) on eye and hand reaction times and vigor. Hand reaction time was not
434 affected by block type, but we found an effect of jump size ($F_{1,12} = 5.68; p = 0.03; \eta^2 = 0.32$) and a
435 significant interaction ($F_{1,12} = 13.31; p = 0.003; \eta^2 = 0.53$). Post hoc comparison showed that
436 participants responded on average 7.3 ms earlier to 3 cm jumps compared to 6 cm jumps in the
437 mixed blocks ($t(12) = 7.7; p_{adjust} < 0.001; d = 2.1$), but no difference in hand reaction time was
438 found between 3 cm and 6 cm jump blocks. Eye reaction time was affected by block type ($F_{1,12} =$
439 12.77; $p = 0.004; \eta^2 = 0.52$) and jump size ($F_{1,12} = 43.40; p < 0.001; \eta^2 = 0.78$) with no significant
440 interaction. Specifically, participants initiated eye movements on average 5 ms earlier in blocks
441 with constant jump size compared to mixed jump size, and 13.5 ms earlier in 6 cm compared to
442 3 cm jump trials. These results indicate that eye and hand reaction times were differentially
443 affected, with the hands responding earlier to small target jumps and the eyes responding earlier
444 to large target jumps.

445 Hand vigor was not affected by block type, but we found an effect of jump size ($F_{1,12} =$
446 8.35; $p < 0.001; \eta^2 = 0.87$) and a significant interaction ($F_{1,12} = 23.08; p < 0.001; \eta^2 = 0.87$). Post
447 hoc comparison showed that participants responded more vigorously in 6 cm compared to 3 cm
448 jump trials in the 3 cm and 6 cm blocks ($t = 8.1; p_{adjust} < 0.001; d = 2.2$) and mixed jump size blocks
449 ($t = 8.9; p_{adjust} < 0.001; d = 2.5$). Eye vigor was not affected by block type but by jump size ($F_{1,12} =$
450 13..36; $p < 0.003; \eta^2 = 0.53$), with participants responding more vigorously in 6 cm compared to 3
451 cm jump trials. There was no significant interaction. These results indicate that the strength of the
452 response (i.e., the vigor) was affected similarly for the eye and hand movement system.
453

454 Discussion

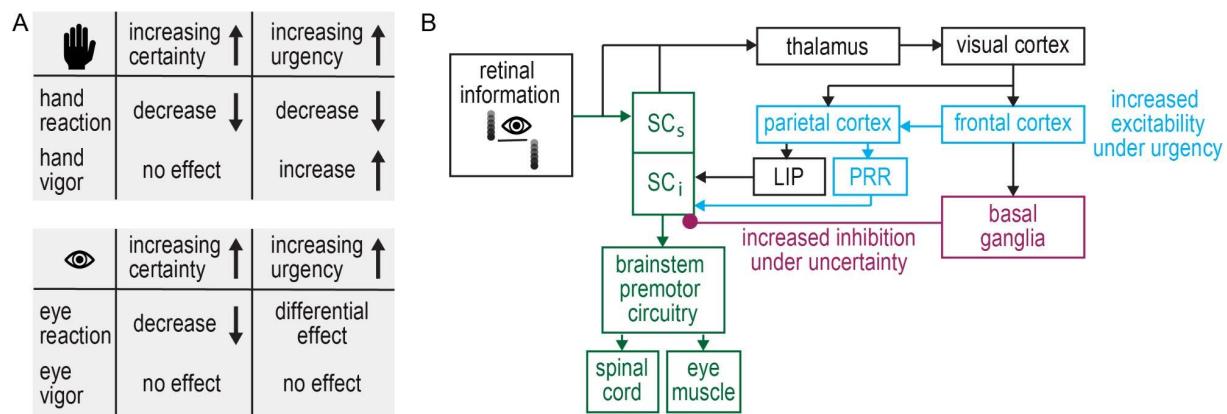
455 In this study, we investigated the coordination of eye and hand responses during a rapid
456 interception task. We found that eye and hand responses were differentially affected by various
457 levels of jump certainty and response urgency (Fig. 7A). Low-certainty conditions caused a delay
458 in both eye and hand reaction times compared to high-certainty conditions. However, high-
459 urgency conditions systematically led to earlier and more vigorous hand responses, while eye
460 responses were largely unaffected by changes in response urgency.

461 Eye-hand coordination depends on task demands

462 Goal-directed actions in natural environments require an integration of bottom-up sensory
463 information and top-down cognitive goals (Fooken et al., 2023; Scott, 2016). Past research has
464 shown that when reaching towards and manipulating stationary objects, eye and hand
465 movements are highly coordinated in space and time (de Brouwer et al., 2021). When reaching
466 to stationary visual targets, eye and hand reaction times are generally moderately correlated (Fisk
467 & Goodale, 1985; Prablanc et al., 1979)). Interestingly, the correlation between eye and hand
468 reaction time is weaker when the visual stimulus elicits rapid eye responses, such as in the gap
469 paradigm, in which the initial fixation target is extinguished before the saccade target appears
470 (Saslow, 1967). Moreover, the correlation between eye and hand responses is stronger when the
471 task requires a cognitive component, such as memory-guided movements or movements to the
472 opposite side of the cued target (Gribble et al., 2002; Sailer et al., 2000). The rapid interception
473 task used in this study elicited rapid eye and hand responses to visual perturbations. Similar to
474 stationary reaching, we found that rapid eye and hand responses to intercept a perturbed moving
475 target were only weakly correlated ($r \approx 0.25$). Taken together, these results indicate that
476 correlation between eye and hand movements depends on the visual information available and
477 the cognitive task demands (Frens & Erkelens, 1991).

478 When intercepting or manually tracking moving objects, observers naturally keep their
479 eyes on the target until they hit or catch it (Cesqui et al., 2015; Coudiere & Danion, 2024; Mrotek
480 & Soechting, 2007). To compensate for high target speeds, the eyes typically track moving objects
481 with a combination of smooth pursuit and saccadic eye movements (Binaee & Diaz, 2019; Fooken
482 et al., 2016; Goettker, Brenner, et al., 2019). In interception tasks that involve distinct visual
483 predictions, such as a target bounce or spatially restricted interception zones, observers make
484 anticipatory saccades to the future target location (Diaz et al., 2013; Fooken & Spering, 2020;
485 Land & McLeod, 2000; Mann et al., 2019). Whereas better object tracking is correlated with higher
486 interception accuracy when target motion is unpredictable and uncertain, eye-hand coordination
487 is more flexible in situations of high motion predictability and visual certainty (Fooken et al., 2021).
488 In our study, we found that participants did not reliably track the moving target prior to the target
489 jump (Fig. 4). Eye position between the time of target movement onset and the time of target jump
490 varied extensively between participants, and the average eye velocity in the same time window
491 was well below target velocity. These results indicate that participants did not attempt to keep
492 their eyes on the moving target, but instead kept their eyes relatively still to detect the target jump.

