

1     **Perceptual decisions about object shape bias visuomotor coordination during**  
2                                   **rapid interception movements**

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35

36 **Abstract**

37 Visual processing in parietal areas of the dorsal stream facilitates sensorimotor  
38 transformations for rapid movement. This action-related visual processing is hypothesized to  
39 play a distinct functional role from the perception-related processing in the ventral stream.  
40 However, it is unclear how the two streams interact when perceptual identification is a  
41 prerequisite to executing an accurate movement. In the current study, we investigated how  
42 perceptual decision-making involving the ventral stream influences arm and eye movement  
43 strategies. Participants ( $N = 26$ ) moved a robotic manipulandum using right whole-arm  
44 movements to rapidly reach a stationary object or intercept a moving object on an augmented-  
45 reality display. On some blocks of trials, participants needed to identify the shape of the object  
46 (circle or ellipse) as a cue to either hit the object (circle) or move to a pre-defined location away  
47 from the object (ellipse). We found that during perceptual decision-making, there was an  
48 increased urgency to act during interception movements relative to reaching, which was  
49 associated with more decision errors. Faster hand reaction times were correlated with a  
50 strategy to adjust the movement post-initiation, and this strategy was more prominent during  
51 interception. Saccadic reaction times were faster and initial gaze lags and gains greater during  
52 decisions, suggesting that eye movements adapt to perceptual demands for guiding limb  
53 movements. Together, our findings suggest that the integration of ventral stream information  
54 with visuomotor planning depends on imposed (or perceived) task demands.

55

56 **New and Noteworthy**

57 Visual processing for perception and for action are thought to be mediated by two specialized  
58 neural pathways. Using a visuomotor decision-making task, we show that participants  
59 differentially utilized online perceptual decision-making in reaching and interception, and that  
60 eye movements necessary for perception influenced motor decision strategies. These results  
61 provide evidence that task complexity modulates how pathways processing perception versus  
62 action information interact during the visual control of movement.

63

## 64 Introduction

65 Many functional sensorimotor skills require rapid visual processing and perceptual  
66 decision-making. A very commonly encountered situation during driving is when drivers must  
67 decide whether to yield or stop at an intersection. The decision should be made from a  
68 distance by judging the shape of the sign at an intersection. If the shape is judged as a stop  
69 sign, the driver would slowly press their foot on the brake to bring the car to a gradual stop.  
70 However, if the shape is judged as a yield sign, the driver might just slow down or even hit the  
71 accelerator if there is no incoming traffic. The driver's ability to make the correct decision and  
72 movement depends on efficient real-time processing of visual sensory information in the two  
73 visual processing streams (Goodale and Milner 1992; Mishkin et al. 1983). The distance  
74 between the sign and the car, the presence of other incoming traffic, and the associated motor  
75 actions are likely processed by the posterior parietal cortex along the dorsal visual stream  
76 (Culham et al. 2006; Rizzolatti et al. 2002; Rizzolatti and Matelli 2003). The shape and  
77 symbols on the sign are perceived by the lateral occipital and inferior temporal cortex along the  
78 ventral visual stream (Ales et al. 2013; Grill-Spector et al. 2001; Lehky and Tanaka 2016;  
79 Schwartz et al. 1983). Though the contributions of these streams to visuomotor and  
80 visuoperceptual processing is well delineated, it is still unclear how these two streams interact  
81 and process sensory information in real-time to facilitate rapid visuomotor actions.

82 The goal of the present study was to understand how engaging the ventral stream  
83 affects the spatiotemporal course of movement selection and execution. Many behavioral  
84 (reviewed in Gallivan et al. 2018; Hecht et al. 2008; Rosenbaum et al. 2007; Song and  
85 Nakayama 2009) as well as neurophysiological studies (reviewed in Cisek and Kalaska 2010)  
86 have provided empirical support for simultaneous specification of competing motor plans in the  
87 dorsal visual stream. Rapid movement modifications have also been shown when a perceptual  
88 decision is made based on ventral stream related attributes, such as object color or shape  
89 (Cressman et al. 2007; Schmidt 2002; Song and Nakayama 2008; Veerman et al. 2008),  
90 though at slower time scales than motor decisions based on dorsal stream processing of  
91 spatial or motion-related properties (Day and Lyon 2000; Franklin et al. 2016; Gritsenko et al.  
92 2009; Sarlegna and Mutha 2015). These results imply that despite functionally segregated  
93 roles, goal-directed visuomotor actions ultimately necessitate online interaction between the  
94 ventral and dorsal streams (Gallivan and Goodale 2018; Milner 2017; Song and Nakayama  
95 2009).

96 In these previous studies, the movement required is typically a simple reach executed to  
97 a spatially defined goal. However, the capacity for integration of ventral stream information with  
98 online decision-making and motor planning may depend on the computational complexity of  
99 the movement (van Polanen and Davare 2015). In contrast to simple reaching, interception  
100 movements present a challenge for the motor system due to the uncertainty in estimating the  
101 velocity and future position of the target and in specifying an appropriate motor plan to hit the  
102 target at the desired time and location (Brenner and Smeets 2009; Merchant et al. 2009; Zago  
103 et al. 2009). Humans can achieve high interception accuracy via continuous updating of  
104 movement trajectories under visual feedback control (Brenner and Smeets 2018), but it is  
105 unclear how these interception mechanisms may be modulated by perceptual decision  
106 processes mediated by the ventral visual stream.

107 In the present study, we developed a rapid visuomotor decision-making task where  
108 participants were asked to make reaching or interception movements under relatively fast or  
109 slow time constraints. In some blocks of trials, participants were simply required to hit a

110 stationary (reaching) or moving (interception) object as quickly and as accurately as possible.  
111 In separate blocks, participants needed to select among two alternative actions that required  
112 correctly identifying the object's shape (hit the circle and avoid the ellipse). Our first hypothesis  
113 was that engaging the ventral stream would elicit stronger interference between ventral and  
114 dorsal stream processes during interception than reaching movements. We predicted that both  
115 decisional and aiming accuracy would be lower for interception movements.

116 In contrast to fixations on static targets during reaching movements, smooth-pursuit eye  
117 movements track moving targets and engage additional neural resources (Lencer and  
118 Trillenber 2008; Lisberger 2015) during interception movements. Once the moving target is  
119 stabilized on the retina, the limb motor system may rely on oculomotor efferent signals during  
120 pursuit eye movements to perform continuous retinotopic to limb-centric coordinate  
121 transformations (Gauthier et al. 1990) and guide limb movements. The neural regions involved  
122 in eye movement processing overlap with those involved in decision-related signals (Fooker  
123 and Spering 2019; Gold and Shadlen 2007; Heekeren et al. 2008; Joo et al. 2016), and this  
124 likely affects recognition of object features during fast smooth-pursuits (Ludvigh and Miller  
125 1958a; Schutz et al. 2009; Westheimer and McKee 1975). Thus, our second hypothesis was  
126 that when the ventral stream is engaged during interception movements, the oculomotor  
127 signature of pursuit eye movements will change. Specifically, we expected higher gaze gains  
128 (computed as ratio of gaze velocity and target velocity) during perceptual decisions.

129

## 130 **Methods**

### 131 *Participants*

132 Twenty-six healthy, right-handed participants (16 women;  $23.7 \pm 5.5$  years) completed  
133 the experiment. All participants had no known history of neurological disorders and had normal  
134 or corrected-to-normal vision. Each participant provided written informed consent prior to  
135 participating and were compensated for their participation. All study procedures were approved  
136 by the Institutional Review Board at the University of Georgia.

137

### 138 *Apparatus*

139 Participants were seated in a chair and used their right hand to grasp the handle of a  
140 robotic manipulandum that could move in a horizontal plane (KINARM End-Point Lab, BKIN  
141 Technologies, Kingston, Ontario, Canada) (see Fig.1A). All visual stimuli were projected at 60  
142 Hz onto a semi-transparent mirror from a monitor above the workspace. This set-up allowed  
143 the stimuli to appear on the same horizontal plane as the handle and to occlude direct vision of  
144 the hand. During task performance, the robot applied a small background load (-3 N in the Y  
145 direction) to the handle and recorded movement position and velocity at 1000 Hz. The  
146 monocular eye position of each participant was recorded at 500 Hz using a video-based  
147 remote eye-tracking system (Eyelink 1000; SR Research, Ottawa, ON Canada) integrated with  
148 the robot and calibrated for the 2D horizontal workspace. Data from the eye-tracker and robot  
149 were time-synced offline using MATLAB (version 9.5.0; The MathWorks, Natick, MA).

150

### 151 *Experimental design and procedure*

152 Participants performed rapid whole-arm reaching and interception movements in which  
153 they were instructed to either hit or avoid an object based on the object's shape. At the  
154 beginning of each trial, participants moved a cursor (white circle, 1 cm diameter) representing  
155 their veridical hand position to a start position (yellow circle, 2 cm diameter) located at the

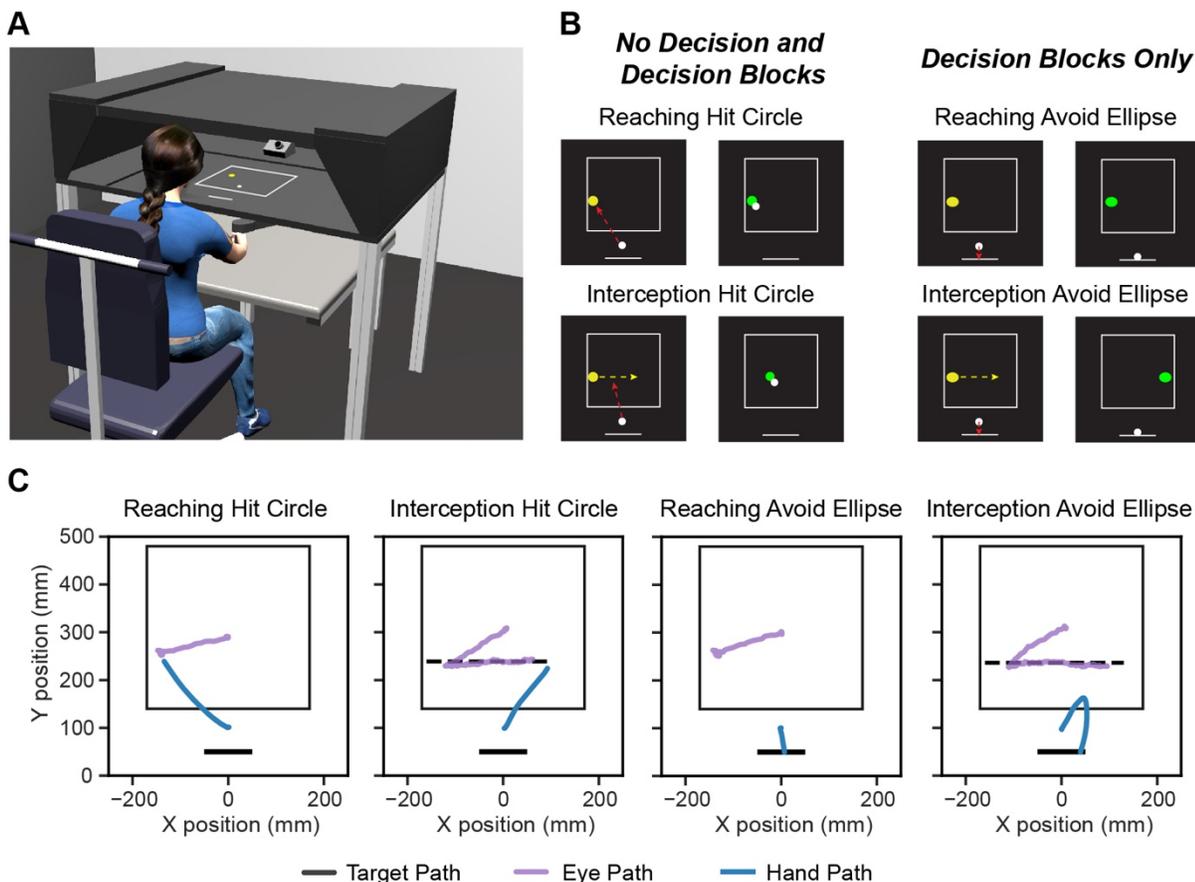
156 midline of the visual display ( $x=0$ ). After reaching the start position, a fixation cross appeared at  
157 the midline 22 cm from the start position in the Y direction. Participants were required to  
158 maintain fixation and keep their hand at the start position for 500 ms, after which the fixation  
159 cross and start position disappeared.

