1	Perceptual decisions about object shape bias visuomotor coordination during
2	rapid interception movements
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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-
- reality display. On some blocks of trials, participants needed to identify the shape of the object
 (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
- 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

Many functional sensorimotor skills require rapid visual processing and perceptual 65 decision-making. A very commonly encountered situation during driving is when drivers must 66 decide whether to yield or stop at an intersection. The decision should be made from a 67 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. However, if the shape is judged as a yield sign, the driver might just slow down or even hit the 70 accelerator if there is no incoming traffic. The driver's ability to make the correct decision and 71 movement depends on efficient real-time processing of visual sensory information in the two 72 visual processing streams (Goodale and Milner 1992; Mishkin et al. 1983). The distance 73 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 (Culham et al. 2006; Rizzolatti et al. 2002; Rizzolatti and Matelli 2003). The shape and 76 77 symbols on the sign are perceived by the lateral occipital and inferior temporal cortex along the ventral visual stream (Ales et al. 2013; Grill-Spector et al. 2001; Lehky and Tanaka 2016; 78 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 and process sensory information in real-time to facilitate rapid visuomotor actions. 81

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 (reviewed in Gallivan et al. 2018; Hecht et al. 2008; Rosenbaum et al. 2007; Song and 84 Nakayama 2009) as well as neurophysiological studies (reviewed in Cisek and Kalaska 2010) 85 have provided empirical support for simultaneous specification of competing motor plans in the 86 dorsal visual stream. Rapid movement modifications have also been shown when a perceptual 87 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. 2009; Sarlegna and Mutha 2015). These results imply that despite functionally segregated 92 roles, goal-directed visuomotor actions ultimately necessitate online interaction between the 93 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 online decision-making and motor planning may depend on the computational complexity of 98 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 et al. 2009). Humans can achieve high interception accuracy via continuous updating of 103 104 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 guickly and as accurately as possible. In separate blocks, participants needed to select among two alternative actions that required 111 correctly identifying the object's shape (hit the circle and avoid the ellipse). Our first hypothesis 112 was that engaging the ventral stream would elicit stronger interference between ventral and 113 114 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 Trillenberg 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 in eye movement processing overlap with those involved in decision-related signals (Fooken 122 123 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

Twenty-six healthy, right-handed participants (16 women; 23.7 ± 5.5 years) completed 132 133 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 Technologies, Kingston, Ontario, Canada) (see Fig.1A). All visual stimuli were projected at 60 141 142 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 direction) to the handle and recorded movement position and velocity at 1000 Hz. The 145 monocular eye position of each participant was recorded at 500 Hz using a video-based 146 147 remote eye-tracking system (Eyelink 1000; SR Research, Ottawa, ON Canada) integrated with the robot and calibrated for the 2D horizontal workspace. Data from the eye-tracker and robot 148 149 were time-synced offline using MATLAB (version 9.5.0; The MathWorks, Natick, MA).

150

Experimental design and procedure

151 152 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

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

160 Following a fixed 200 ms delay, a vellow object was presented on the display near either the left or right edge of a rectangular box (34 x 34 cm) centered on the midline and 22 161 162 cm above the start position (see Fig. 1B). The possible object shape on a given trial, and the participant's task, depended on the experimental block. During No Decision blocks, 163 164 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 when the cursor first touched the circle—participants were not required to stop at the circle. 166 167 During Decision blocks, participants were informed that the object would appear as either a circle or an ellipse (major axis = 2.3 cm; minor axis = 2 cm) with equal probability. The lengths 168 169 of the ellipse axes were selected based on pilot experiments to ensure that the object must be foveated to differentiate it from a circle. As in the No Decision blocks, if the participants saw a 170 171 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 required the participant to accurately identify the object shape in order to perform the correct 176 action (i.e., hit the circle or avoid the ellipse). Therefore, in addition to the No Decision blocks, 177 178 the Decision condition required two additional steps, object identification and selection of an appropriate motor plan. 179