493 These results support the hypothesis that the oculomotor response was driven by the
494 salient sensory event rather than by planning an anticipatory saccade to the future interception
495 location (Fig. 1B-C). Participants initiated saccades towards the location of the jumped target with
496 latencies of ~135 ms, which is slightly slower than human express saccades elicited in the gap
497 paradigm (Fischer & Ramsperger, 1984) but faster than 'regular' visually-driven saccades (Irving
498 et al., 2006). Previous work has shown that saccade reaction times to moving targets depend on
499 the visual features of the target, such as target velocity (Gellman & Carl, 1991; Ron et al., 1989)
500 or target contrast (Goettker, Braun, et al., 2019). Importantly, these saccades are initiated with
501 latencies of at least 170 ms and are able to compensate for target motion during saccade planning
502 and execution (Engel et al., 1999; Etchells et al., 2010; Gellman & Carl, 1991; Goettker et al.,
503 2019; Ron et al., 1989). Here, we found that saccades in response to target jumps landed ahead
504 of the moving target in low-urgency trials and behind the moving target in high-urgency trials.
505 These results indicate that saccades were reactive, with limited time for anticipating the
506 interception location (Findlay, 1983; Robinson, 2022). Interestingly, we found that participants did
507 not make a second saccade to the interception location, even when participants had up to 500
508 ms to intercept following the target jump (low-urgency condition). This finding is in line with
509 previous research showing that participants tend to suppress saccades shortly before intercepting



510
511 **Figure 7.** Summary of results and proposed neural modulations. (A) Effects of jump certainty and response
512 urgency on hand (top) and eye (bottom) reaction time and vigor. (B) Simplified visuomotor circuit,
513 highlighting areas involved in rapid responses. Retinal information is directly projected to the superficial
514 layers of the superior colliculus (SC_s) and transferred to the intermediate layers (SC_i) that are involved in
515 limb- and oculomotor control (Green). Retinal information also travels through the thalamus to the visual
516 cortex and higher cortical areas. The parietal reach region (PRR) and the lateral intraparietal area (LIP)
517 may drive signals to generate limb and eye responses in parallel.

518 moving objects (Goettker et al., 2019; Mrotek & Soechting, 2007). Overall, our results
519 demonstrate that eye and hand responses are generally coordinated—but not necessarily
520 correlated—to accomplish rapid goal-directed interceptions.

521 Rapid visuomotor responses depend on target predictability

522 When reaching to or looking at visual targets, humans are able to quickly react to sudden changes
523 in the target position, a phenomenon that has been termed express visuomotor or stimulus-locked
524 responses (Goonetilleke et al., 2015; Gu et al., 2016; Pruszynski et al., 2010; Wood et al., 2015).
525 These fast orienting responses can be behaviourally measured across different movement
526 systems, including the oculomotor and limb motor system. Previous work has shown that humans
527 reliably elicit express visuomotor responses when intercepting a vertically moving target that is
528 displaced behind an occluder (Kozak et al., 2020), and that these responses depend on temporal
529 predictability (Contemori et al., 2021; Jakobs et al., 2009). Here, we use a similar experimental
530 paradigm to investigate coordinated eye and hand responses to moving targets. We found that
531 both eye and hand responses following the target jump were initiated earlier in trials in which a
532 target perturbation was highly predictable (high-certainty blocks). Although the possible timings
533 of the perturbation did not change across the experiment, participants had to inhibit a movement
534 in 40% of the low-certainty blocks. These results suggest that participants' state of response
535 readiness was reduced in the low-certainty condition, similar to an observed decrease in eye
536 reaction time when catch trials are included in the gap paradigm (Kingstone & Klein, 1993; Paré
537 & Munoz, 1996). Response readiness is also increased when targets rapidly move to a new
538 location rather than being instantaneously displaced from one location to another (Rescheczkko
539 et al., 2023), indicating that continuous motion prediction is important for rapid visuomotor
540 responses.

541 In dynamic environments, humans are able to rapidly integrate contextual information to
542 generate motor corrections (Kalidindi & Crévécoeur, 2023). The onset and strength of express
543 visuomotor responses following visual perturbations depend not only on visual target features,
544 such as stimulus luminance, orientation, or spatial frequency (Kozak et al., 2019; Marino et al.,
545 2012; Veerman et al., 2008), but also on the behavioural context, such as target shape, texture,
546 colour, or contextual cues (Contemori et al., 2022; Cross et al., 2019; Dimitriou et al., 2013;
547 Veerman et al., 2008). Moreover, following mechanical perturbations, muscle responses and
548 movement kinematics scale with the time available to respond (Crévécoeur et al., 2013; Poscente
549 et al., 2021). Similarly, we found that hand responses were initiated earlier and more vigorously

550 with increasing urgency, in their respective certainty conditions. The fact that we did not
551 manipulate visual features at the time of perturbation suggests that hand response modulations
552 across urgency levels were driven by the behavioural rather than visual context.

553 In contrast to the systematic effect of urgency on hand responses, we found that eye
554 reaction time was lowest for medium compared to low and high-urgency trials, and that eye vigor
555 was generally unaffected. Previous research has shown that saccade vigor is indicative of the
556 subjective and economic value of visual targets in value-based decision-making tasks (Korbisch
557 et al., 2022; Reppert et al., 2015; Shadmehr et al., 2019; Yoon et al., 2020). Moreover, saccade
558 vigor is increased when observers have to make a perceptual decision about a moving target in
559 a manual interception task (Barany et al., 2020). Perceptual decisions in urgent visuomotor tasks
560 requiring saccade choices between two possible target locations have been shown to occur after
561 an initial sensorimotor processing time of 90-180 ms (Salinas et al., 2019; Seideman et al., 2018;
562 Stanford et al., 2010; Stanford & Salinas, 2021). Taken together, our results suggest that eye
563 vigor is indicative of perceptual decisions and might be computed after an initial bottom-up
564 sensory processing period.

565 Neural mechanisms underlying rapid visuomotor responses

566 To successfully respond to a visual or mechanical perturbation within a few hundred milliseconds,
567 the brain must rapidly transform visual input into motor output, a process that has been shown to
568 involve subcortical circuits. In both the oculomotor and limb motor systems, the superior colliculus
569 (SC)—a midbrain structure that interfaces sensory and premotor circuits—is involved in
570 generating rapid orienting responses (Boehnke & Munoz, 2008; Cooper & McPeek, 2021; Corneil
571 & Munoz, 2014; Gandhi & Katnani, 2011). In the oculomotor system, it has been shown that
572 reduced activity of fixation-related neurons in the SC is linked to the generation of express
573 saccades in the gap paradigm (Dorris et al., 1997, 2002; Marino et al., 2015; Sparks et al., 2000).
574 In the limb motor system, muscle responses to visual or mechanical perturbations can be detected
575 as early as 90 ms (Corneil et al., 2004; Gu et al., 2016; Pruszynski et al., 2010; Wood et al., 2015),
576 and rapid muscle activity is highly correlated with neural activity in collicular reach cells (Philipp &
577 Hoffmann, 2014; Stuphorn et al., 1999; Werner et al., 1997). Moreover, when intercepting a
578 moving target that abruptly shifts its position, muscle activity of human participants is modulated
579 90-110 ms after the perturbation, indicating that the speed of these rapid responses would likely
580 involve subcortical pathways (Perfiliev et al., 2010). We believe that the rapid visuomotor
581 responses observed in our study involve pathways through the superior colliculus-brainstem loop.