160 Following a fixed 200 ms delay, a yellow object was presented on the display near  
161 either the left or right edge of a rectangular box (34 x 34 cm) centered on the midline and 22  
162 cm above the start position (see Fig. 1B). The possible object shape on a given trial, and the  
163 participant's task, depended on the experimental block. During No Decision blocks,  
164 participants were informed that the object shape would always be a circle (2 cm diameter), and  
165 that they should hit the circle as quickly and as accurately as possible. A "hit" was recorded  
166 when the cursor first touched the circle—participants were not required to stop at the circle.  
167 During Decision blocks, participants were informed that the object would appear as either a  
168 circle or an ellipse (major axis = 2.3 cm; minor axis = 2 cm) with equal probability. The lengths  
169 of the ellipse axes were selected based on pilot experiments to ensure that the object must be  
170 foveated to differentiate it from a circle. As in the No Decision blocks, if the participants saw a  
171 circle, they were instructed to hit it as quickly and as accurately as possible. However, if an  
172 ellipse appeared, participants were instructed to avoid hitting the ellipse and instead move in  
173 the opposite direction toward a horizontal bar (10 cm width) centered on the midline and -4 cm  
174 from the start position in the y direction (see Fig. 1B). Thus, in contrast to No Decision blocks,  
175 in which participants could simply plan to hit the object on every trial, Decision block trials  
176 required the participant to accurately identify the object shape in order to perform the correct  
177 action (i.e., hit the circle or avoid the ellipse). Therefore, in addition to the No Decision blocks,  
178 the Decision condition required two additional steps, object identification and selection of an  
179 appropriate motor plan.

180 For each block of trials, the object either moved horizontally across the display  
181 (Interception) or remained in the same position (Reaching). On Interception trials, the object  
182 appeared  $\pm 16$  cm to the left or right of the midline (Y position range 14.5 - 17 cm from the start  
183 position, uniform distribution) and traversed at a constant Euclidean velocity of  $\pm 40$  cm/s (Fast)  
184 or  $\pm 34$  cm/s (Slow) toward the other horizontal boundary of the rectangular box. The varying  
185 object velocity was added to test the hypotheses under stricter conditions of time constraints.  
186 On Reaching trials, the object appeared to the left or right of the midline with starting positions  
187 drawn from a uniform distribution (X position range:  $\pm 13$  - 16 cm from midline; Y position range  
188 14.5 - 17 cm in front of start position) and remained stationary. For both types of trials, the  
189 object remained on the visual display until it was hit or for the maximum trial duration. On  
190 Interception trials, the maximum trial duration equaled the time it took for the object to arrive at  
191 the horizontal boundary given its velocity: 800 ms for fast velocities ( $\pm 40$  cm/s) and 950 ms for  
192 slow velocities ( $\pm 34$  cm/s). To match the Interception trial durations, objects remained on the  
193 screen for a maximum of 800 ms (Fast) or 950 ms (Slow) during Reaching trials. Before each  
194 block, participants were informed about the object motion (moving or stationary) but were not  
195 given any information about the object speed or trial duration.

196 Performance feedback was provided for 500 ms once the object was hit (i.e., the cursor  
197 overlapped with the object) or the maximum trial duration was reached. If a circle was correctly  
198 hit, the circle would turn green; if the circle was missed it would turn red. An ellipse would turn  
199 red if it was incorrectly hit instead of avoided and would turn green if correctly avoided. The  
200 next trial began following a 1500 - 2000 ms delay.

201 Participants performed 8 experimental blocks of 90 trials each (720 trials total). Block  
202 order was counterbalanced across participants. Each experimental block consisted of a unique  
203 combination of decision type (No Decision or Decision), movement type (Reach or Intercept),  
204 and trial duration (Fast or Slow). Object shape (during Decision blocks) and the object start  
205 location were randomized across trials within each block.  
206



207  
208 *Figure 1: Experimental design and example trials. A: Experimental setup. Participants moved a robotic*  
209 *manipulandum with their right hand to control a cursor (white circle) in response to an object (yellow circle) on the*  
210 *visual display. A remote gaze-tracker at the back of the workspace recorded eye positions in Cartesian*  
211 *coordinates of the workspace. B: Trial types. On every trial, participants were instructed to hit or avoid depending*  
212 *on object shape (hit circle, avoid ellipse). No Decision blocks consisted of only circles; Decision blocks mixed*  
213 *circle and ellipse trials with equal probability. Participants either reached a stationary object (Reaching) or*  
214 *intercepted a moving object (Interception). The object turned green for correct hits (circle hits) and red for*  
215 *incorrect (if ellipses were hit). Similarly, if a circle was missed, it turned red at the end of the trial (Fast blocks trial*  
216 *duration: 800 ms; Slow blocks: 950 ms), and if movement was made towards the bar when an ellipse appeared in*  
217 *the workspace, it turned green at the end of the trial. C: Sample 2D eye and hand paths for each trial type from a*  
218 *representative participant.*

### 219 Data Analysis

220 All hand and eye movement data were analyzed using MATLAB (version 9.5.0, The  
221 MathWorks, Natick, MA) and Python (version 3.7). Statistical analyses were performed in R  
222 (version 3.6.0).  
223

## 224 *Arm Movements*

225 Hand position and velocity data were first smoothed using a fourth-order Butterworth  
226 low-pass filter with a 5 Hz cutoff. Movement onset was defined as the time the tangential  
227 velocity first exceeded 5% of the first local peak. Reaction time (RT) was calculated as the time  
228 from appearance of object in the workspace to movement onset. Trials were excluded if there  
229 was no identifiable RT or if RT was less than 100 ms (1.4% of all trials). Trials were also  
230 excluded if participants received correct feedback despite inaccurate motor performance; this  
231 was the case when the participant hit the circle only after missing the object on the initial  
232 attempt (2.3% of all trials). Peak speed (PS) was defined as the maximum tangential velocity  
233 of the hand position at the first local peak. Since PS could differ depending on the object  
234 decision in Decision blocks, only trials in which the participant continually moved toward the  
235 circle throughout the trial were included (49.3% of all Decision trials).

236 For each trial, we examined the hand kinematics to determine decisional and motor  
237 performance accuracy at different stages of the movement. The initial direction (ID) of the  
238 movement was calculated as the angle between the midline and the vector linking the hand  
239 position at the start to the hand position at peak acceleration. In Decision blocks, the initial  
240 decision was based on the ID of the movement: movements were classified either as being  
241 aimed toward the object or toward the bar. Initial decision errors were computed for each  
242 participant as the percentage of trials in which the initial decision did not match the expected  
243 movement direction given the true object identify (i.e., aimed toward the bar on trials with a  
244 circle or aimed toward the object on trials with an ellipse). Likewise, final decision errors were  
245 calculated as the percentage of trials the participants' final hand position was closer to the bar  
246 on circle trials or closer to the object on ellipse trials. Trials in which the initial decision and the  
247 final decision were different (e.g., aimed toward the circle but attempted to hit the bar) were  
248 classified as "redirect" movements, indicating a change-of-mind after movement initiation  
249 (Resulaj et al. 2009). We quantified both the total percentage of redirect movements across all  
250 Decision trials, as well as the percentage of initial decision errors that were redirected. This  
251 latter index characterizes how well participants were able to correct wrong initial decisions  
252 online.

253 Finally, to compare motor performance across No Decision and Decision blocks, we  
254 calculated aiming accuracy on trials continually directed toward the circle (i.e., all valid No  
255 Decision trials and Decision circle trials in which both the initial and final decision were  
256 correct). An *aiming error* was defined as whenever the hand position reached the Y-position of  
257 the object, but nevertheless did not successfully hit the object before the trial elapsed.

## 258 *Eye Movements*

260 Details of gaze processing and gaze-event identification are provided in more detail in  
261 previous work (Singh et al. 2017; Singh et al. 2016). Briefly, gaze data were low-pass filtered  
262 at 20 Hz and preprocessed to remove blinks, one-sample spikes (due to incorrect detection of  
263 corneal reflection), and screen outliers (due to instances when gaze drifts outside the  
264 workspace). Gaze events were identified as saccades and fixations using adaptive velocity  
265 and acceleration thresholds (Singh et al. 2016). Our previous analyses showed that velocity  
266 thresholds vary substantially between participants but that acceleration threshold is relatively  
267 constant ( $6,000^\circ/\text{s}^2$ ). For each velocity peak that exceeded the velocity threshold, we  
268 confirmed that the peak acceleration leading up to the velocity peak also exceeded the  
269 acceleration threshold. If both thresholds were exceeded, we classified the gaze event as a

270 saccade. For each saccade, we found the first inflection point before and after the local peak in  
271 gaze angular velocity. Saccade onset corresponded to the first inflection point before the local  
272 peak in gaze angular velocity. Saccade offset was determined by starting at the first inflection  
273 point after the local peak in gaze angular velocity and finding the first point in time at which the  
274 gaze velocity and acceleration remained continuously lower than the respective thresholds for  
275 at least 40 ms.

