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Perceptual decisions about object shape bias visuomotor coordination during rapid reaching and interception

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Abstract

Visual processing in parietal areas of the dorsal stream facilitates sensorimotor transformations for rapid movement. This action-related visual processing is hypothesized to play a distinct functional role from the perception-related processing in the ventral stream. However, it is unclear how the two streams interact when perceptual identification is a prerequisite to executing an accurate movement. In the current study, we investigated how perceptual decision-making involving the ventral stream influences eye and arm movement strategies. Participants (*N* = 26) moved a robotic manipulandum using right whole-arm movements to rapidly reach a stationary object or intercept a moving object on a virtual 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 from the object (ellipse). We found that interception movements were initiated sooner and performed less accurately than reaches, a difference that increased in trials when perceptual decisions about object shape were made. Faster hand reaction times were correlated with a deliberate strategy to adjust the movement post-initiation - this strategy was more prominent during interception, when there is a greater perceived urgency to act. Saccadic reaction times were faster and initial smooth pursuit lags and gains greater during decisions, suggesting an interference between how eye movements are used for perception and for guiding limb movements. Together, our findings suggest that the extent to which ventral stream information is incorporated in into visuomotor planning depends on imposed (or perceived) task demands.

New and Noteworthy

Visual processing for perception and for action are thought to be mediated by two specialized neural pathways. Using a novel visuomotor decision-making task, we show that participants differentially depended on online perceptual decision-making in reaching and interception, and that eye movements necessary for perception influence movement coordination strategies. These results provide evidence that task complexity modulates how pathways processing perception versus action information interact during the visuomotor control of movement.

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Introduction

Many functional sensorimotor skills require rapid visual processing and perceptual decision-making. A very commonly encountered situation during driving is when drivers must decide whether to yield or stop at an intersection. The decision should be made from a distance by judging the shape of the sign at the intersection. If the shape is judged as a stop 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 accelerator if there is no incoming traffic. The driver's ability to make the correct decision and movement depends on efficient real-time processing of visual sensory information in the two visual processing streams (Goodale and Milner 1992; Mishkin et al. 1983). The distance between the sign and the car, the presence of other incoming traffic, and the associated motor actions are almost certainly 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 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; Schwartz et al. 1983). Though the contributions of these streams to visuomotor and 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.

Simple visuomotor reaching to stationary targets has been studied using the center-out reaching paradigm (Archambault et al. 2015; Clower et al. 1996; Goodale et al. 1986; Jax and Rosenbaum 2009) where participants fixate on a center-cross while waiting for a cue to initiate a reaching movement to a peripheral target. These studies have shown that the reciprocal connections between the parietal areas in the dorsal stream and the premotor areas subserve visuomotor processing and transformations during reaching movements (Caminiti et al. 1998; Pesaran et al. 2006). When a target appears in the periphery, participants first make a rapid saccade to it. The saccadic reaction times varies anywhere from 120-220 ms based on when the central fixation cross is turned off prior to the appearance of the peripheral target (Munoz and Corneil 1995; Stevenson et al. 2009). This is followed by the initiation of a reaching movement within 50-100 ms (Prablanc et al. 2003); the delay simply reflects the larger inertia of the arm (Biguer et al. 1982; Pélisson et al. 1986; Prablanc et al. 1979). The overall reaction time between target appearance and initiation of a limb movement encompasses the sensory,

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cognitive, and motor processes involved in movement preparation (Haith et al. 2016; Prablanc et al. 1986; Smeets et al. 2016).

Based on Donders' framework of neural information processing (Donders 1969), the reaction time for simple visuomotor reaching movements consists of a two-stage process: (1) detection and localization of the stimulus in space; and (2) specification of an appropriate motor plan. Reflexive detection of visual stimuli is primarily accomplished by lower order neurons in the primary visual cortex, but target localization in space involves the parietal areas in the dorsal stream (Andersen et al. 1985; Colby and Goldberg 1992). Specification of motor plans involves coordinate transformations of target and hand locations into a single frame of reference (Beurze et al. 2006). The target locations are transformed in two steps; first from a world-centered to a retinotopic coordinate frame and then finally to a limb-centered reference frame (reviewed in Andersen and Buneo 2002; Boussaoud and Bremmer 1999; Pesaran et al. 2006). These transformations are computationally intensive and involve different frontoparietal nodes along the dorsal visual stream and the premotor cortex.