582 Extensive work on visually guided eye movements has highlighted the subcortical
583 mechanisms contributing to saccade generation and suppression (for a review, see Coe & Munoz,
584 2017). We propose that in our task, two factors may modulate eye and hand responses: 1) a
585 reduced inhibition and 2) an increased excitability of the intermediate layers of the SC. Our
586 observation that both eye and hand responses occurred earlier in high-certainty compared to low-
587 certainty blocks suggests a common mechanism modulating visuomotor responses. We
588 speculate that a change in certainty about an upcoming target jump affected inhibitory control
589 from the basal ganglia to the SC (Fig. 7B). Whereas inhibitory mechanisms were upregulated in
590 low-certainty blocks and visuomotor responses had to be withheld in 40% of the trials, inhibition
591 was reduced in high-certainty blocks. This potential regulation of inhibition affected both the
592 oculomotor and limb motor systems similarly.

593 Our observation that eye and hand responses were differentially affected by urgency
594 suggests that shared sensory information is used differently by the oculomotor and limb motor
595 systems. We speculate that increasing urgency led to an increase in excitability along the limb
596 motor pathway, possibly driven by top-down cortical processes (Fig. 7B). Previous work on the
597 neural control of eye-hand coordination has elucidated that both movement systems are
598 controlled by shared early sensory and visuomotor processing areas (Battaglia-Mayer et al., 2003;
599 Crawford et al., 2004; Dean et al., 2012; Hwang et al., 2014; Vesia & Crawford, 2012). More
600 recently, the idea that the oculomotor and limb systems use the same task-specific sensory
601 information, but operate in parallel to attain task goals has been brought forward (Kang et al.,
602 2024). Our results support the idea of a parallel functional organisation of eye-hand coordination
603 stem that relies on shared sensory information but may serve separate behavioural goals (Fig.
604 1).

605 Eye-hand coordination depends on spatiotemporal task constraints
606 When controlling goal-directed actions, the human motor system must compensate for inherent
607 delays that arise from transmitting and processing sensory input through neural pathways. For
608 example, to accurately plan a saccade to a moving target, the oculomotor system has to rely on
609 internal information about the trajectory and duration of the eye movement to compensate for the
610 object motion (Schlag & Schlag-Rey, 2002). When planning a hand movement to a moving target,
611 there is a similar delay of ~100 ms to transform visual information into the limb motor command
612 (Brenner & Smeets, 1997). However, unlike saccades, hand movements can be corrected online
613 after the movement has been initiated and decisions about movement goals can be rapidly

614 updated (Contemori et al., 2023; Nashed et al., 2014). We found that hand reaction times were
615 shorter when intercepting targets at a distance of 3 compared to 6 cm. These results suggest that
616 planning a shorter, or lower amplitude hand response took slightly less time (~7 ms) than the
617 longer, or higher amplitude response. This effect could be related to the observation that the hand
618 responded more vigorously when intercepting targets at 6 compared to 3 cm, and thus higher
619 muscle recruitment was required. Future work investigating muscle activity is required to elucidate
620 this idea.

621 In contrast to hand responses, we found that eye reaction times were shorter for targets
622 that jumped 6 cm, or 9.2 deg, compared to 3 cm, or 4.6 deg. This is in contrast to previous findings
623 in human and non-human primates, showing that when making visually-guided saccades to
624 targets that are further than 1 deg away, saccade latency increases with increasing target
625 eccentricity (Hafed & Goffart, 2020; Kalesnykas & Hallett, 1994; Zhang & Fries, 2023). It should
626 be noted that in these studies, saccades were made to stationary targets at ‘regular’ saccade
627 latencies. Interestingly, short-latency saccades to predictable targets in the periphery are initiated
628 earlier toward more eccentric compared to less eccentric targets (Cohen & Ross, 1977). Further,
629 saccades to auditory targets are initiated earlier the more eccentric the target position (Gabriel et
630 al., 2010). Taken together, these results suggest that salient sensory events may evoke even
631 earlier orienting responses for targets of relatively high eccentricity.

632 Conclusion

633 This paper highlights system-specific mechanisms guiding rapid eye and hand responses. We
634 found that both eye and hand responses were similarly modulated by jump certainty, with reaction
635 times decreasing when perturbations were highly predictable. However, we found that increasing
636 levels of response urgency impacted eye and hand responses differently. Whereas hand
637 responses scaled to the level of urgency, eye responses were relatively unaffected. We proposed
638 a framework that links our behavioural results to the neural mechanisms involved in the
639 visuomotor coordination of the eye and hand. This framework can potentially offer a foundation
640 for future research on motor actions in the face of unpredictable changes in our dynamic world.
641

642 Citation diversity statement

643 Recent work in several fields of science has identified a bias in citation practices such that papers
644 from women and other minority scholars are under-cited relative to the number of such papers in
645 the field (Bertolero et al., 2020; Caplar et al., 2017; Chatterjee & Werner, 2021; Dion et al., 2018;
646 Dworkin et al., 2020; Fulvio et al., 2021; Maliniak et al., 2013; Mitchell et al., 2013; Wang et al.,
647 2021). Here we sought to proactively consider choosing references that reflect the diversity of the
648 field in thought, form of contribution, gender, race, ethnicity, and other factors. First, we obtained
649 the predicted gender of the first and last author of each reference by using databases that store
650 the probability of a first name being carried by a woman (Dworkin et al., 2020; Zhou et al., 2020).
651 By this measure (and excluding self-citations to the first and last authors of our current paper),
652 our references contain 7.14% woman(first)/woman(last), 8.16% man/woman, 19.39%
653 woman/man, and 65.31% man/man. This method is limited in that a) names, pronouns, and social
654 media profiles used to construct the databases may not, in every case, be indicative of gender
655 identity and b) it cannot account for intersex, non-binary, or transgender people. Second, we
656 obtained the predicted racial/ethnic category of the first and last author of each reference by
657 databases that store the probability of a first and last name being carried by an author of colour
658 (Ambekar et al., 2009; Chintalapati et al., 2023). By this measure (and excluding self-citations),
659 our references contain 4.67% author of colour (first)/author of colour(last), 23.22% white
660 author/author of colour, 17.89% author of colour/white author, and 54.22% white author/white
661 author. This method is limited in that a) names and Florida Voter Data to make the predictions
662 may not be indicative of racial/ethnic identity, and b) it cannot account for Indigenous and mixed-
663 race authors, or those who may face differential biases due to the ambiguous racialization or
664 ethnicization of their names. We look forward to future work that could help us to better understand
665 how to support equitable practices in science.