276 For interception movements, smooth-pursuits were identified when gaze and target  
277 locations and velocities were continuously within a *foveal visual radius* as described in Singh et  
278 al. (2016). Briefly, because targets were presented in a transverse plane, the foveal visual  
279 radius accounts for larger spatial distances for the same foveal visual acuity (2-3°) when the  
280 objects were presented farther away from the body. Note that a gaze event was only classified  
281 as a smooth-pursuit if the target was foveated. Individual saccades were discarded if the  
282 duration was <5 ms, and smooth-pursuits/fixations were discarded if the duration was <40 ms.  
283 On some trials, participants made predictive saccades anticipating the location of the object.  
284 Since we were only concerned with visually-guided performance, we eliminated any saccade  
285 initiated <100 ms after target onset and any initial saccade not directed to the object (>100 mm  
286 from object). Following exclusion of individual saccades, we defined a valid trial for the task as  
287 one containing an initial saccade to the target followed by a fixation or smooth-pursuit. Thus,  
288 gaze for a trial was not analyzed if the trial did not contain a valid saccade and a gaze event  
289 (fixation or pursuit) or if a gaze event (fixation or pursuit) occurred before any saccade. Overall,  
290 gaze data were included for 90.7% of Reaching trials and 88.6% of Interception trials. Data  
291 from two subjects were not included in the eye movement analyses because fewer than 50%  
292 of their trials were identified as valid according to the above criteria.

293 Saccadic reaction time (SRT) for both Reaching and Interception trials was calculated  
294 as the onset of the initial saccade for a given trial. For interception movements, we also  
295 determined the gaze lag as the horizontal distance (mm) between the moving object and the  
296 eye position at the end of the first saccade, and throughout the gaze duration (excluding catch-  
297 up saccades occurring during the smooth-pursuit period). Gaze gain was calculated as the  
298 gaze angular velocity divided by the object angular velocity and average gain was quantified  
299 for the open-loop (15-100 ms of gaze), first 100 ms of the closed-loop (next 100 ms of gaze),  
300 and full closed-loop (gaze after first 100 ms) phases (excluding catch-up saccades). Gaze gain  
301 for the first 15 ms was not analyzed due to the potential for artificially high velocities from the  
302 offset of the preceding saccade. Removal of the first 15 ms did not affect differences in gaze  
303 gain across conditions. Of note, smooth-pursuit gains are typically computed using eye-  
304 trackers with chin rests (Brostek et al. 2017; Churchland and Lisberger 2002) or eye-trackers  
305 that are head-mounted (Spering et al. 2005). With these eye-trackers, gaze movements are  
306 computed as eye-in-head movements. In contrast, we used a remote eye-tracker which  
307 allowed small head movements to occur. Thus, we chose to report gaze gains instead of  
308 smooth-pursuit gains (Barnes 1993; Ranalli and Sharpe 1988). Finally, we determined the  
309 number of catch-up saccades as a function of time after gaze onset and quantified the average  
310 number of catch-up saccades during the entire gaze duration.

### 311 312 *Statistical Analyses*

313 To assess how the introduction of perceptual decision-making influenced RT, PS, and  
314 SRT, we computed the means for each combination of decision type, movement type, object  
315 velocity, and object start location (left or right). We then subtracted the No Decision block

316 means from the Decision block means, separately for each participant and movement type/  
317 trial duration combination. A one-sample  $t$ -test was used to determine whether the change  
318 between Decision and No Decision means were significantly different from zero, and a 2  
319 (Reaching or Interception) x 2 (Fast or Slow) repeated-measures ANOVA assessed whether  
320 the effect of decision-making differed across movement type and trial duration. Measures of  
321 decision-making and hand and eye motor performance were assessed across conditions using  
322 repeated-measures ANOVAs. For all ANOVA tests, the alpha level was set at 0.05 and effect  
323 sizes are reported using generalized  $\eta^2$ . Post hoc pairwise comparisons were conducted using  
324 the Holm correction (Holm 1979). Linear regression was used for bivariate comparisons, with  
325 alpha set to 0.05, and the statistical comparison of correlations between conditions was  
326 evaluated using the Dunn and Clark's  $z$  for dependent groups with nonoverlapping variables  
327 (Dunn and Clark 1969), as implemented in *cocor* package in R (Diedenhofen and Musch  
328 2015).

329

## 330 Results

331

### 332 *Final decision errors occurred more frequently for interception than reaching movements*

333 In the task, participants made rapid eye and arm movements in response to an object  
334 appearing on the visual display. As illustrated in Figure 1C, after object onset participants  
335 typically made saccades directly to the object, followed by fixation on a stationary object near  
336 the right or left edge of the display boundary (Reaching trials) or pursuit of an object moving at  
337 a constant Euclidean velocity from one boundary to the other (Interception trials). Participants  
338 either attempted to hit any circle that appeared by moving the cursor (representing hand  
339 position) to the object before the end of the trial or avoid any ellipse that appeared by moving  
340 in the opposite direction toward a bar on the display.

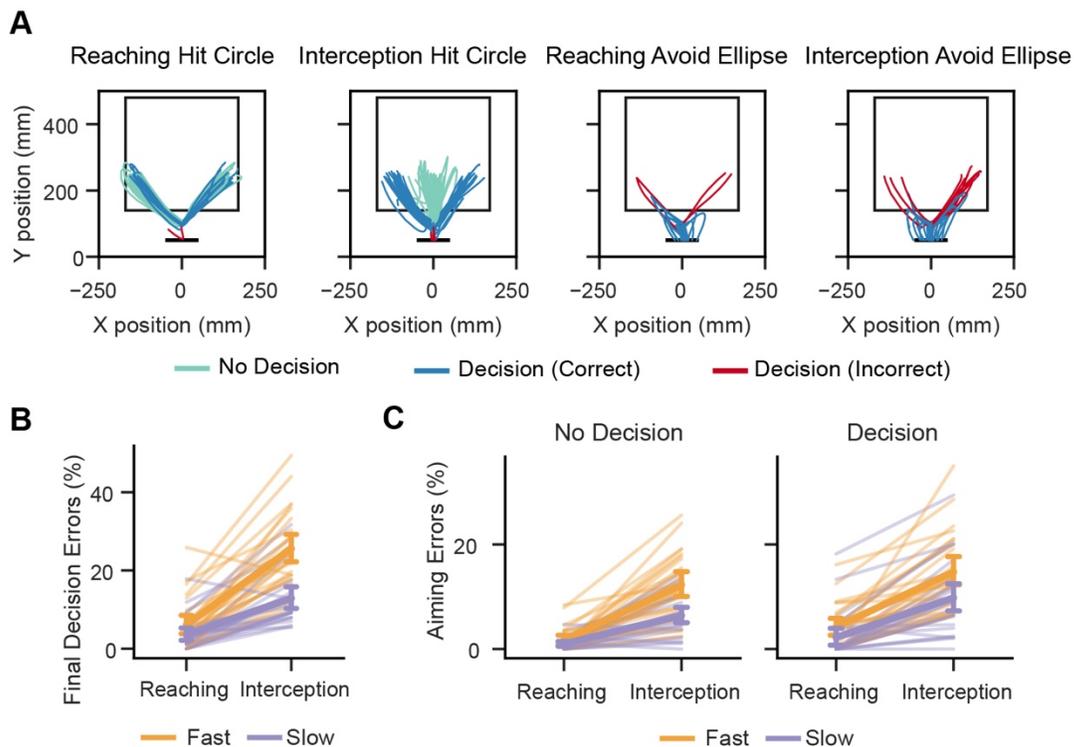
341 Figure 2A shows the hand trajectories for a representative participant. Each line  
342 indicates the hand path from object onset until the participant hit their intended target (object or  
343 bar), or until the maximum trial duration (if neither the object nor the bar was hit). During No  
344 Decision blocks, the object was always a circle, whereas in Decision blocks, the object could  
345 be either a circle or ellipse. The addition of the decision-making task component led to clear  
346 differences in where participants chose to intercept the object. In No Decision blocks, on  
347 average, participants tended to intercept the object slightly after it crossed the midline ( $M =$   
348  $20.1 \pm 5.9$  mm from midline). In contrast, there was a significant shift in object hit locations  
349 during Decision blocks ( $M = 75.0 \pm 5.6$  mm from midline) [main effect of decision:  $F(1,25) =$   
350  $228.77$ ,  $p < 0.001$ ,  $\eta^2 = 0.66$ ]. As expected, interceptions were made later when the object was  
351 moving faster [main effect of trial duration:  $F(1,25) = 110.32$ ,  $p < 0.001$ ,  $\eta^2 = 0.13$ ].

352 In Decision blocks, final decisions were classified as either correctly attempting to hit the  
353 circle or avoid the ellipse, or incorrectly attempting to hit the ellipse or avoid the circle (Fig. 2B).  
354 The percentage of final decision errors was higher for interceptions than for reaching  
355 movements [main effect of movement type:  $F(1,25) = 113.03$ ,  $p < 0.001$ ,  $\eta^2 = 0.52$ ] and for  
356 faster trial durations [main effect of trial duration:  $F(1,25) = 107.72$ ,  $p < 0.001$ ,  $\eta^2 = 0.23$ ]. The  
357 increase in errors at faster durations was larger for interceptions [interaction of movement type  
358 and trial duration:  $F(1,25) = 47.38$ ,  $p < 0.001$ ,  $\eta^2 = 0.12$ ], indicating that faster object velocity  
359 reduced interception decision accuracy beyond decreasing the time possible to hit the object.

360 For Decision blocks, we then computed aiming errors for only those trials where the  
361 final decision was correct. As expected, the additional computational costs associated with

362 estimating object velocity and movement timing led to more aiming errors during interception  
 363 movements. In both No Decision and Decision blocks, there were a higher percentage of  
 364 aiming errors for Interception [main effect of movement type:  $F(1,25) = 129.22, p < 0.001, \eta^2 =$   
 365  $0.43$ ], especially at faster trial durations [interaction of movement type and trial duration:  
 366  $F(1,25) = 20.88, p < 0.001, \eta^2 = 0.04$ ], reflective of the greater difficulty in intercepting an object  
 367 at higher speeds (Fig. 2C). There was an increase in aiming errors in Decision blocks [main  
 368 effect of decision:  $F(1,25) = 11.49, p = 0.002, \eta^2 = 0.06$ ], but the increase did not differ  
 369 between Reaching and Interception [interaction of movement type and decision:  $F(1,25) =$   
 370  $1.48, p = 0.24, \eta^2 = 0.003$ ]. Together, these results suggest that during time-constrained  
 371 perceptual decision-making, the added task demands of interceptive movements affected the  
 372 decisional accuracy more than the motor accuracy.