180 For each block of trials, the object either moved horizontally across the display (Interception) or remained in the same position (Reaching). On Interception trials, the object 181 appeared ±16 cm to the left or right of the midline (Y position range 14.5 - 17 cm from the start 182 183 position, uniform distribution) and traversed at a constant Euclidean velocity of ±40 cm/s (Fast) or ±34 cm/s (Slow) toward the other horizontal boundary of the rectangular box. The varying 184 object velocity was added to test the hypotheses under stricter conditions of time constraints. 185 On Reaching trials, the object appeared to the left or right of the midline with starting positions 186 drawn from a uniform distribution (X position range: ±13 - 16 cm from midline; Y position range 187 188 14.5 - 17 cm in front of start position) and remained stationary. For both types of trials, the object remained on the visual display until it was hit or for the maximum trial duration. On 189 190 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 (±40 cm/s) and 950 ms for 192 slow velocities (±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.

Performance feedback was provided for 500 ms once the object was hit (i.e., the cursor overlapped with the object) or the maximum trial duration was reached. If a circle was correctly hit, the circle would turn green; if the circle was missed it would turn red. An ellipse would turn red if it was incorrectly hit instead of avoided and would turn green if correctly avoided. The next trial began following a 1500 - 2000 ms delay. Participants performed 8 experimental blocks of 90 trials each (720 trials total). Block order was counterbalanced across participants. Each experimental block consisted of a unique combination of decision type (No Decision or Decision), movement type (Reach or Intercept), and trial duration (Fast or Slow). Object shape (during Decision blocks) and the object start location were randomized across trials within each block.





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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 (vellow 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

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

223

224 Arm Movements

Hand position and velocity data were first smoothed using a fourth-order Butterworth 225 low-pass filter with a 5 Hz cutoff. Movement onset was defined as the time the tangential 226 velocity first exceeded 5% of the first local peak. Reaction time (RT) was calculated as the time 227 228 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 attempt (2.3% of all trials). Peak speed (PS) was defined as the maximum tangential velocity 232 233 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).

For each trial, we examined the hand kinematics to determine decisional and motor 236 237 performance accuracy at different stages of the movement. The initial direction (ID) of the movement was calculated as the angle between the midline and the vector linking the hand 238 239 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 aimed toward the object or toward the bar. Initial decision errors were computed for each 241 242 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 circle or aimed toward the object on trials with an ellipse). Likewise, final decision errors were 244 245 calculated as the percentage of trials the participants' final hand position was closer to the bar on circle trials or closer to the object on ellipse trials. Trials in which the initial decision and the 246 final decision were different (e.g., aimed toward the circle but attempted to hit the bar) were 247 248 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.

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

258 259 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 corneal reflection), and screen outliers (due to instances when gaze drifts outside the 263 264 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 constant $(6,000^{\circ}/s^2)$. For each velocity peak that exceeded the velocity threshold, we 267 268 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

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

For interception movements, smooth-pursuits were identified when gaze and target 276 locations and velocities were continuously within a foveal visual radius as described in Singh et 277 al. (2016). Briefly, because targets were presented in a transverse plane, the foveal visual 278 279 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 duration was <5 ms, and smooth-pursuits/fixations were discarded if the duration was <40 ms. 282 283 On some trials, participants made predictive saccades anticipating the location of the object. Since we were only concerned with visually-guided performance, we eliminated any saccade 284 285 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 one containing an initial saccade to the target followed by a fixation or smooth-pursuit. Thus, 287 288 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, gaze data were included for 90.7% of Reaching trials and 88.6% of Interception trials. Data 290 291 from two subjects were not included in the eye movement analyses because fewer than 50% of their trials were identified as valid according to the above criteria. 292