666

- 667 References
- 668 Ambekar, A., Ward, C., Mohammed, J., Male, S., & Skiena, S. (2009). Name-ethnicity
669 classification from open sources. *Proceedings of the 15th ACM SIGKDD International
670 Conference on Knowledge Discovery and Data Mining*, 49–58.
671 <https://doi.org/10.1145/1557019.1557032>
- 672 Barany, D. A., Gómez-Granados, A., Schrayer, M., Cutts, S. A., & Singh, T. (2020). Perceptual
673 decisions about object shape bias visuomotor coordination during rapid interception
674 movements. *Journal of Neurophysiology*, 123(6), 2235–2248.
675 <https://doi.org/10.1152/jn.00098.2020>
- 676 Battaglia-Mayer, A., Caminiti, R., Lacquaniti, F., & Zago, M. (2003). Multiple Levels of
677 Representation of Reaching in the Parieto-frontal Network. *Cerebral Cortex*, 13(10),
678 1009–1022. <https://doi.org/10.1093/cercor/13.10.1009>
- 679 Bertolero, M. A., Dworkin, J. D., David, S. U., Lloreda, C. L., Srivastava, P., Stiso, J., Zhou, D.,
680 Dzirasa, K., Fair, D. A., Kaczkurkin, A. N., Marlin, B. J., Shohamy, D., Uddin, L. Q., Zurn,
681 P., & Bassett, D. S. (2020). *Racial and ethnic imbalance in neuroscience reference lists
682 and intersections with gender*. <https://doi.org/10.1101/2020.10.12.336230>
- 683 Binaee, K., & Diaz, G. (2019). Movements of the eyes and hands are coordinated by a common
684 predictive strategy. *Journal of Vision*, 19(12), 3. <https://doi.org/10.1167/19.12.3>
- 685 Boehnke, S. E., & Munoz, D. P. (2008). On the importance of the transient visual response in
686 the superior colliculus. *Current Opinion in Neurobiology*, 18(6), 544–551.
687 <https://doi.org/10.1016/j.conb.2008.11.004>
- 688 Bosco, G., Delle Monache, S., Gravano, S., Indovina, I., La Scaleia, B., Maffei, V., Zago, M., &
689 Lacquaniti, F. (2015). Filling gaps in visual motion for target capture. *Frontiers in
690 Integrative Neuroscience*, 9. <https://doi.org/10.3389/fnint.2015.00013>
- 691 Brenner, E., & Smeets, J. B. J. (1997). Fast Responses of the Human Hand to Changes in
692 Target Position. *Journal of Motor Behavior*, 29(4), 297–310.
693 <https://doi.org/10.1080/00222899709600017>
- 694 Brenner, E., & Smeets, J. B. J. (2018). Continuously updating one's predictions underlies
695 successful interception. *Journal of Neurophysiology*, 120(6), 3257–3274.
696 <https://doi.org/10.1152/jn.00517.2018>
- 697 Caplar, N., Tacchella, S., & Birrer, S. (2017). Quantitative evaluation of gender bias in
698 astronomical publications from citation counts. *Nature Astronomy*, 1(6), 0141.
699 <https://doi.org/10.1038/s41550-017-0141>
- 700 Carpenter, R. H. S., & Williams, M. L. L. (1995). Neural computation of log likelihood in control
701 of saccadic eye movements. *Nature*, 377(6544), 59–62.
702 <https://doi.org/10.1038/377059a0>
- 703 Cesqui, B., Mezzetti, M., Lacquaniti, F., & d'Avella, A. (2015). Gaze Behavior in One-Handed
704 Catching and Its Relation with Interceptive Performance: What the Eyes Can't Tell.
705 *PLOS ONE*, 10(3), e0119445. <https://doi.org/10.1371/journal.pone.0119445>
- 706 Chatterjee, P., & Werner, R. M. (2021). Gender Disparity in Citations in High-Impact Journal

- 707 Articles. *JAMA Network Open*, 4(7), e2114509.
708 <https://doi.org/10.1001/jamanetworkopen.2021.14509>

709 Chintalapati, R., Laohaprapanon, S., & Sood, G. (2023). *Predicting Race and Ethnicity From the*
710 *Sequence of Characters in a Name* (No. arXiv:1805.02109). arXiv.
711 <http://arxiv.org/abs/1805.02109>

712 Coe, B. C., & Munoz, D. P. (2017). Mechanisms of saccade suppression revealed in the anti-
713 saccade task. *Philosophical Transactions of the Royal Society B: Biological Sciences*,
714 372(1718), 20160192. <https://doi.org/10.1098/rstb.2016.0192>

715 Cohen, M. E., & Ross, L. E. (1977). Saccade latency in children and adults: Effects of warning
716 interval and target eccentricity. *Journal of Experimental Child Psychology*, 23(3), 539–
717 549. [https://doi.org/10.1016/0022-0965\(77\)90044-3](https://doi.org/10.1016/0022-0965(77)90044-3)

718 Contemori, S., Loeb, G. E., Corneil, B. D., Wallis, G., & Carroll, T. J. (2021). The influence of
719 temporal predictability on express visuomotor responses. *Journal of Neurophysiology*,
720 125(3), 731–747. <https://doi.org/10.1152/jn.00521.2020>

721 Contemori, S., Loeb, G. E., Corneil, B. D., Wallis, G., & Carroll, T. J. (2022). Symbolic cues
722 enhance express visuomotor responses in human arm muscles at the motor planning
723 rather than the visuospatial processing stage. *Journal of Neurophysiology*, 128(3), 494–
724 510. <https://doi.org/10.1152/jn.00136.2022>

725 Contemori, S., Loeb, G. E., Corneil, B. D., Wallis, G., & Carroll, T. J. (2023). Express
726 Visuomotor Responses Reflect Knowledge of Both Target Locations and Contextual
727 Rules during Reaches of Different Amplitudes. *The Journal of Neuroscience*, 43(42),
728 7041–7055. <https://doi.org/10.1523/JNEUROSCI.2069-22.2023>

729 Cooper, B., & McPeek, R. M. (2021). Role of the Superior Colliculus in Guiding Movements Not
730 Made by the Eyes. *Annual Review of Vision Science*, 7(1), 279–300.
731 <https://doi.org/10.1146/annurev-vision-012521-102314>

732 Corneil, B. D., & Munoz, D. P. (2014). Overt Responses during Covert Orienting. *Neuron*, 82(6),
733 1230–1243. <https://doi.org/10.1016/j.neuron.2014.05.040>

734 Corneil, B. D., Munoz, D. P., Chapman, B. B., Admans, T., & Cushing, S. L. (2008).
735 Neuromuscular consequences of reflexive covert orienting. *Nature Neuroscience*, 11(1),
736 13–15. <https://doi.org/10.1038/nn2023>