373



374

375 Figure 2: Final decision errors for interception and reaching movements. A: Sample hand paths from a  
 376 representative participant. During No Decision blocks, participants were required to reach or intercept a circle  
 377 appearing on the display (green paths, left two panels). During Decision blocks, participants were required to hit a  
 378 circle if it appeared (blue and red paths, left two panels), or avoid an ellipse (right two panels). Final decisions on  
 379 these trials were classified as correct if the final hand position was closer to the correct location (object or bar)  
 380 given the object's identify (blue paths), and incorrect if not (red paths). B: Final decision errors were higher for  
 381 interception than reaching and for fast (800 ms) than slow (950 ms) trial durations. C: Aiming errors were higher  
 382 for during interception, and aiming errors increased similarly for both reaching and interception during Decision  
 383 blocks. Errors were calculated as the percentage of all trials in which the y-position of the object was reached but  
 384 the object was not hit. Individual lines represent the means for one participant. Error bars show the 95%  
 385 confidence interval of the group mean estimate.

386 *Perceptual decisions increase urgency to act more for interception relative to reaching*

387 One potential strategy participants could have employed in the Decision trials is to  
 388 complete the recognition of the object shape before initiating a movement. Such a strategy  
 389 would minimize an erroneous commitment to a movement that would later have to be

390 reversed. If this were the case, initial decisions should have been similar between Reaching  
391 and Interception movements. In contrast, there was a large increase in initial decision errors  
392 during Interception relative to Reaching [main effect of movement type:  $F(1,25) = 121.09$ ,  $p <$   
393  $0.001$ ,  $\eta^2 = 0.48$ ] (Fig. 3A). Most of these errors (91.4 %) were due to initially aiming toward the  
394 ellipse (which had to be avoided), suggesting a default initial strategy of trying to hit rather than  
395 avoid the object and then correct the movement if the object shape was correctly identified  
396 during the movement. This default strategy was used more often during faster trials [main  
397 effect of trial duration:  $F(1,25) = 19.09$ ,  $p < 0.001$ ,  $\eta^2 = 0.05$ ], when there were greater  
398 constraints to hit the object in time.

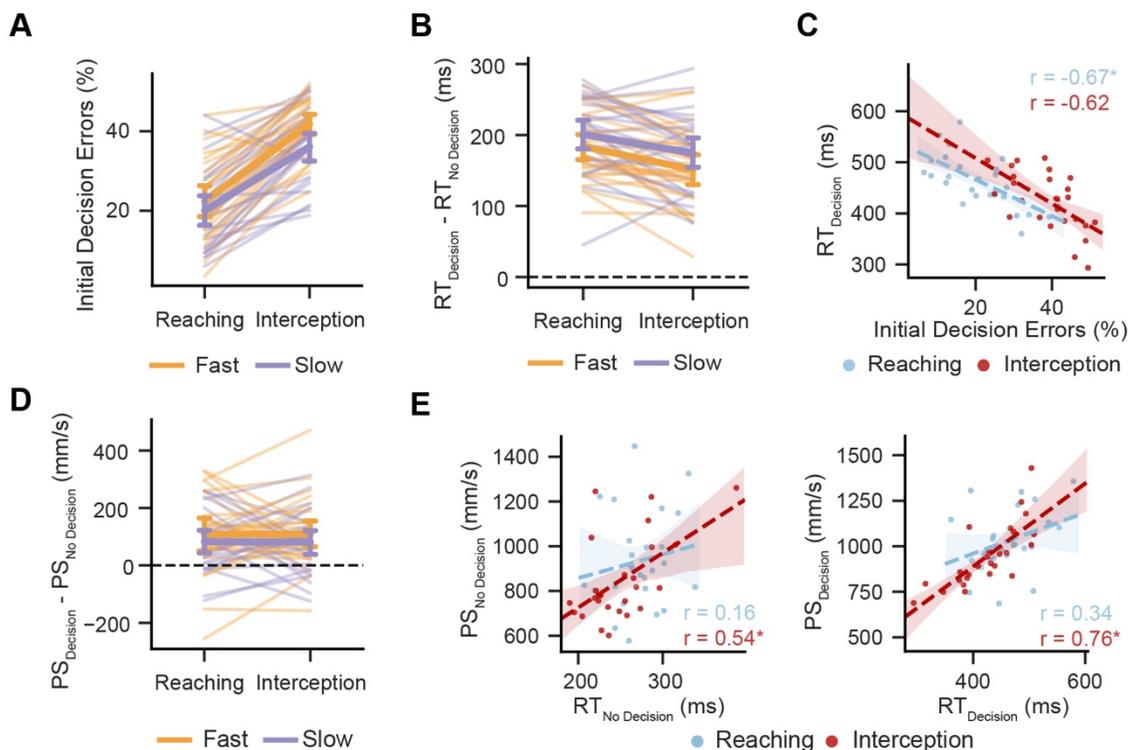
399 As expected, perceptual decision-making led to a significant reaction time (RT) delay.  
400 Relative to No Decision blocks, RTs for Decision blocks were on average  $178 \pm 11$  ms longer  
401 [ $t(1,25) = 20.04$ ,  $p < 0.001$ ] (Fig. 3B). Thus, perceptual decisions based on ventral stream  
402 processing clearly increased the time taken for object identification (circle or ellipse) and motor  
403 response selection (hit or avoid). However, the increase in RT for the Decision blocks differed  
404 depending on the type of movement and time constraints: RT increase was smaller for  
405 Interception [main effect of movement type:  $F(1,25) = 13.63$ ,  $p = 0.001$ ,  $\eta^2 = 0.07$ ], and for Fast  
406 movement blocks [main effect of trial duration:  $F(1,25) = 9.83$ ,  $p = 0.004$ ,  $\eta^2 = 0.04$ ]. This  
407 suggests that even though decisions added processing time, participants chose to limit pre-  
408 movement processing time when an interception was required or under more restrictive time  
409 constraints. The increased urgency to act came at the expense of initial decision accuracy:  
410 participants with shorter RTs during Decision blocks exhibited more initial decision errors for  
411 both reaching and interception movements (Reaching:  $r = -0.67$ ,  $p < 0.001$ ; Interception:  $r = -$   
412  $0.62$ ,  $p < 0.001$ ) (Fig. 3C).

413 During decision-making, there was also an increase in the speed of the response: on  
414 average, peak speed (PS) of movements attempting to hit the object increased by  $95.4$  mm/s  
415 [ $t(1,25) = 5.46$ ,  $p < 0.001$ ] (Fig. 3D). The change in PS did not vary based on movement type  
416 [main effect of movement type:  $F(1,25) = 0.00$ ,  $p = 0.98$ ,  $\eta^2 < 0.01$ ] or trial duration [main effect  
417 of trial duration:  $F(1,25) = 2.70$ ,  $p = 0.11$ ,  $\eta^2 = 0.01$ ]. For reaching movements, the increase in  
418 PS may reflect a general urgency to complete the movement more quickly after a prolonged  
419 decision period. For interception movements, where participants have a salient visual cue for  
420 time remaining (the object approaching the boundary), changes in PS are likely more directly  
421 related to changes in RT: the longer the participant waited to initiate movement, the less time  
422 available and longer movement amplitude necessary to hit the object. Indeed, for both No  
423 Decision and Decision blocks, there was a significant positive correlation between PS and RT  
424 (No Decision:  $r = 0.54$ ,  $p = 0.003$ ; Decision:  $r = 0.76$ ,  $p < 0.001$ ), which was not the case for  
425 reaching movements (No Decision:  $r = 0.16$ ,  $p = 0.43$ ; Decision:  $r = 0.34$ ,  $p = 0.08$ ) (Fig. 3E).  
426 The PS-RT correlation was significantly greater for Decision, Interception blocks than for No  
427 Decision, Reaching blocks ( $z = 2.98$ ,  $p = 0.003$ ), indicating that the lower RTs during decision-  
428 making for interception may be in part to allow for slower, shorter movement trajectories.  
429 Overall, the results suggest that perceived time constraints—amplified during both interception  
430 movements and faster trial durations—encourage earlier movement initiation even if the  
431 decision process is incomplete.

432  
433 *Interception strategies favor ongoing decision-making after movement initiation*

434 To further investigate how movements are planned relative to time-sensitive decision  
435 processing, we analyzed how often participants adjusted their movements online. To do this,

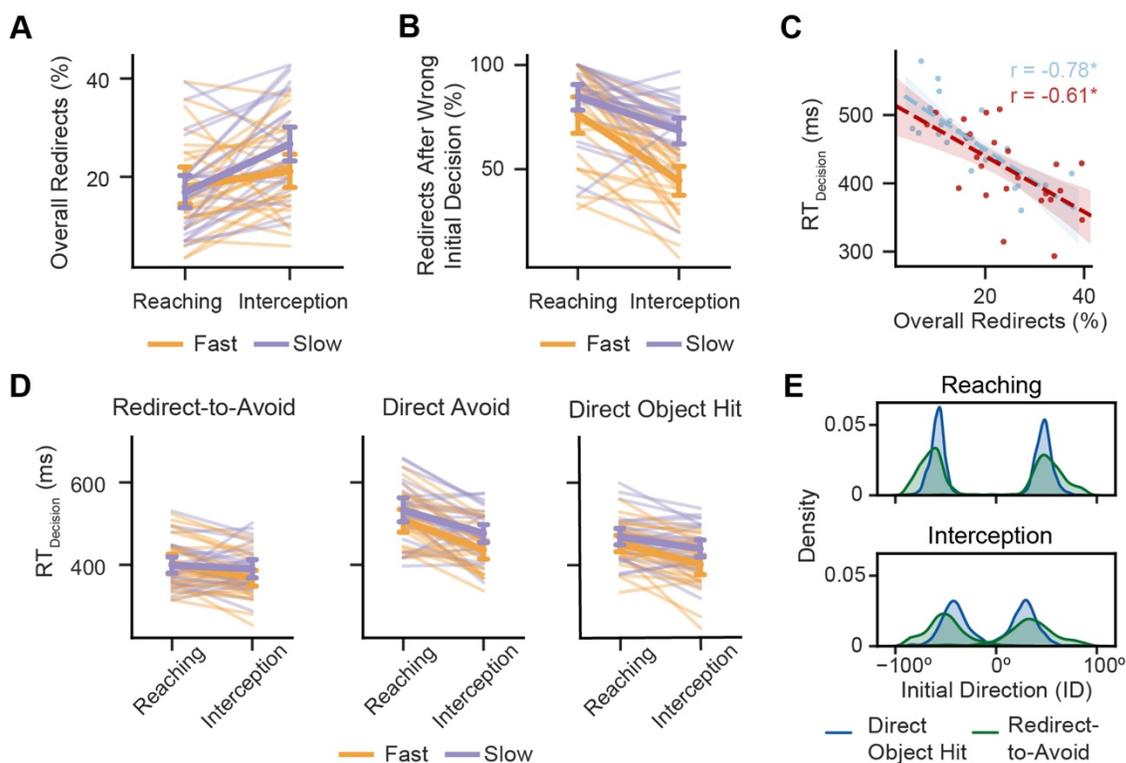
436 we distinguished between “direct” and “redirect” movements. Direct movements were when  
 437 both the initial and final decisions were directed toward the object (direct object hit) or to the  
 438 bar (direct avoid). Redirect movements occurred when the final decision differed from the initial  
 439 decision: as can be seen in Figure 2A, redirects were predominantly observed when the  
 440 participant made an initial decision toward the object, only to curve back around to hit the bar  
 441 (redirect-to-avoid). The opposite pattern—moving to the object after initially moving to avoid it  
 442 (redirect-to-hit), rarely occurred (<0.01% of Decision trials), highlighting the greater accuracy  
 443 demands imposed by hitting the object vs. hitting the bar.