Saccadic reaction time (SRT) for both Reaching and Interception trials was calculated 293 294 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 guantified for the open-loop (15-100 ms of gaze), first 100 ms of the closed-loop (next 100 ms of gaze), 299 and full closed-loop (gaze after first 100 ms) phases (excluding catch-up saccades). Gaze gain 300 for the first 15 ms was not analyzed due to the potential for artificially high velocities from the 301 302 offset of the preceding saccade. Removal of the first 15 ms did not affect differences in gaze gain across conditions. Of note, smooth-pursuit gains are typically computed using eye-303 304 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

To assess how the introduction of perceptual decision-making influenced RT, PS, and SRT, we computed the means for each combination of decision type, movement type, object 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/ trial duration combination. A one-sample *t*-test was used to determine whether the change 317 between Decision and No Decision means were significantly different from zero, and a 2 318 (Reaching or Interception) x 2 (Fast or Slow) repeated-measures ANOVA assessed whether 319 320 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 repeated-measures ANOVAs. For all ANOVA tests, the alpha level was set at 0.05 and effect 322 sizes are reported using generalized η^2 . Post hoc pairwise comparisons were conducted using 323 the Holm correction (Holm 1979). Linear regression was used for bivariate comparisons, with 324 325 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 (Dunn and Clark 1969), as implemented in *cocor* package in R (Diedenhofen and Musch 327 328 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 typically made saccades directly to the object, followed by fixation on a stationary object near 335 336 the right or left edge of the display boundary (Reaching trials) or pursuit of an object moving at a constant Euclidean velocity from one boundary to the other (Interception trials). Participants 337 either attempted to hit any circle that appeared by moving the cursor (representing hand 338 339 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 bar), or until the maximum trial duration (if neither the object nor the bar was hit). During No 343 344 Decision blocks, the object was always a circle, whereas in Decision blocks, the object could be either a circle or ellipse. The addition of the decision-making task component led to clear 345 differences in where participants chose to intercept the object. In No Decision blocks, on 346 average, participants tended to intercept the object slightly after it crossed the midline (M =347 348 20.1 ± 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 moving faster [main effect of trial duration: F(1,25) = 110.32, p < 0.001, $n^2 = 0.13$]. 351

In Decision blocks, final decisions were classified as either correctly attempting to hit the 352 circle or avoid the ellipse, or incorrectly attempting to hit the ellipse or avoid the circle (Fig. 2B). 353 The percentage of final decision errors was higher for interceptions than for reaching 354 355 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, $n^2 = 0.23$]. The increase in errors at faster durations was larger for interceptions [interaction of movement type 357 and trial duration: F(1,25) = 47.38, p < 0.001, $\eta^2 = 0.12$], indicating that faster object velocity 358 359 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 movements. In both No Decision and Decision blocks, there were a higher percentage of 363 aiming errors for Interception [main effect of movement type: F(1,25) = 129.22, p < 0.001, $n^2 =$ 364 0.43], especially at faster trial durations [interaction of movement type and trial duration: 365 F(1,25) = 20.88, p < 0.001, $\eta^2 = 0.04$], reflective of the greater difficulty in intercepting an object 366 at higher speeds (Fig. 2C). There was an increase in aiming errors in Decision blocks [main 367 effect of decision: F(1,25) = 11.49, p = 0.002, $\eta^2 = 0.06$], but the increase did not differ 368 between Reaching and Interception [interaction of movement type and decision: F(1,25) =369 1.48, p = 0.24, $n^2 = 0.003$]. Together, these results suggest that during time-constrained 370 perceptual decision-making, the added task demands of interceptive movements affected the 371 372 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

reversed. If this were the case, initial decisions should have been similar between Reaching 390 391 and Interception movements. In contrast, there was a large increase in initial decision errors during Interception relative to Reaching [main effect of movement type: F(1,25) = 121.09, p < 121.09392 393 0.001, $n^2 = 0.48$] (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 during the movement. This default strategy was used more often during faster trials [main 396 effect of trial duration: F(1,25) = 19.09, p < 0.001, $\eta^2 = 0.05$], when there were greater 397 constraints to hit the object in time. 398