737 Corneil, B. D., Olivier, E., & Munoz, D. P. (2004). Visual Responses on Neck Muscles Reveal
738 Selective Gating that Prevents Express Saccades. *Neuron*, 42(5), 831–841.
739 [https://doi.org/10.1016/S0896-6273\(04\)00267-3](https://doi.org/10.1016/S0896-6273(04)00267-3)

740 Coudiere, A., & Danion, F. R. (2024). Eye-hand coordination all the way: From discrete to
741 continuous hand movements. *Journal of Neurophysiology*, 131(4), 652–667.
742 <https://doi.org/10.1152/jn.00314.2023>

743 Crawford, J. D., Medendorp, W. P., & Marotta, J. J. (2004). Spatial Transformations for Eye–
744 Hand Coordination. *Journal of Neurophysiology*, 92(1), 10–19.
745 <https://doi.org/10.1152/jn.00117.2004>

746 Crévécoeur, F., Kurtzer, I., Bourke, T., & Scott, S. H. (2013). Feedback responses rapidly scale

- 747 with the urgency to correct for external perturbations. *Journal of Neurophysiology*,
748 110(6), 1323–1332. <https://doi.org/10.1152/jn.00216.2013>
- 749 Cross, K. P., Cluff, T., Takei, T., & Scott, S. H. (2019). Visual Feedback Processing of the Limb
750 Involves Two Distinct Phases. *The Journal of Neuroscience*, 39(34), 6751–6765.
751 <https://doi.org/10.1523/JNEUROSCI.3112-18.2019>
- 752 de Brouwer, A. J., Flanagan, J. R., & Spering, M. (2021). Functional Use of Eye Movements for
753 an Acting System. *Trends in Cognitive Sciences*, 25(3), 252–263.
754 <https://doi.org/10.1016/j.tics.2020.12.006>
- 755 de la Malla, C., Rushton, S. K., Clark, K., Smeets, J. B. J., & Brenner, E. (2019). The
756 predictability of a target's motion influences gaze, head, and hand movements when
757 trying to intercept it. *Journal of Neurophysiology*, 121(6), 2416–2427.
758 <https://doi.org/10.1152/jn.00917.2017>
- 759 Dean, H. L., Hagan, M. A., & Pesaran, B. (2012). Only Coherent Spiking in Posterior Parietal
760 Cortex Coordinates Looking and Reaching. *Neuron*, 73(4), 829–841.
761 <https://doi.org/10.1016/j.neuron.2011.12.035>
- 762 Diaz, G. J., Cooper, J., Rothkopf, C., & Hayhoe, M. M. (2013). Saccades to future ball location
763 reveal memory-based prediction in a virtual-reality interception task. *Journal of Vision*,
764 13(1), 20–20. <https://doi.org/10.1167/13.1.20>
- 765 Dimitriou, M., Wolpert, D. M., & Franklin, D. W. (2013). The Temporal Evolution of Feedback
766 Gains Rapidly Update to Task Demands. *Journal of Neuroscience*, 33(26), 10898–
767 10909. <https://doi.org/10.1523/JNEUROSCI.5669-12.2013>
- 768 Dion, M. L., Sumner, J. L., & Mitchell, S. M. (2018). Gendered Citation Patterns across Political
769 Science and Social Science Methodology Fields. *Political Analysis*, 26(3), 312–327.
770 <https://doi.org/10.1017/pan.2018.12>
- 771 Dorris, M. C., Klein, R. M., Everling, S., & Munoz, D. P. (2002). Contribution of the Primate
772 Superior Colliculus to Inhibition of Return. *Journal of Cognitive Neuroscience*, 14(8),
773 1256–1263. <https://doi.org/10.1162/089892902760807249>
- 774 Dorris, M. C., Paré, M., & Munoz, D. P. (1997). Neuronal Activity in Monkey Superior Colliculus
775 Related to the Initiation of Saccadic Eye Movements. *The Journal of Neuroscience*,
776 17(21), 8566–8579. <https://doi.org/10.1523/JNEUROSCI.17-21-08566.1997>
- 777 Dworkin, J. D., Linn, K. A., Teich, E. G., Zurn, P., Shinohara, R. T., & Bassett, D. S. (2020). The
778 extent and drivers of gender imbalance in neuroscience reference lists. *Nature
779 Neuroscience*, 23(8), 918–926. <https://doi.org/10.1038/s41593-020-0658-y>
- 780 Engel, K. C., Anderson, J. H., & Soechting, J. F. (1999). Oculomotor Tracking in Two
781 Dimensions. *Journal of Neurophysiology*, 81(4), 1597–1602.
782 <https://doi.org/10.1152/jn.1999.81.4.1597>
- 783 Etchells, P. J., Benton, C. P., Ludwig, C. J. H., & Gilchrist, I. D. (2010). The target velocity
784 integration function for saccades. *Journal of Vision*, 10(6), 7–7.
785 <https://doi.org/10.1167/10.6.7>
- 786 Findlay, J. M. (1983). Visual Information Processing for Saccadic Eye Movements. In A. Hein &

- 787 M. Jeannerod (Eds.), *Spatially Oriented Behavior* (pp. 281–303). Springer New York.
788 https://doi.org/10.1007/978-1-4612-5488-1_16
- 789 Fischer, B., & Ramsperger, E. (1984). Human express saccades: Extremely short reaction times
790 of goal directed eye movements. *Experimental Brain Research*, 57(1).
791 <https://doi.org/10.1007/BF00231145>
- 792 Fisk, J. D., & Goodale, M. A. (1985). The organization of eye and limb movements during
793 unrestricted reaching to targets in contralateral and ipsilateral visual space. *Experimental*
794 *Brain Research*, 60(1). <https://doi.org/10.1007/BF00237028>
- 795 Fooken, J., Baltaretu, B. R., Barany, D. A., Diaz, G., Semrau, J. A., Singh, T., & Crawford, J. D.
796 (2023). Perceptual-Cognitive Integration for Goal-Directed Action in Naturalistic
797 Environments. *Journal of Neuroscience*, 43(45), 7511–7522.
798 <https://doi.org/10.1523/JNEUROSCI.1373-23.2023>
- 799 Fooken, J., Kreyenmeier, P., & Spering, M. (2021). The role of eye movements in manual
800 interception: A mini-review. *Vision Research*, 183, 81–90.
801 <https://doi.org/10.1016/j.visres.2021.02.007>
- 802 Fooken, J., & Spering, M. (2019). Decoding go/no-go decisions from eye movements. *Journal of*
803 *Vision*, 19(2), 5. <https://doi.org/10.1167/19.2.5>
- 804 Fooken, J., & Spering, M. (2020). Eye movements as a readout of sensorimotor decision
805 processes. *Journal of Neurophysiology*, 123(4), 1439–1447.
806 <https://doi.org/10.1152/jn.00622.2019>
- 807 Fooken, J., Yeo, S.-H., Pai, D. K., & Spering, M. (2016). Eye movement accuracy determines
808 natural interception strategies. *Journal of Vision*, 16(14), 1.
809 <https://doi.org/10.1167/16.14.1>
- 810 Frens, M., & Erkelens, C. J. (1991). Coordination of hand movements and saccades: Evidence
811 for a common and a separate pathway. *Experimental Brain Research*, 85(3).
812 <https://doi.org/10.1007/BF00231754>
- 813 Fulvio, J. M., Akinnola, I., & Postle, B. R. (2021). Gender (Im)balance in Citation Practices in
814 Cognitive Neuroscience. *Journal of Cognitive Neuroscience*, 33(1), 3–7.
815 https://doi.org/10.1162/jocn_a_01643
- 816 Gabriel, D. N., Munoz, D. P., & Boehnke, S. E. (2010). The eccentricity effect for auditory
817 saccadic reaction times is independent of target frequency. *Hearing Research*, 262(1–2),
818 19–25. <https://doi.org/10.1016/j.heares.2010.01.016>
- 819 Gandhi, N. J., & Katnani, H. A. (2011). Motor Functions of the Superior Colliculus. *Annual*
820 *Review of Neuroscience*, 34(1), 205–231. <https://doi.org/10.1146/annurev-neuro-061010-113728>
- 822 Gellman, R. S., & Carl, J. R. (1991). Motion processing for saccadic eye movements in humans.
823 *Experimental Brain Research*, 84(3). <https://doi.org/10.1007/BF00230979>
- 824 Goettker, A., Braun, D. I., & Gegenfurtner, K. R. (2019). Dynamic combination of position and
825 motion information when tracking moving targets. *Journal of Vision*, 19(7), 2.
826 <https://doi.org/10.1167/19.7.2>