444  
 445 Figure 3: Reaction times and limb kinematics for interception and reaching movements. A: Initial decision errors  
 446 were higher for interception and for fast (800 ms) trial durations. B: The increase in reaction time from No  
 447 Decision to Decision blocks was smaller for interception relative to reaching. C: Participants were shorter reaction  
 448 times during Decision blocks were exhibited a higher number of initial decision errors. D: Peak speed increased  
 449 for Decision blocks similarly for reaching and interception. E: Reaction time and peak speed tended to be more  
 450 correlated during interception and Decision blocks. For line plots, individual lines represent the means for one  
 451 participant and error bars show the 95% confidence interval of the group mean estimate. For regression plots,  
 452 each dot represents the mean value for one participant and shaded area represents the 95% confidence interval  
 453 of the regression estimate. \* indicates  $p < 0.05$ .

454 All participants had both direct and redirect movements, indicating a mixture of  
 455 strategies used during the task. Overall, redirect movements were more common during  
 456 Interception [main effect of movement type:  $F(1,25) = 16.82$ ,  $p < 0.001$ ,  $\eta^2 = 0.11$ ], especially at  
 457 Slow trial durations [interaction of movement type and trial duration:  $F(1,25) = 9.61$ ,  $p = 0.005$ ,  
 458  $\eta^2 = 0.03$ ] (Fig. 4A). This suggests that decisions about object shape could be modified after  
 459 movement initiation. Furthermore, participants were more likely to rely on this strategy for  
 460 complex interceptive movements and when there was more time for online corrections (Slow  
 461 trials).

462 Though redirect movements were used more during Interception, they were employed  
 463 more effectively during Reaching. As shown in Figure 4B, after an initial decision error, a  
 464 correct redirect of an initially wrong decision was more likely to occur for Reaching [main effect  
 465 of movement type:  $F(1,25) = 50.82, p < 0.001, \eta^2 = 0.30$ ] and for Slow trial durations [main  
 466 effect of trial duration:  $F(1,25) = 55.83, p < 0.001, \eta^2 = 0.16$ ]. Therefore, task difficulty limited  
 467 the ability to implement a corrective movement when they were necessary.  
 468



469  
 470 Figure 4: Redirected movements and Initial Directions (ID) reveal ongoing decision-making after movement  
 471 initiation. A: Redirect movements (change between initial and final decision) during Decision blocks were higher  
 472 for interception, suggesting more online adjustments after movement initiation. B: Initial decision errors were more  
 473 likely to be corrected for reaching and slow trial durations. C: Participants were shorter reaction times during  
 474 Decision blocks were exhibited a higher number of redirect movements. Each dot represents the mean value for  
 475 one participant and shaded area represents the 95% confidence interval of the regression estimate. \* indicates  $p$   
 476  $< 0.05$ . D: Mean reaction times were shortest for redirect-to-avoid movements (initially aimed toward object then  
 477 redirected to bar), longest for direct avoid movements (directed toward bar throughout), and intermediate for  
 478 direct object hits (directed to object throughout). In all cases, interception reaction times were shorter than those  
 479 for reaching. Individual lines represent the means for one participant and error bars show the 95% confidence  
 480 interval of the group mean estimate. E: Kernel density estimate of the initial movement direction ( $0^\circ$  = aimed at  
 481 midline) for redirect-to-avoid and direct object hit movements. IDs were aimed farther from the midline for redirect-  
 482 to-avoids during Decision blocks for both reaching (upper panel) and interception (lower panel).

483 If initial decisions were less likely to be corrected, why were participants more likely to  
 484 redirect their movements during Interception trials? In Decision blocks, movements might have  
 485 been initiated early (during both Reaching and Interception trials) before the perceptual  
 486 decision was complete, but once the movements were underway the complexity of the  
 487 interception movements may have made it much harder to correct them. If this is the case,  
 488 initiation of redirect movements should be associated with shorter RTs. Indeed, for both

489 Reaching and Interception, participants with a higher proportion of redirect movements  
490 exhibited shorter decision RTs [Reaching:  $r = -0.78$ ,  $p < 0.001$ ; Interception:  $r = -0.61$ ,  $p <$   
491  $0.001$ ], suggesting a greater reliance on online adjustments and ongoing decision-making after  
492 movement initiation (Fig. 4C). Furthermore, there were RT differences depending on the  
493 movement strategy (redirect-to-avoid, direct avoid, direct object hit) ultimately executed.  
494 Redirect-to-avoid movements (i.e., movements initiated towards ellipse but subsequently  
495 corrected) had an average RT of  $390 \pm 11$  ms, relative to  $489 \pm 15$  ms for direct avoids [main  
496 effect of movement strategy:  $F(1.32, 33.12) = 71.64$ ,  $p < 0.001$ ,  $\eta^2 = 0.35$ , Greenhouse-Geisser  
497 corrected] (Fig. 4D). The average RT for direct object hits was approximately halfway in-  
498 between the RTs for the two types of avoid movements ( $439 \pm 12$  ms), reflecting that  
499 participants defaulted towards initiating a movement towards the object even when their  
500 decision was incomplete. Interestingly, RTs were shorter for Interception than Reaching for  
501 redirect-to-avoid, direct avoids, and direct hits [all  $t$ 's  $> 2.2$ , all  $p$ 's  $< 0.05$ ], and the RT  
502 difference was largest for direct avoids [interaction of movement type and strategy:  $F(1.34,$   
503  $33.48) = 8.51$ ,  $p = 0.003$ ,  $\eta^2 = 0.02$ , Greenhouse-Geisser corrected]. This suggests that simply  
504 preparing for an interception movement, even when it was not selected, contributed to earlier  
505 movement initiation.

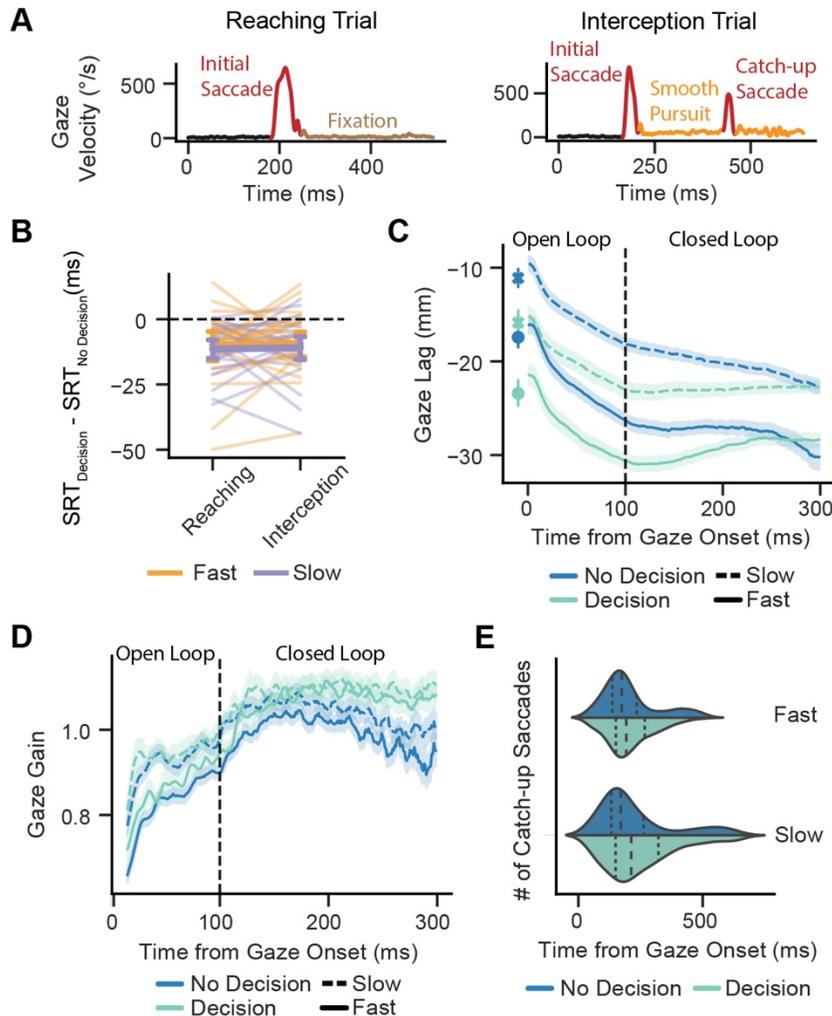
506 A closer analysis of the movement trajectories suggests that the initial movement plans  
507 carried a signature of an incomplete decision during movement initiation. Both direct object hit  
508 and redirect-to-avoid movements were initially aimed toward the object, indicating an early  
509 motor plan to hit the object. However, as shown in Figure 4E, trajectories of movements that  
510 were ultimately redirected were on average initially aimed farther from the midline than direct  
511 movements (longer tail for redirect-to-avoid) [main effect of movement strategy:  $F(1,25) =$   
512  $131.91$ ,  $p < 0.001$ ,  $\eta^2 = 0.28$ ], and this difference was larger for Interception [interaction of  
513 movement type and strategy:  $F(1, 25) = 10.59$ ,  $p = 0.003$ ,  $\eta^2 = 0.01$ ]. The deviation of the initial  
514 direction away from the midline likely reflects an intermediate motor plan between hitting the  
515 circle and the bar, suggesting a more conservative approach when the decision is not fully  
516 formed.

517  
518 *Perceptual decision-making influences eye movement strategies*

519 Saccades and gaze events were identified using a geometric method to transform eye  
520 movement data to the horizontal plane and adaptive velocity-based thresholds (Singh et al.  
521 2016) for each participant (see Fig. 5A). Standard task performance consisted of an initial  
522 saccade followed by onset of gaze (fixation or smooth-pursuit) on the target - we restricted our  
523 eye movement analysis to the trials that followed that structure (see Methods for details).