In contrast to reaching movements made to stationary targets, moving targets add additional complexities for target localization and motor plan specification. Specifically, suboptimal temporal integration of retinal and extraretinal signals during smooth pursuit eye movements create errors in spatial localization of targets (Brenner et al. 2001; Honda 1990; Schlag and Schlag-Rey 2002). Furthermore, the neural processes associated with coordinate transformation for moving targets are also computationally demanding. One study suggests that suboptimal transformation from the real-world to the retinotopic reference frame may result in higher number of movement errors during interception movements (Dessing et al. 2011). Taken together, these studies suggest that for moving targets, planning and execution of smooth pursuits and interception movements may constitute a significant computational burden for both target localization and movement specification, respectively.

Another way to add computational complexity to visuomotor reaching movements is to include a perceptual decision-making component to the task. This could be in the form of selection of alternative motor responses based on visuoperceptual decision-making, such as identification of visual features of stimuli (shape, color, etc.). The identification of visual properties, such as two-dimensional shape and color, is performed by the ventral visual stream (Konen and Kastner 2008; Lehky and Sereno 2007), whereas the appropriate limb motor

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responses are selected by the dorsal visual stream and the dorsal premotor cortex (Grafton et al. 1998; Kalaska and Crammond 1995; Rushworth et al. 2003). The additional neural processing adds two intermediate stages to Donder's model of information-processing. Now the four information-processing stages for visuoperceptual motor tasks are: (1) detection of the stimulus, (2) identification of the stimulus, (3) selection of an appropriate motor response and (4) execution of the motor response (Donders 1969; Hecht et al. 2008; Smeets et al. 2016; Sternberg 1969). In humans, geometric shape recognition in the ventral stream approximately takes ~250 ms (Delorme et al. 2000; Doniger et al. 2000) and it takes another ~100-200 ms to initiate an arm movement (Thorpe and Fabre-Thorpe 2001). In contrast to the 50-100 ms delays associated with arm movements initiation during simple visuomotor reaching movements, the relatively longer time to initiate movements during ventral stream processing may be due to delays in integration of neural information between the two streams. Indeed, an indirect synaptic pathway between the inferior temporal neurons in the ventral stream and the motor cortex passes through the prefrontal and premotor cortices adding additional conductional and processing delays (Hegdé 2008; Thorpe and Fabre-Thorpe 2001). If processed perceptual information converges at the motor cortex only through this pathway, then ventral stream processing would be the rate-limiting step for movement specification.

The goal of the present study was to understand how adding computational complexity to dorsal stream and ventral stream processing affects the spatiotemporal course of movement specification. We asked two questions. First, compared to reaching movements, what are the additional computational costs associated with movement specification of interception movements? Our hypothesis for this question was that the reaction time of interception movements would be longer and accuracy reduced because of additional computations associated with rapid reference frame transformations from the real-world to the retinotopic reference frame. Second, how does engaging the ventral visual stream impact dorsal stream processes associated with movement specification?

To propose a hypothesis for the second question, we again drew from Donder's framework that suggests that the four stages of information processing are functionally distinct (Ulrich et al. 1999) and that information is processed sequentially at every stage, i.e. output of a stage serves as the input to the next stage. This would suggest that the neural processing in the ventral visual stream for object identification and response selection should be completed

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before the dorsal stream processes an appropriate arm movement plan. However, many behavioral (reviewed in Gallivan et al. 2018; Hecht et al. 2008; Rosenbaum et al. 2007; Song and Nakayama 2008) as well as neurophysiological studies (reviewed in Cisek and Kalaska 2010) have challenged the sequential-processing view. Recently, empirical support has been provided for simultaneous selection of multiple motor plans in the form of intermediate movements that reflect a spontaneous averaging of the kinematics of competing motor plans (Gallivan et al. 2016; Haith et al. 2015). Other studies, however, have suggested that movement specification may involve both simultaneous and sequential processing of different sensorimotor attributes (Dekleva et al. 2018; Wong and Haith 2017). Therefore, in time-constrained rapid visuomotor and perceptual decision-making tasks, movements may be initiated even before the object identification is complete (Haith et al. 2016). This would suggest that hand trajectories would be corrected online under visual feedback control. Thus, our second hypothesis was that under imposed (or perceived) time constraints, neural processing in the ventral and dorsal visual streams becomes more parallel and less sequential, resulting in more online adjustments of trajectories after movement initiation.