- 827 Goettker, A., Brenner, E., Gegenfurtner, K. R., & de la Malla, C. (2019). Corrective saccades
828 influence velocity judgments and interception. *Scientific Reports*, 9(1), 5395.
829 <https://doi.org/10.1038/s41598-019-41857-z>
- 830 Goonetilleke, S. C., Katz, L., Wood, D. K., Gu, C., Huk, A. C., & Corneil, B. D. (2015). Cross-
831 species comparison of anticipatory and stimulus-driven neck muscle activity well before
832 saccadic gaze shifts in humans and nonhuman primates. *Journal of Neurophysiology*,
833 114(2), 902–913. <https://doi.org/10.1152/jn.00230.2015>
- 834 Gribble, P. L., Everling, S., Ford, K., & Mattar, A. (2002). Hand-eye coordination for rapid
835 pointing movements: Arm movement direction and distance are specified prior to
836 saccade onset. *Experimental Brain Research*, 145(3), 372–382.
837 <https://doi.org/10.1007/s00221-002-1122-9>
- 838 Gu, C., Wood, D. K., Gribble, P. L., & Corneil, B. D. (2016). A Trial-by-Trial Window into
839 Sensorimotor Transformations in the Human Motor Periphery. *Journal of Neuroscience*,
840 36(31), 8273–8282. <https://doi.org/10.1523/JNEUROSCI.0899-16.2016>
- 841 Hafed, Z. M., & Goffart, L. (2020). Gaze direction as equilibrium: More evidence from spatial
842 and temporal aspects of small-saccade triggering in the rhesus macaque monkey.
843 *Journal of Neurophysiology*, 123(1), 308–322. <https://doi.org/10.1152/jn.00588.2019>
- 844 Hwang, E. J., Hauschild, M., Wilke, M., & Andersen, R. A. (2014). Spatial and Temporal Eye-
845 Hand Coordination Relies on the Parietal Reach Region. *Journal of Neuroscience*,
846 34(38), 12884–12892. <https://doi.org/10.1523/JNEUROSCI.3719-13.2014>
- 847 Irving, E. L., Steinbach, M. J., Lillakas, L., Babu, R. J., & Hutchings, N. (2006). Horizontal
848 Saccade Dynamics across the Human Life Span. *Investigative Ophthalmology & Visual
849 Science*, 47(6), 2478. <https://doi.org/10.1167/iovs.05-1311>
- 850 Jakobs, O., Wang, L. E., Dafotakis, M., Grefkes, C., Zilles, K., & Eickhoff, S. B. (2009). Effects
851 of timing and movement uncertainty implicate the temporo-parietal junction in the
852 prediction of forthcoming motor actions. *NeuroImage*, 47(2), 667–677.
853 <https://doi.org/10.1016/j.neuroimage.2009.04.065>
- 854 Johansson, R. S., Westling, G., Bäckström, A., & Flanagan, J. R. (2001). Eye-Hand
855 Coordination in Object Manipulation. *The Journal of Neuroscience*, 21(17), 6917–6932.
856 <https://doi.org/10.1523/JNEUROSCI.21-17-06917.2001>
- 857 Kalesnykas, R. P., & Hallett, P. E. (1994). Retinal eccentricity and the latency of eye saccades.
858 *Vision Research*, 34(4), 517–531. [https://doi.org/10.1016/0042-6989\(94\)90165-1](https://doi.org/10.1016/0042-6989(94)90165-1)
- 859 Kalidindi, H. T., & Crévécoeur, F. (2023). Human reaching control in dynamic environments.
860 *Current Opinion in Neurobiology*, 83, 102810.
861 <https://doi.org/10.1016/j.conb.2023.102810>
- 862 Kang, J. U., Mooshagian, E., & Snyder, L. H. (2024). Functional organization of posterior
863 parietal cortex circuitry based on inferred information flow. *Cell Reports*, 43(4), 114028.
864 <https://doi.org/10.1016/j.celrep.2024.114028>
- 865 Kingstone, A., & Klein, R. M. (1993). What are human express saccades? *Perception &
866 Psychophysics*, 54(2), 260–273. <https://doi.org/10.3758/BF03211762>