524 As shown in Figure 5B, SRTs during Decision blocks were on average  $10.4 (\pm 2.3)$  ms  
525 faster during Decision blocks than No Decision blocks [ $t(1,23) = -5.52$ ,  $p < 0.001$ ]. The  
526 decrease in SRTs was similar for both Reaching and Interception [main effect of movement  
527 type:  $F(1,23) = 0.08$ ,  $p = 0.79$ ,  $\eta^2 < 0.01$ ], suggesting that adding a perceptual decision  
528 increased the general urgency to launch a saccade. However, as can be seen for Interception  
529 movements, there was likely a speed-accuracy trade-off associated with faster SRTs: the initial  
530 saccade landed farther behind the moving object during Decision blocks [see Fig. 5C; main  
531 effect of decision:  $F(1,23) = 13.93$ ,  $p = 0.001$ ,  $\eta^2 = 0.04$ ] and for Fast trial durations (i.e., when  
532 the object was moving at faster velocities) [main effect of trial duration:  $F(1,23) = 37.25$ ,  $p <$   
533  $0.001$ ,  $\eta^2 = 0.07$ ]. Eye position lag persisted during approximately the first 300 ms of the  
534 smooth-pursuit period [main effect of decision type:  $F(1,23) = 17.74$ ,  $p < 0.001$ ,  $\eta^2 = 0.14$ ; main

535 effect of trial duration:  $F(1,23) = 114.18, p < 0.001, \eta^2 = 0.32$ ]. This result suggests that the  
 536 urgency of the initial saccade led to less precise oculomotor movement during decision-  
 537 making.  
 538



539 Figure 5: Perceptual decision-making influences eye movement strategies. A: Two representative trials showing classification  
 540 of gaze events using adaptive velocity-based thresholds for reaching to stationary targets and intercepting moving targets. B:  
 541 Saccadic reaction times decreased for Decision blocks similarly for reaching and interception. C: Gaze lag across interception  
 542 trials for the end of the initial saccade and as a function of time from gaze onset. Positive values indicate that the gaze led the  
 543 object, whereas negative values indicate lag. Participants lagged more during Decision blocks and at fast trial durations  
 544 (higher object velocity). The error bars and shaded area represents the 95% confidence interval of the mean estimate. D:  
 545 Gaze gain across interception trials as a function of time from gaze onset. Gaze gain was higher for faster velocities during the  
 546 open-loop period and higher for Decision blocks during the closed-loop period. The shaded area represents the 95%  
 547 confidence interval of the mean estimate. E: Distribution of catch-up saccades after gaze onset during interception. Catch-up  
 548 saccades were more frequent during Decision blocks. The dotted lines denote the quartiles of the distribution.  
 549

550 Participants compensated for the initial lag in pursuit by increasing the gaze gain.  
 551 Though gaze gain in the open-loop period (15-100 ms after pursuit initiation) was driven mainly  
 552 by differences in object velocity [main effect of trial duration:  $F(1,23) = 58.67, p < 0.001, \eta^2 =$   
 553  $0.13$ ], during the closed-loop period gaze gain increased for Decision blocks relative to No  
 554 Decision blocks [main effect of decision:  $F(1,23) = 49.02, p < 0.001, \eta^2 = 0.15$ ] (Fig. 5D). This  
 555 effect is not simply due to longer pursuit durations during Decision blocks, as gains are also

556 longer when the analysis is restricted to the first 100 ms of the closed-loop period [main effect  
557 of decision:  $F(1,23) = 8.71$ ,  $p = 0.007$ ,  $\eta^2 = 0.04$ ]. This suggests that the negative closed  
558 feedback loop that minimizes retinal error between gaze and target is engaged differently  
559 when perceptual decision-making task-constraints are imposed during pursuit eye movements.

560 Participants also initiated more catch-up saccades during Decision blocks ( $M = 0.99 \pm$   
561  $0.30$  saccades/s) than No Decision blocks ( $M = 0.68 \pm 0.30$  saccades/s) to make up for the lag  
562 in object pursuit [main effect of decision type:  $F(1,23) = 16.23$ ,  $p < 0.001$ ,  $\eta^2 = 0.10$ ] (see Fig.  
563 5E). The mean latency of when the catch-up saccade occurred relative to pursuit onset did not  
564 differ across decision type blocks [main effect of decision:  $F(1,23) = 1.06$ ,  $p = 0.31$ ,  $\eta^2 < 0.01$ ]  
565 or trial duration [main effect of trial duration:  $F(1,23) = 2.25$ ,  $p = 0.15$ ,  $\eta^2 = 0.02$ ]. Together,  
566 these results suggest that ocular movements are altered when decision about object features  
567 have to be made in addition to estimating its spatial location.

568

## 569 Discussion

570 In the current study, we asked the question: how does perceptual decision-making  
571 involving the two visual streams affect visuomotor coordination during reaching and  
572 interception movements? To address this question, we manipulated ventral stream  
573 involvement in a rapid visuomotor task. In one condition, participants made reaching or  
574 interception movements to hit an object shaped like a circle. In another condition, participants  
575 had to judge the shape of the object: if a circle appeared, they were instructed to reach or  
576 intercept it, but if an ellipse appeared, they were instead instructed to make a movement away  
577 from the ellipse and towards a horizontal bar. Our results support our first hypothesis of  
578 differential effects of ventral stream engagement on dorsal stream processing during  
579 interception relative to reaching movements. Furthermore, we also found support for our  
580 second hypothesis - that changes in oculomotor behavior when the ventral visual stream is  
581 engaged may contribute to differences in limb motor performance.

582 Many studies have probed the interactions between dorsal and ventral stream  
583 processes during reaching movements (reviewed in Song and Nakayama 2009) but to the best  
584 of our knowledge only a handful of studies have extended this type of paradigm to interception  
585 movements (de la Malla et al. 2019; Lacquaniti and Maioli 1989). Our approach also differs  
586 from the classical *backward masking* approach used by some researchers to quantify how  
587 object recognition affects planning and execution of reaching movements (Cressman et al.  
588 2007; Schmidt 2002). In this approach, a brief target stimulus (prime) is followed by a mask  
589 that impedes recognition of the target. These studies showed that reaching movement  
590 trajectories were strongly affected by the prime target, even when blocked from awareness by  
591 masking, suggesting a flow of object property information from the ventral visual stream to the  
592 dorsal action stream. In our approach, we presented the same stimulus for the entire trial  
593 duration to afford participants flexibility in how they processed object shape. We chose two trial  
594 times of 800 ms (Fast) and 950 ms (Slow) to give participants enough time to identify object  
595 shape (~250-300 ms) and plan movements (~100-200 ms) in a sequential fashion, i.e. to  
596 minimize decision errors participants could first ascertain the object shape and then plan the  
597 movement trajectory. Our paradigm also allowed participants to judge the object shape and  
598 prepare a motor plan simultaneously. If the slower ventral stream process of shape recognition  
599 took longer than the preparation of the motor plan, we predicted that effective ventral-dorsal  
600 stream integration would allow participants to take corrective action by completing shape  
601 recognition after the movement had been initiated. Our results show that participants used

602 both strategies. Longer reaction times of ~500 ms were associated with fewer decision errors  
603 and redirected movements (see Fig. 3C and 4C). In contrast, average reaction times of ~400  
604 ms were associated with more decision errors as well as corrective redirected movements.

605

#### 606 *Online integration of ventral stream and decision processing during interception*

607 Vision for goal selection based on object properties and vision guiding the online control  
608 of movement have been conceptualized as two specialized processes mediated by the ventral  
609 and dorsal streams, respectively (Goodale and Milner 1992; Goodale and Westwood 2004).  
610 While much work has concerned how the two visual streams serve unique functional roles  
611 operating largely independent of each other, less is known about the interaction in more  
612 complex task environments. The current task was designed to force this interaction—that is, in  
613 order to perform the correct action (hit the object or avoid it), participants must accurately  
614 identify the object's shape (circle or ellipse). We found that even under time constraints (800  
615 ms to hit the object in the Fast condition), participants could recognize objects and formulate a  
616 decision prior to movement initiation. Relative to No Decision blocks, in which participants only  
617 needed to process spatial information to facilitate movement, there was an average RT delay  
618 of 178 ms in Decision blocks (see Fig. 3B), suggesting additional processing time for shape  
619 recognition and motor goal selection (Cisek and Kalaska 2010; Thorpe and Fabre-Thorpe  
620 2001; Veerman et al. 2008). Thus, it is reasonable to assume from the average RTs that  
621 perceptual processing in the ventral stream could precede dorsal stream processing of  
622 visuomotor transformations for action execution.

623 However, closer investigation of the movement trajectories and corresponding RTs  
624 provides evidence that processing of object information and decision-making continues after  
625 movement initiation. During both reaching and interception, we observed that participants  
626 would often initiate their movements toward the circle only to curve around past the original  
627 start location and hit the bar. The presence of these “redirect-to-avoid” movements (see Fig.  
628 4D) provide evidence of an evolving decision given accumulating stimulus information (Resulaj  
629 et al. 2009; Selen et al. 2012). In contrast to previous studies investigating sensorimotor  
630 decisions of the limb that vary the motion or spatial location of the target (Burk et al. 2014;  
631 Gallivan et al. 2016; van den Berg et al. 2016), here we show that sensorimotor  
632 transformations computed in the dorsal stream can seamlessly integrate incoming information  
633 about object shape that originates in the ventral stream (Davare et al. 2007; Konen and  
634 Kastner 2008; Lehky and Tanaka 2016; Sereno and Maunsell 1998). The distribution of initial  
635 movement directions (see Fig. 4E) of redirected movements toward the direction of the bar  
636 suggests that movements are planned to optimize task success given uncertainty about the  
637 impending decision (Haith et al. 2015; Nashed et al. 2017; Wong and Haith 2017). Thus, even  
638 though the imposed time constraints allowed for sequential stimulus identification, decision-  
639 making, and movement execution, participants tended to favor an alternative strategy in which  
640 both these processes co-occurred during preparation and execution (Haith et al. 2016; Orban  
641 de Xivry et al. 2017).

642 What determines the reliance on integration of ventral and dorsal stream information  
643 during visuomotor control? In the present task, the complexity of the motor response  
644 modulated the perceived urgency to act (Thura 2020; Thura and Cisek 2016). Both initial and  
645 final decision errors increased during interception relative to reaching during decision-making,  
646 largely due to participants initially aiming toward and then unable to correct a response toward  
647 a moving ellipse. In addition, movements were more likely to be redirected during interception,

648 indicating a stronger bias toward initiating a hit movement prior to making a perceptual  
649 decision about object shape. Furthermore, an individual's initial decision error rate and  
650 tendency to perform redirect movements were each associated with shorter RTs, indicating  
651 that the shorter RTs during interceptions in Decision blocks were likely due to a greater  
652 dependency on online decision-making and motor control (Brenner and Smeets 2018).