As expected, perceptual decision-making led to a significant reaction time (RT) delay. 399 400 Relative to No Decision blocks, RTs for Decision blocks were on average 178 ± 11 ms longer 401 [t(1,25) = 20.04, p < 0.001] (Fig. 3B). Thus, perceptual decisions based on ventral stream processing clearly increased the time taken for object identification (circle or ellipse) and motor 402 403 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 Interception [main effect of movement type: F(1,25) = 13.63, p = 0.001, $n^2 = 0.07$], and for Fast 405 movement blocks [main effect of trial duration: F(1,25) = 9.83, p = 0.004, $n^2 = 0.04$]. This 406 suggests that even though decisions added processing time, participants chose to limit pre-407 408 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: participants with shorter RTs during Decision blocks exhibited more initial decision errors for 410 both reaching and interception movements (Reaching: r = -0.67, p < 0.001; Interception: r = -411 0.62, *p* <0.001) (Fig. 3C). 412

During decision-making, there was also an increase in the speed of the response: on 413 414 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 [main effect of movement type: F(1,25) = 0.00, p = 0.98, $\eta^2 < 0.01$] or trial duration [main effect 416 of trial duration: F(1,25) = 2.70, p = 0.11, $n^2 = 0.01$]. For reaching movements, the increase in 417 PS may reflect a general urgency to complete the movement more quickly after a prolonged 418 decision period. For interception movements, where participants have a salient visual cue for 419 time remaining (the object approaching the boundary), changes in PS are likely more directly 420 421 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 (No Decision: r = 0.54, p = 0.003; Decision: r = 0.76, p < 0.001), which was not the case for 424 reaching movements (No Decision: r = 0.16, p = 0.43; Decision: r = 0.34, p = 0.08) (Fig. 3E). 425 426 The PS-RT correlation was significantly greater for Decision, Interception blocks than for No Decision, Reaching blocks (z = 2.98, p = 0.003), indicating that the lower RTs during decision-427 428 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

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</p>

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 strategies used during the task. Overall, redirect movements were more common during 455 Interception [main effect of movement type: F(1,25) = 16.82, p < 0.001, $\eta^2 = 0.11$], especially at 456 457 Slow trial durations [interaction of movement type and trial duration: F(1,25) = 9.61, p = 0.005, $n^2 = 0.03$ (Fig. 4A). This suggests that decisions about object shape could be modified after 458 movement initiation. Furthermore, participants were more likely to rely on this strategy for 459 460 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 more effectively during Reaching. As shown in Figure 4B, after an initial decision error, a 463 correct redirect of an initially wrong decision was more likely to occur for Reaching [main effect 464 of movement type: F(1,25) = 50.82, p < 0.001, $\eta^2 = 0.30$] and for Slow trial durations [main 465 effect of trial duration: F(1,25) = 55.83, p < 0.001, $\eta^2 = 0.16$]. Therefore, task difficulty limited 466 the ability to implement a corrective movement when they were necessary. 467 468



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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 one participant and shaded area represents the 95% confidence interval of the regression estimate. * indicates p 475 476 < 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° = 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).

If initial decisions were less likely to be corrected, why were participants more likely to 483 484 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 decision was complete, but once the movements were underway the complexity of the 486 487 interception movements may have made it much harder to correct them. If this is the case, initiation of redirect movements should be associated with shorter RTs. Indeed, for both 488