- 867 Korbisch, C. C., Apuan, D. R., Shadmehr, R., & Ahmed, A. A. (2022). Saccade vigor reflects the
868 rise of decision variables during deliberation. *Current Biology*, 32(24), 5374-5381.e4.
869 <https://doi.org/10.1016/j.cub.2022.10.053>
- 870 Kozak, R. A., Cecala, A. L., & Corneil, B. D. (2020). An Emerging Target Paradigm to Evoke
871 Fast Visuomotor Responses on Human Upper Limb Muscles. *Journal of Visualized
872 Experiments*, 162, 61428. <https://doi.org/10.3791/61428>
- 873 Kozak, R. A., Kreyenmeier, P., Gu, C., Johnston, K., & Corneil, B. D. (2019). Stimulus-Locked
874 Responses on Human Upper Limb Muscles and Corrective Reaches Are Preferentially
875 Evoked by Low Spatial Frequencies. *eNeuro*, 6(5), ENEURO.0301-19.2019.
876 <https://doi.org/10.1523/ENEURO.0301-19.2019>
- 877 Kreyenmeier, P., Kämmer, L., Fooken, J., & Spering, M. (2022). Humans Can Track But Fail to
878 Predict Accelerating Objects. *Eneuro*, 9(5), ENEURO.0185-22.2022.
879 <https://doi.org/10.1523/ENEURO.0185-22.2022>
- 880 Land, M. F. (2006). Eye movements and the control of actions in everyday life. *Progress in
881 Retinal and Eye Research*, 25(3), 296–324.
882 <https://doi.org/10.1016/j.preteyeres.2006.01.002>
- 883 Land, M. F., & McLeod, P. (2000). From eye movements to actions: How batsmen hit the ball.
884 *Nature Neuroscience*, 3(12), 1340–1345. <https://doi.org/10.1038/81887>
- 885 Maliniak, D., Powers, R., & Walter, B. F. (2013). The Gender Citation Gap in International
886 Relations. *International Organization*, 67(4), 889–922.
887 <https://doi.org/10.1017/S0020818313000209>
- 888 Mann, D. L., Nakamoto, H., Logt, N., Sikkink, L., & Brenner, E. (2019). Predictive eye
889 movements when hitting a bouncing ball. *Journal of Vision*, 19(14), 28.
890 <https://doi.org/10.1167/19.14.28>
- 891 Marino, R. A., Levy, R., Boehnke, S., White, B. J., Itti, L., & Munoz, D. P. (2012). Linking visual
892 response properties in the superior colliculus to saccade behavior. *European Journal of
893 Neuroscience*, 35(11), 1738–1752. <https://doi.org/10.1111/j.1460-9568.2012.08079.x>
- 894 Marino, R. A., Levy, R., & Munoz, D. P. (2015). Linking express saccade occurrence to stimulus
895 properties and sensorimotor integration in the superior colliculus. *Journal of
896 Neurophysiology*, 114(2), 879–892. <https://doi.org/10.1152/jn.00047.2015>
- 897 Maurus, P., Jackson, K., Cashaback, J. G. A., & Cluff, T. (2023). The nervous system tunes
898 sensorimotor gains when reaching in variable mechanical environments. *iScience*, 26(6),
899 106756. <https://doi.org/10.1016/j.isci.2023.106756>
- 900 Mitchell, S. M., Lange, S., & Brus, H. (2013). Gendered Citation Patterns in International
901 Relations Journals. *International Studies Perspectives*, 14(4), 485–492.
902 <https://doi.org/10.1111/insp.12026>
- 903 Mrotek, L. A. (2013). Following and intercepting scribbles: Interactions between eye and hand
904 control. *Experimental Brain Research*, 227(2), 161–174. [https://doi.org/10.1007/s00221-013-3496-2](https://doi.org/10.1007/s00221-
905 013-3496-2)
- 906 Mrotek, L. A., & Soechting, J. F. (2007). Target Interception: Hand–Eye Coordination and

- 907 Strategies. *The Journal of Neuroscience*, 27(27), 7297–7309.
908 <https://doi.org/10.1523/JNEUROSCI.2046-07.2007>
- 909 Nashed, J. Y., Crévécoeur, F., & Scott, S. H. (2014). Rapid Online Selection between Multiple
910 Motor Plans. *The Journal of Neuroscience*, 34(5), 1769–1780.
911 <https://doi.org/10.1523/JNEUROSCI.3063-13.2014>
- 912 Paré, M., & Munoz, D. P. (1996). Saccadic reaction time in the monkey: Advanced preparation
913 of oculomotor programs is primarily responsible for express saccade occurrence.
914 *Journal of Neurophysiology*, 76(6), 3666–3681.
915 <https://doi.org/10.1152/jn.1996.76.6.3666>
- 916 Park, K., Ritsma, B. R., Dukelow, S. P., & Scott, S. H. (2023). A robot-based interception task to
917 quantify upper limb impairments in proprioceptive and visual feedback after stroke.
918 *Journal of NeuroEngineering and Rehabilitation*, 20(1), 137.
919 <https://doi.org/10.1186/s12984-023-01262-0>
- 920 Perfiliev, S., Isa, T., Johnels, B., Steg, G., & Wessberg, J. (2010). Reflexive Limb Selection and
921 Control of Reach Direction to Moving Targets in Cats, Monkeys, and Humans. *Journal of
922 Neurophysiology*, 104(5), 2423–2432. <https://doi.org/10.1152/jn.01133.2009>
- 923 Philipp, R., & Hoffmann, K.-P. (2014). Arm Movements Induced by Electrical Microstimulation in
924 the Superior Colliculus of the Macaque Monkey. *The Journal of Neuroscience*, 34(9),
925 3350–3363. <https://doi.org/10.1523/JNEUROSCI.0443-13.2014>
- 926 Poscente, S. V., Peters, R. M., Cashaback, J. G. A., & Cluff, T. (2021). Rapid Feedback
927 Responses Parallel the Urgency of Voluntary Reaching Movements. *Neuroscience*, 475,
928 163–184. <https://doi.org/10.1016/j.neuroscience.2021.07.014>
- 929 Prablanc, C., Echallier, J. F., Komilis, E., & Jeannerod, M. (1979). Optimal response of eye and
930 hand motor systems in pointing at a visual target: I. Spatio-temporal characteristics of
931 eye and hand movements and their relationships when varying the amount of visual
932 information. *Biological Cybernetics*, 35(2), 113–124. <https://doi.org/10.1007/BF00337436>
- 933 Pruszynski, J. A., King, G. L., Boisse, L., Scott, S. H., Flanagan, J. R., & Munoz, D. P. (2010).
934 Stimulus-locked responses on human arm muscles reveal a rapid neural pathway linking
935 visual input to arm motor output. *European Journal of Neuroscience*, 32(6), 1049–1057.
936 <https://doi.org/10.1111/j.1460-9568.2010.07380.x>
- 937 Reppert, T. R., Lempert, K. M., Glimcher, P. W., & Shadmehr, R. (2015). Modulation of Saccade
938 Vigor during Value-Based Decision Making. *The Journal of Neuroscience*, 35(46),
939 15369–15378. <https://doi.org/10.1523/JNEUROSCI.2621-15.2015>
- 940 Reschchtko, S., Gnanaseelan, C., & Pruszynski, J. A. (2023). Reach Corrections Toward
941 Moving Objects are Faster Than Reach Corrections Toward Instantaneously Switching
942 Targets. *Neuroscience*, 526, 135–143.
943 <https://doi.org/10.1016/j.neuroscience.2023.06.021>
- 944 Robinson, D. A. (2022). Behavior of the saccadic system: Metrics of timing and accuracy. In
945 *Progress in Brain Research* (Vol. 267, pp. 329–353). Elsevier.
946 <https://doi.org/10.1016/bs.pbr.2021.10.016>
- 947 Ron, S., Vieville, T., & Droulez, J. (1989). Target velocity based prediction in saccadic vector