653 However, given that the urgency to act during interception had clear consequences on  
654 task performance (more decisional errors), the capacity for integration of ventral stream  
655 information with visuomotor performance may be limited. Our results suggest that the urgency  
656 of the response may interfere with, rather than be a consequence of, differential ventral-dorsal  
657 stream interactions. Further work directly addressing different stimulus attributes associated  
658 with separate areas along the ventral pathway (e.g., orientation, color, size) can help clarify  
659 how movements are planned relative to the time-course of sensory processing and decision-  
660 making. Notably, the errors in interception during decision-making were associated with the  
661 inability to adjust initial movement trajectories that account for decisional demands, but the  
662 increase in aiming errors was no different between interception and reaching. This suggests  
663 that the interference in the time-course of ventral-dorsal stream interactions mainly affects  
664 decision processes rather than the online control of movement per se.

665 Our study does not address how the dorsal stream receives ventral stream information  
666 about object shape, but recent work has identified pathways between the two streams that  
667 could facilitate direct communication during ongoing sensorimotor control (Budisavljevic et al.  
668 2018; Takemura et al. 2016). The present findings suggest that that the motor system can  
669 integrate prolonged processing of sensory information originating in the ventral stream, but  
670 how the extent to which this integrated information can be accessed depends on movement  
671 complexity.

672  
673 *Modulation of gaze gains during perceptual decision-making*

674 During Decision blocks, saccades were launched about 10 ms earlier than No-Decision  
675 blocks. It appears that the earlier launch of the saccade was because of a perceived urgency  
676 to recognize the object shape and make the correct motor decision. Saccades to visible targets  
677 are generally imprecise and undershoot target position (Krappmann 1998). Thus, the earlier  
678 launch may have occurred before the spatial planning of the saccade was complete, resulting  
679 in larger undershoots farther away from the object (larger gaze lags in Decision blocks, Fig.  
680 5C). Since in our study objects had to be foveated to be recognized, the oculomotor system  
681 may have increased the gaze gains (Fig. 5D) and made more catch-up saccades (Fig. 5E) to  
682 the target during Decision blocks to compensate for the large lags at the end of the saccades.

683 Smooth-pursuit gains have been conventionally defined as the ratio of target and gaze  
684 velocity in angular coordinates in head-fixed conditions. The first 100 ms of the smooth-pursuit  
685 movement is referred to as the open-loop phase (Barnes 2008; Tychsen and Lisberger 1986).  
686 This is followed by the onset of closed-loop pursuit, which is mainly controlled by a negative  
687 feedback loop to ensure that the eye velocity closely matches the target velocity. However,  
688 pursuit gains are defined for head-fixed conditions to ensure that the vestibular-ocular reflex  
689 does not interfere with gaze movements. Since our eye-tracker could have allowed small head  
690 movements, we decided to report gaze gains (Barnes 1993; Collins and Barnes 1999; Ranalli  
691 and Sharpe 1988) instead of pursuit gains. One study in primates has shown that when the  
692 head is unrestrained, pursuit and gaze gains are similar suggesting that eye and head  
693 movements are controlled together within the pursuit pathways (Dubrovsky and Cullen 2002).

694 Thus, we compared both open-loop (first 100 ms) and closed-loop gaze gains (>100 ms) as a  
695 proxy for pursuit gains for the Interception blocks for the No Decision and Decision conditions.

696 As expected, changes in the open-loop gains were driven predominantly by object  
697 velocity (Fast versus Slow). However, the closed-loop gains were significantly higher for the  
698 Decision than No Decision blocks. An important question is whether these higher gains for the  
699 Decision blocks reflected the constraints imposed by shape recognition or were simply a  
700 compensation for the large errors in where the saccade landed. Previously, it has been shown  
701 that object recognition is impaired when targets move at high speeds (Ludvigh and Miller  
702 1958b; Schütz et al. 2009; Westheimer and McKee 1975). In contrast to the slow speed of 1-  
703 10°/sec used in these studies, the objects in our experiment moved at approximately 80-  
704 90°/sec. This speed approaches the limit of smooth-pursuit in humans (Meyer et al. 1985) and  
705 we expected that participants would not only have trouble in pursuing objects at high speeds,  
706 but that it would also compromise their ability to recognize objects. However, the closed-loop  
707 pursuit gains were similar between Fast and Slow blocks, and only differed between the  
708 Decision blocks. Thus, it seems that the gaze lag (caused by earlier release of the saccade)  
709 and the need to foveate the object to recognize the shape together contributed to a higher  
710 closed-loop gaze gain. This suggests that the negative closed feedback loop that minimizes  
711 retinal error between gaze and target is engaged differently when the ventral stream is  
712 engaged for perceptual decision-making during pursuit eye movements.

713 Our result suggests that the visual perceptual decision-making network, that includes  
714 the ventral visual stream, dorsolateral prefrontal regions and frontal eye fields (Heekeren et al.  
715 2004; Heekeren et al. 2008; Sakagami and Pan 2007), may provide either a predictive or  
716 urgency signal to the smooth-pursuit system to increase the gain and minimize the retinal error  
717 between the target and the gaze. Indeed, stimulation and lesion studies have implicated the  
718 frontal eye fields with the modulation of smooth-pursuit gain during object tracking (Gagnon et  
719 al. 2006; Keating 1991; Morrow and Sharpe 1995; Shi et al. 1998). Furthermore, anatomical  
720 tracer studies in primates have shown that the dorsal and ventral processing streams converge  
721 in the lateral frontal eye fields (Schall et al. 1995). Taken together with our data, this suggests  
722 that in tasks where perceptual decision-making is necessary during pursuit eye movements,  
723 the frontal eye fields may modulate gaze gains to meet task demands.

724

## 725 *Conclusions*

726 In this study, we introduced a visuomotor decision-making task in which a successful  
727 reaching or interception movement depended on visual processing for perception and action in  
728 the ventral and dorsal streams. We found that engagement of the ventral stream led to more  
729 decision errors and a smaller increase in hand RTs for interception movements relative to  
730 reaching movements, reflective of a greater perceived urgency to act during interception.  
731 During decision-making, participants had faster saccadic RTs and adopted online movement  
732 strategies that incorporated an evolving decision about object shape. Additionally, participants  
733 exhibited higher gaze gains to adapt to the demands of integrating the perceptual decision with  
734 visuomotor control. These results suggest that the capacity to effectively integrate ventral-  
735 dorsal stream information during ongoing movement depends on the perceived urgency to act,  
736 which is greater when intercepting a moving target.

## References

- Ales JM, Appelbaum LG, Cottureau BR, and Norcia AM.** The time course of shape discrimination in the human brain. *Neuroimage* 67: 77-88, 2013.
- Barnes GR.** Cognitive processes involved in smooth pursuit eye movements. *Brain and Cognition* 68: 309-326, 2008.
- Barnes GR.** Visual-vestibular interaction in the control of head and eye movement: The role of visual feedback and predictive mechanisms. *Progress in Neurobiology* 41: 435-472, 1993.
- Brenner E, and Smeets JB.** Sources of variability in interceptive movements. *Exp Brain Res* 195: 117-133, 2009.
- Brenner E, and Smeets JBJ.** Continuously updating one's predictions underlies successful interception. *J Neurophysiol* 120: 3257-3274, 2018.
- Brostek L, Eggert T, and Glasauer S.** Gain Control in Predictive Smooth Pursuit Eye Movements: Evidence for an Acceleration-Based Predictive Mechanism. *eNeuro* 4: 2017.
- Budisavljevic S, Dell'Acqua F, and Castiello U.** Cross-talk connections underlying dorsal and ventral stream integration during hand actions. *Cortex* 103: 224-239, 2018.
- Burk D, Ingram JN, Franklin DW, Shadlen MN, and Wolpert DM.** Motor effort alters changes of mind in sensorimotor decision making. *PLoS One* 9: e92681, 2014.
- Churchland AK, and Lisberger SG.** Gain control in human smooth-pursuit eye movements. *J Neurophysiol* 87: 2936-2945, 2002.
- Cisek P, and Kalaska JF.** Neural mechanisms for interacting with a world full of action choices. *Annu Rev Neurosci* 33: 269-298, 2010.
- Collins C, and Barnes G.** Independent control of head and gaze movements during head-free pursuit in humans. *Journal of Physiology* 515: 299-314, 1999.
- Cressman EK, Franks IM, Enns JT, and Chua R.** On-line control of pointing is modified by unseen visual shapes. *Consciousness and Cognition* 16: 265-275, 2007.
- Culham JC, Cavina-Pratesi C, and Singhal A.** The role of parietal cortex in visuomotor control: what have we learned from neuroimaging? *Neuropsychologia* 44: 2668-2684, 2006.
- Davare M, Andres M, Clerget E, Thonnard JL, and Olivier E.** Temporal dissociation between hand shaping and grip force scaling in the anterior intraparietal area. *J Neurosci* 27: 3974-3980, 2007.
- Day BL, and Lyon IN.** Voluntary modification of automatic arm movements evoked by motion of a visual target. *Exp Brain Res* 130: 159-168, 2000.
- de la Malla C, Brenner E, de Haan EHF, and Smeets JBJ.** A visual illusion that influences perception and action through the dorsal pathway. *Communications Biology* 2: 38, 2019.
- Diedenhofen B, and Musch J.** cocor: a comprehensive solution for the statistical comparison of correlations. *PLoS One* 10: e0121945, 2015.
- Dubrovsky AS, and Cullen KE.** Gaze-, eye-, and head-movement dynamics during closed-and open-loop gaze pursuit. *Journal of Neurophysiology* 87: 859-875, 2002.
- Dunn OJ, and Clark V.** Correlation coefficients measured on the same individuals. *Journal of the American Statistical Association* 64: 366-377, 1969.
- Fooken J, and Spering M.** Decoding go/no-go decisions from eye movements. *J Vis* 19: 5, 2019.
- Franklin DW, Reichenbach A, Franklin S, and Diedrichsen J.** Temporal Evolution of Spatial Computations for Visuomotor Control. *J Neurosci* 36: 2329-2341, 2016.
- Gagnon D, Paus T, Grosbras M-H, Pike GB, and O'Driscoll GA.** Transcranial magnetic stimulation of frontal oculomotor regions during smooth pursuit. *Journal of Neuroscience* 26: 458-466, 2006.
- Gallivan JP, Chapman CS, Wolpert DM, and Flanagan JR.** Decision-making in sensorimotor control. *Nat Rev Neurosci* 19: 519-534, 2018.
- Gallivan JP, and Goodale MA.** The dorsal "action" pathway. In: *Handbook of clinical neurology* Elsevier, 2018, p. 449-466.
- Gallivan JP, Logan L, Wolpert DM, and Flanagan JR.** Parallel specification of competing sensorimotor control policies for alternative action options. *Nat Neurosci* 19: 320-326, 2016.