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 < 0.001; Interception: r491 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 corrected) had an average RT of 390 ± 11 ms, relative to 489 ± 15 ms for direct avoids [main 495 effect of movement strategy: F(1.32, 33.12) = 71.64, p < 0.001, $\eta^2 = 0.35$, Greenhouse-Geisser 496 corrected] (Fig. 4D). The average RT for direct object hits was approximately halfway in-497 498 between the RTs for the two types of avoid movements $(439 \pm 12 \text{ ms})$, reflecting that 499 participants defaulted towards initiating a movement towards the object even when their decision was incomplete. Interestingly, RTs were shorter for Interception than Reaching for 500 redirect-to-avoid, direct avoids, and direct hits [all t's > 2.2, all p's < 0.05], and the RT 501 502 difference was largest for direct avoids [interaction of movement type and strategy: F(1.34), 503 (33.48) = 8.51, p = 0.003, $n^2 = 0.02$, Greenhouse-Geisser corrected]. This suggests that simply preparing for an interception movement, even when it was not selected, contributed to earlier 504 505 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 motor plan to hit the object. However, as shown in Figure 4E, trajectories of movements that 509 510 were ultimately redirected were on average initially aimed farther from the midline than direct movements (longer tail for redirect-to-avoid) [main effect of movement strategy: F(1,25) =511 131.91, p < 0.001, $n^2 = 0.28$], and this difference was larger for Interception [interaction of 512 movement type and strategy: F(1, 25) = 10.59, p = 0.003, $\eta^2 = 0.01$]. The deviation of the initial 513 514 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 (± 2.3) ms 525 faster during Decision blocks than No Decision blocks [t(1,23) = -5.52, p < 0.001]. The decrease in SRTs was similar for both Reaching and Interception [main effect of movement 526 527 type: F(1,23) = 0.08 p = 0.79, $\eta^2 < 0.01$], suggesting that adding a perceptual decision increased the general urgency to launch a saccade. However, as can be seen for Interception 528 529 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 effect of decision: F(1,23) = 13.93, p = 0.001, $\eta^2 = 0.04$] and for Fast trial durations (i.e., when 531 the object was moving at faster velocities) [main effect of trial duration: F(1,23) = 37.25, p < 100532 533 0.001, $n^2 = 0.07$]. 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

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

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Participants compensated for the initial lag in pursuit by increasing the gaze gain. Though gaze gain in the open-loop period (15-100 ms after pursuit initiation) was driven mainly by differences in object velocity [main effect of trial duration: F(1,23) = 58.67, p < 0.001, $\eta^2 =$ 0.13], during the closed-loop period gaze gain increased for Decision blocks relative to No Decision blocks [main effect of decision: F(1,23) = 49.02, p < 0.001, $\eta^2 = 0.15$] (Fig. 5D). This effect is not simply due to longer pursuit durations during Decision blocks, as gains are also longer when the analysis is restricted to the first 100 ms of the closed-loop period [main effect of decision: F(1,23) = 8.71, p = 0.007, $\eta^2 = 0.04$]. This suggests that the negative closed feedback loop that minimizes retinal error between gaze and target is engaged differently when perceptual decision-making task-constraints are imposed during pursuit eye movements.

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

569 Discussion

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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 guestion, 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 intercept it, but if an ellipse appeared, they were instead instructed to make a movement away 576 from the ellipse and towards a horizontal bar. Our results support our first hypothesis of 577 differential effects of ventral stream engagement on dorsal stream processing during 578 interception relative to reaching movements. Furthermore, we also found support for our 579 580 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 movements (de la Malla et al. 2019; Lacquaniti and Maioli 1989). Our approach also differs 585 586 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 that impedes recognition of the target. These studies showed that reaching movement 589 590 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 shape (~250-300 ms) and plan movements (~100-200 ms) in a sequential fashion, i.e. to 595 596 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 took longer than the preparation of the motor plan, we predicted that effective ventral-dorsal 599 600 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