- 948 programming. *Vision Research*, 29(9), 1103–1114. [https://doi.org/10.1016/0042-6989\(89\)90059-X](https://doi.org/10.1016/0042-6989(89)90059-X)
- 950 Sailer, U., Eggert, T., Ditterich, J., & Straube, A. (2000). Spatial and temporal aspects of eye-hand coordination across different tasks. *Experimental Brain Research*, 134(2), 163–173. <https://doi.org/10.1007/s002210000457>
- 953 Salinas, E., Steinberg, B. R., Sussman, L. A., Fry, S. M., Hauser, C. K., Anderson, D. D., & 954 Stanford, T. R. (2019). Voluntary and involuntary contributions to perceptually guided 955 saccadic choices resolved with millisecond precision. *eLife*, 8, e46359. 956 <https://doi.org/10.7554/eLife.46359>
- 957 Saslow, M. G. (1967). Effects of Components of Displacement-Step Stimuli Upon Latency for 958 Saccadic Eye Movement. *Journal of the Optical Society of America*, 57(8), 1024. 959 <https://doi.org/10.1364/JOSA.57.001024>
- 960 Schlag, J., & Schlag-Rey, M. (2002). Through the eye, slowly; Delays and localization errors in 961 the visual system. *Nature Reviews Neuroscience*, 3(3), 191–191. 962 <https://doi.org/10.1038/nrn750>
- 963 Scott, S. H. (2016). A Functional Taxonomy of Bottom-Up Sensory Feedback Processing for 964 Motor Actions. *Trends in Neurosciences*, 39(8), 512–526. 965 <https://doi.org/10.1016/j.tins.2016.06.001>
- 966 Seideman, J. A., Stanford, T. R., & Salinas, E. (2018). Saccade metrics reflect decision-making 967 dynamics during urgent choices. *Nature Communications*, 9(1), 2907. 968 <https://doi.org/10.1038/s41467-018-05319-w>
- 969 Shadmehr, R., Reppert, T. R., Summerside, E. M., Yoon, T., & Ahmed, A. A. (2019). Movement 970 Vigor as a Reflection of Subjective Economic Utility. *Trends in Neurosciences*, 42(5), 971 323–336. <https://doi.org/10.1016/j.tins.2019.02.003>
- 972 Sparks, D., Rohrer, W. H., & Zhang, Y. (2000). The role of the superior colliculus in saccade 973 initiation: A study of express saccades and the gap effect. *Vision Research*, 40(20), 974 2763–2777. [https://doi.org/10.1016/S0042-6989\(00\)00133-4](https://doi.org/10.1016/S0042-6989(00)00133-4)
- 975 Spering, M., Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2011). Keep your eyes on the 976 ball: Smooth pursuit eye movements enhance prediction of visual motion. *Journal of 977 Neurophysiology*, 105(4), 1756–1767. <https://doi.org/10.1152/jn.00344.2010>
- 978 Stanford, T. R., & Salinas, E. (2021). Urgent Decision Making: Resolving Visuomotor 979 Interactions at High Temporal Resolution. *Annual Review of Vision Science*, 7(1), 323–980 348. <https://doi.org/10.1146/annurev-vision-100419-103842>
- 981 Stanford, T. R., Shankar, S., Massoglia, D. P., Costello, M. G., & Salinas, E. (2010). Perceptual 982 decision making in less than 30 milliseconds. *Nature Neuroscience*, 13(3), 379–385. 983 <https://doi.org/10.1038/nn.2485>
- 984 Stuphorn, V., Hoffmann, K.-P., & Miller, L. E. (1999). Correlation of Primate Superior Colliculus 985 and Reticular Formation Discharge With Proximal Limb Muscle Activity. *Journal of 986 Neurophysiology*, 81(4), 1978–1982. <https://doi.org/10.1152/jn.1999.81.4.1978>
- 987 Todorov, E., & Jordan, M. I. (2002). Optimal feedback control as a theory of motor coordination.

- 988 *Nature Neuroscience*, 5(11), 1226–1235. <https://doi.org/10.1038/nn963>
- 989 Veerman, M. M., Brenner, E., & Smeets, J. B. J. (2008). The latency for correcting a movement
990 depends on the visual attribute that defines the target. *Experimental Brain Research*,
991 187(2), 219–228. <https://doi.org/10.1007/s00221-008-1296-x>
- 992 Vesia, M., & Crawford, J. D. (2012). Specialization of reach function in human posterior parietal
993 cortex. *Experimental Brain Research*, 221(1), 1–18. <https://doi.org/10.1007/s00221-012-3158-9>
- 995 Wang, X., Dworkin, J. D., Zhou, D., Stiso, J., Falk, E. B., Bassett, D. S., Zurn, P., & Lydon-
996 Staley, D. M. (2021). Gendered citation practices in the field of communication. *Annals*
997 of the International Communication Association, 45(2), 134–153.
998 <https://doi.org/10.1080/23808985.2021.1960180>
- 999 Werner, W., Dannenberg, S., & Hoffmann, K.-P. (1997). Arm-movement-related neurons in the
1000 primate superior colliculus and underlying reticular formation: Comparison of neuronal
1001 activity with EMGs of muscles of the shoulder, arm and trunk during reaching:
1002 *Experimental Brain Research*, 115(2), 191–205. <https://doi.org/10.1007/PL00005690>
- 1003 Wood, D. K., Gu, C., Corneil, B. D., Gribble, P. L., & Goodale, M. A. (2015). Transient visual
1004 responses reset the phase of low-frequency oscillations in the skeletomotor periphery.
1005 *European Journal of Neuroscience*, 42(3), 1919–1932. <https://doi.org/10.1111/ejn.12976>
- 1006 Yoon, T., Jaleel, A., Ahmed, A. A., & Shadmehr, R. (2020). Saccade vigor and the subjective
1007 economic value of visual stimuli. *Journal of Neurophysiology*, 123(6), 2161–2172.
1008 <https://doi.org/10.1152/jn.00700.2019>
- 1009 Zago, M., Iosa, M., Maffei, V., & Lacquaniti, F. (2010). Extrapolation of vertical target motion
1010 through a brief visual occlusion. *Experimental Brain Research*, 201(3), 365–384.
1011 <https://doi.org/10.1007/s00221-009-2041-9>
- 1012 Zago, M., McIntyre, J., Senot, P., & Lacquaniti, F. (2009). Visuo-motor coordination and internal
1013 models for object interception. *Experimental Brain Research*, 192, 571–604.
- 1014 Zhang, Y., & Fries, P. (2023). *Eccentricity-Dependent Saccadic Reaction Time: The Roles of*
1015 *Foveal Magnification and Attentional Orienting*.
1016 <https://doi.org/10.1101/2023.08.08.552339>
- 1017 Zhou, D., Bertolero, M. A., Stiso, J., Cornblath, E. J., Teich, E. G., Blevins, A. S., Virtualmario
1018 Camp, Dworkin, J., & Bassett, D. S. (2020). *Gender diversity statement and code*
1019 *notebook* (v1.1) [Computer software]. <https://github.com/dalejn/cleanBib>