- Gauthier GM, Nommay D, and Vercher JL.** The role of ocular muscle proprioception in visual localization of targets. *Science* 249: 58-61, 1990.
- Gold JI, and Shadlen MN.** The neural basis of decision making. *Annu Rev Neurosci* 30: 535-574, 2007.
- Goodale MA, and Milner AD.** Separate visual pathways for perception and action. *Trends Neurosci* 15: 20-25, 1992.
- Goodale MA, and Westwood DA.** An evolving view of duplex vision: separate but interacting cortical pathways for perception and action. *Curr Opin Neurobiol* 14: 203-211, 2004.
- Grill-Spector K, Kourtzi Z, and Kanwisher N.** The lateral occipital complex and its role in object recognition. *Vision Res* 41: 1409-1422, 2001.
- Gritsenko V, Yakovenko S, and Kalaska JF.** Integration of predictive feedforward and sensory feedback signals for online control of visually guided movement. *J Neurophysiol* 102: 914-930, 2009.
- Haith AM, Huberdeau DM, and Krakauer JW.** Hedging your bets: intermediate movements as optimal behavior in the context of an incomplete decision. *PLoS Comput Biol* 11: e1004171, 2015.
- Haith AM, Pakpoor J, and Krakauer JW.** Independence of Movement Preparation and Movement Initiation. *J Neurosci* 36: 3007-3015, 2016.
- Hecht D, Reiner M, and Karni A.** Multisensory enhancement: gains in choice and in simple response times. *Exp Brain Res* 189: 133-143, 2008.
- Heekeren HR, Marrett S, Bandettini PA, and Ungerleider LG.** A general mechanism for perceptual decision-making in the human brain. *Nature* 431: 859-862, 2004.
- Heekeren HR, Marrett S, and Ungerleider LG.** The neural systems that mediate human perceptual decision making. *Nature Reviews Neuroscience* 9: 467-479, 2008.
- Holm S.** A Simple Sequentially Rejective Multiple Test Procedure. *Scandinavian Journal of Statistics* 6: 65-70, 1979.
- Joo SJ, Katz LN, and Huk AC.** Decision-related perturbations of decision-irrelevant eye movements. *Proc Natl Acad Sci U S A* 113: 1925-1930, 2016.
- Keating E.** Frontal eye field lesions impair predictive and visually-guided pursuit eye movements. *Experimental Brain Research* 86: 311-323, 1991.
- Konen CS, and Kastner S.** Two hierarchically organized neural systems for object information in human visual cortex. *Nat Neurosci* 11: 224-231, 2008.
- Krappmann P.** Accuracy of visually and memory-guided antisaccades in man. *Vision Research* 38: 2979-2985, 1998.
- Lacquaniti F, and Maioli C.** The role of preparation in tuning anticipatory and reflex responses during catching. *Journal of Neuroscience* 9: 134-148, 1989.
- Lehky SR, and Tanaka K.** Neural representation for object recognition in inferotemporal cortex. *Curr Opin Neurobiol* 37: 23-35, 2016.
- Lencer R, and Trillenber P.** Neurophysiology and neuroanatomy of smooth pursuit in humans. *Brain Cogn* 68: 219-228, 2008.
- Lisberger SG.** Visual Guidance of Smooth Pursuit Eye Movements. *Annu Rev Vis Sci* 1: 447-468, 2015.
- Ludvig E, and Miller JW.** Study of visual acuity during the ocular pursuit of moving test objects. I. Introduction. *J Opt Soc Am* 48: 799-802, 1958a.
- Ludvig E, and Miller JW.** Study of visual acuity during the ocular pursuit of moving test objects. I. Introduction. *Journal of the Optical Society of America* 48: 799-802, 1958b.
- Merchant H, Zarco W, Prado L, and Perez O.** Behavioral and neurophysiological aspects of target interception. In: *Progress in Motor Control Advances in Experimental Medicine and Biology*, edited by Sternad D. Boston, MA: Springer, 2009, p. 201-220.
- Meyer CH, Lasker AG, and Robinson DA.** The upper limit of human smooth pursuit velocity. *Vision Research* 25: 561-563, 1985.
- Milner AD.** How do the two visual streams interact with each other? *Experimental brain research* 235: 1297-1308, 2017.

- Mishkin M, Ungerleider LG, and Macko KA.** Object vision and spatial vision: two cortical pathways. *Trends in Neurosciences* 6: 414-417, 1983.
- Morrow MJ, and Sharpe JA.** Deficits of smooth-pursuit eye movement after unilateral frontal lobe lesions. *Annals of Neurology* 37: 443-451, 1995.
- Nashed JY, Diamond JS, Gallivan JP, Wolpert DM, and Flanagan JR.** Grip force when reaching with target uncertainty provides evidence for motor optimization over averaging. *Sci Rep* 7: 11703, 2017.
- Orban de Xivry JJ, Legrain V, and Lefevre P.** Overlap of movement planning and movement execution reduces reaction time. *J Neurophysiol* 117: 117-122, 2017.
- Ranalli PJ, and Sharpe JA.** Vertical vestibulo-ocular reflex, smooth pursuit and eye-head tracking dysfunction in internuclear ophthalmoplegia. *Brain* 111: 1299-1317, 1988.
- Resulaj A, Kiani R, Wolpert DM, and Shadlen MN.** Changes of mind in decision-making. *Nature* 461: 263-266, 2009.
- Rizzolatti G, Fogassi L, and Gallese V.** Motor and cognitive functions of the ventral premotor cortex. *Curr Opin Neurobiol* 12: 149-154, 2002.
- Rizzolatti G, and Matelli M.** Two different streams form the dorsal visual system: anatomy and functions. *Exp Brain Res* 153: 146-157, 2003.
- Rosenbaum DA, Cohen RG, Jax SA, Weiss DJ, and Van Der Wel R.** The problem of serial order in behavior: Lashley's legacy. *Human Movement Science* 26: 525-554, 2007.
- Sakagami M, and Pan X.** Functional role of the ventrolateral prefrontal cortex in decision making. *Current Opinion in Neurobiology* 17: 228-233, 2007.
- Sarlegna FR, and Mutha PK.** The influence of visual target information on the online control of movements. *Vision Res* 110: 144-154, 2015.
- Schall JD, Morel A, King DJ, and Bullier J.** Topography of visual cortex connections with frontal eye field in macaque: convergence and segregation of processing streams. *Journal of Neuroscience* 15: 4464-4487, 1995.
- Schmidt T.** The finger in flight: real-time motor control by visually masked color stimuli. *Psychol Sci* 13: 112-118, 2002.
- Schutz AC, Braun DI, and Gegenfurtner KR.** Object recognition during foveating eye movements. *Vision Research* 49: 2241-2253, 2009.
- Schütz AC, Braun DI, and Gegenfurtner KR.** Object recognition during foveating eye movements. *Vision Research* 49: 2241-2253, 2009.
- Schwartz EL, Desimone R, Albright TD, and Gross CG.** Shape recognition and inferior temporal neurons. *Proc Natl Acad Sci U S A* 80: 5776-5778, 1983.
- Selen LP, Shadlen MN, and Wolpert DM.** Deliberation in the motor system: reflex gains track evolving evidence leading to a decision. *J Neurosci* 32: 2276-2286, 2012.
- Sereno AB, and Maunsell JH.** Shape selectivity in primate lateral intraparietal cortex. *Nature* 395: 500-503, 1998.
- Shi D, Friedman HR, and Bruce CJ.** Deficits in smooth-pursuit eye movements after muscimol inactivation within the primate's frontal eye field. *Journal of Neurophysiology* 80: 458-464, 1998.
- Singh T, Fridriksson J, Perry CM, Tryon SC, Ross A, Fritz S, and Herter TM.** A novel computational model to probe visual search deficits during motor performance. *J Neurophysiol* 117: 79-92, 2017.
- Singh T, Perry CM, and Herter TM.** A geometric method for computing ocular kinematics and classifying gaze events using monocular remote eye tracking in a robotic environment. *Journal of Neuroengineering and Rehabilitation* 13: 10, 2016.
- Song JH, and Nakayama K.** Hidden cognitive states revealed in choice reaching tasks. *Trends Cogn Sci* 13: 360-366, 2009.
- Song JH, and Nakayama K.** Target selection in visual search as revealed by movement trajectories. *Vision Research* 48: 853-861, 2008.
- Spering M, Kerzel D, Braun DI, Hawken MJ, and Gegenfurtner KR.** Effects of contrast on smooth pursuit eye movements. *J Vis* 5: 455-465, 2005.

- Takemura H, Rokem A, Winawer J, Yeatman JD, Wandell BA, and Pestilli F.** A Major Human White Matter Pathway Between Dorsal and Ventral Visual Cortex. *Cereb Cortex* 26: 2205-2214, 2016.
- Thorpe SJ, and Fabre-Thorpe M.** Neuroscience. Seeking categories in the brain. *Science* 291: 260-263, 2001.
- Thura D.** Decision urgency invigorates movement in humans. *Behav Brain Res* 382: 112477, 2020.
- Thura D, and Cisek P.** Modulation of Premotor and Primary Motor Cortical Activity during Volitional Adjustments of Speed-Accuracy Trade-Offs. *J Neurosci* 36: 938-956, 2016.
- Tychsen L, and Lisberger SG.** Visual motion processing for the initiation of smooth-pursuit eye movements in humans. *Journal of Neurophysiology* 56: 953-968, 1986.
- van den Berg R, Anandalingam K, Zylberberg A, Kiani R, Shadlen MN, and Wolpert DM.** A common mechanism underlies changes of mind about decisions and confidence. *Elife* 5: e12192, 2016.
- van Polanen V, and Davare M.** Interactions between dorsal and ventral streams for controlling skilled grasp. *Neuropsychologia* 79, Part B: 186-191, 2015.
- Veerman MM, Brenner E, and Smeets JB.** The latency for correcting a movement depends on the visual attribute that defines the target. *Exp Brain Res* 187: 219-228, 2008.
- Westheimer G, and McKee SP.** Visual acuity in the presence of retinal-image motion. *Journal of the Optical Society of America* 65: 847-850, 1975.
- Wong AL, and Haith AM.** Motor planning flexibly optimizes performance under uncertainty about task goals. *Nature Communications* 8: 14624, 2017.
- Zago M, McIntyre J, Senot P, and Lacquaniti F.** Visuo-motor coordination and internal models for object interception. *Exp Brain Res* 192: 571-604, 2009.