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

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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 of movement have been conceptualized as two specialized processes mediated by the ventral 608 and dorsal streams, respectively (Goodale and Milner 1992; Goodale and Westwood 2004). 609 610 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 complex task environments. The current task was designed to force this interaction-that is, in 612 613 order to perform the correct action (hit the object or avoid it), participants must accurately identify the object's shape (circle or ellipse). We found that even under time constraints (800 614 615 ms to hit the object in the Fast condition), participants could recognize objects and formulate a decision prior to movement initiation. Relative to No Decision blocks, in which participants only 616 617 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 2001; Veerman et al. 2008). Thus, it is reasonable to assume from the average RTs that 620 621 perceptual processing in the ventral stream could precede dorsal stream processing of visuomotor transformations for action execution. 622

However, closer investigation of the movement trajectories and corresponding RTs 623 provides evidence that processing of object information and decision-making continues after 624 movement initiation. During both reaching and interception, we observed that participants 625 626 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 (Resula) 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; Gallivan et al. 2016; van den Berg et al. 2016), here we show that sensorimotor 631 632 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 movement directions (see Fig. 4E) of redirected movements toward the direction of the bar 635 suggests that movements are planned to optimize task success given uncertainty about the 636 637 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 de Xivry et al. 2017). 641

What determines the reliance on integration of ventral and dorsal stream information during visuomotor control? In the present task, the complexity of the motor response modulated the perceived urgency to act (Thura 2020; Thura and Cisek 2016). Both initial and final decision errors increased during interception relative to reaching during decision-making, largely due to participants initially aiming toward and then unable to correct a response toward a moving ellipse. In addition, movements were more likely to be redirected during interception, indicating a stronger bias toward initiating a hit movement prior to making a perceptual
decision about object shape. Furthermore, an individual's initial decision error rate and
tendency to perform redirect movements were each associated with shorter RTs, indicating
that the shorter RTs during interceptions in Decision blocks were likely due to a greater
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 information with visuomotor performance may be limited. Our results suggest that the urgency 655 of the response may interfere with, rather than be a consequence of, differential ventral-dorsal 656 657 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 decisionmaking. Notably, the errors in interception during decision-making were associated with the 660 661 inability to adjust initial movement trajectories that account for decisional demands, but the increase in aiming errors was no different between interception and reaching. This suggests 662 663 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.

673 Modulation of gaze gains during perceptual decision-making

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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 in larger undershoots farther away from the object (larger gaze lags in Decision blocks, Fig. 679 680 5C). Since in our study objects had to be foveated to be recognized, the oculomotor system may have increased the gaze gains (Fig. 5D) and made more catch-up saccades (Fig. 5E) to 681 the target during Decision blocks to compensate for the large lags at the end of the saccades. 682

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 feedback loop to ensure that the eye velocity closely matches the target velocity. However, 687 688 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 and Sharpe 1988) instead of pursuit gains. One study in primates has shown that when the 691 692 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).

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

As expected, changes in the open-loop gains were driven predominantly by object 696 velocity (Fast versus Slow). However, the closed-loop gains were significantly higher for the 697 698 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, but that it would also compromise their ability to recognize objects. However, the closed-loop 706 707 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 retinal error between gaze and target is engaged differently when the ventral stream is 711 712 engaged for perceptual decision-making during pursuit eye movements.

713 Our result suggests that the visual perceptual decision-making network, that includes the ventral visual stream, dorsolateral prefrontal regions and frontal eve fields (Heekeren et al. 714 2004; Heekeren et al. 2008; Sakagami and Pan 2007), may provide either a predictive or 715 urgency signal to the smooth-pursuit system to increase the gain and minimize the retinal error 716 between the target and the gaze. Indeed, stimulation and lesion studies have implicated the 717 718 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.

725 Conclusions

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726 In this study, we introduced a visuomotor decision-making task in which a successful reaching or interception movement depended on visual processing for perception and action in 727 the ventral and dorsal streams. We found that engagement of the ventral stream led to more 728 729 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 exhibited higher gaze gains to adapt to the demands of integrating the perceptual decision with 733 734 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, Cottereau 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 decisionmaking 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 Trillenberg 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. **Ludvigh 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.

Ludvigh 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.