If participants were to guide interception movements under continuous visual feedback control (Brenner and Smeets 2011; Desmurget and Grafton 2000; Saunders and Knill 2003), this would suggest that perceptual decisions about object identity could be completed during movement execution. However, a previous visual perception study (Schütz et al. 2009) has shown that recognition of object properties during object motion is impaired, suggesting that smooth pursuit eye movements may cause disfacilitation in the ventral visual stream when both streams are simultaneously engaged during object tracking. Thus, our third hypothesis was that during interception movements and object recognition, participants would exhibit higher smooth pursuit gains (computed as ratio of eye velocity and target velocity) to compensate for the impaired recognition.

To test the three hypotheses, we designed a rapid visuomotor decision-making task where participants were asked to make either reaching (stationary targets) or interception movements (moving targets) towards an object (hit) if it was a circle and away from it (avoid), if it were an ellipse. We added another condition, in which objects moved either quickly or relatively slowly across the workspace for moving targets and stayed in the workspace for a short and relatively longer duration for the stationary targets. We expected that this additional

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temporal constraint would elicit stronger interference between visuomotor processing and perceptual decision-making.

Methods

Participants

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

Apparatus

Participants were seated in a chair and used their right hand to grasp the handle of a robotic manipulandum that could move in a horizontal plane (KINARM End-Point Lab, BKIN Technologies, Kingston, Ontario, Canada) (Fig.1A). All visual stimuli were projected at 60 Hz onto a semi-transparent mirror from a monitor above the workspace. This set-up allowed the stimuli to appear on the same horizontal plane as the handle and to occlude direct vision of the hand. During task performance, the robot applied a constant background force (-3 N in the Y direction) to the handle and recorded movement position and velocity at 1000 Hz. The monocular eye position of each participant was recorded at 500 Hz using a video-based 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 were time-synced offline using MATLAB (version 9.5.0; The MathWorks, Natick, MA).

Experimental design and procedure

Participants performed rapid whole-arm reaching and interception movements in which they were instructed to either hit or avoid an object based on the object's shape. At the beginning of each trial, participants moved a cursor (white circle, 1 cm diameter) representing 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

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maintain fixation and keep their hand at the start position for 500 ms, after which the fixation cross and start position disappeared.

Following a fixed 200 ms delay, a yellow 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 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 (Table 1). During No Decision blocks, participants were informed that the object shape would always be a circle (2 cm diameter), and that they should hit the circle as quickly and as accurately as possible. 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 of the ellipse axes were selected to ensure that the object must be foveated to differentiate it from a circle. As in No Decision blocks, if the participants saw a circle, they were instructed to hit it as quickly and as accurately as possible. However, if an ellipse appeared, participants were instructed to avoid hitting the ellipse and instead move in the opposite direction toward a horizontal bar (10 cm width) centered on the midline and -4 cm from the start position in the y direction (see Fig. 1B). Thus, in contrast to No Decision blocks, in which participants could simply plan to hit the object on every trial, Decision block trials required the participant to correctly identify the object shape in order to perform the appropriate action (i.e., hit the circle or avoid the ellipse). Therefore, in addition to the No Decision blocks, the Decision condition required two additional steps, object identification and selection of an appropriate motor plan.

For each block of trials, the object either moved horizontally across the display (Intercept) or remained in the same position (Reach). On Intercept trials, the object appeared ±16 cm to the left or right of the midline (Y position range 14.5 - 17 cm from the start 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 object velocity (see Table 1) was added to test the hypotheses under stricter conditions of time constraints. On Reach trials, the object appeared to the left or right of the midline with starting positions drawn from a uniform distribution (X position range: ±13 - 16 cm from midline; Y position range 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 the maximum trial duration was reached. On Intercept trials, the maximum trial duration equaled the time it took for the

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object to reach the horizontal boundary given its velocity: 800 ms for fast velocities (±40 cm/s) and 950 ms for slow velocities (±34 cm/s). To match the Intercept trial durations, objects that were not hit remained on the screen for 800 ms (Fast) or 950 ms (Slow) during Reach trials.

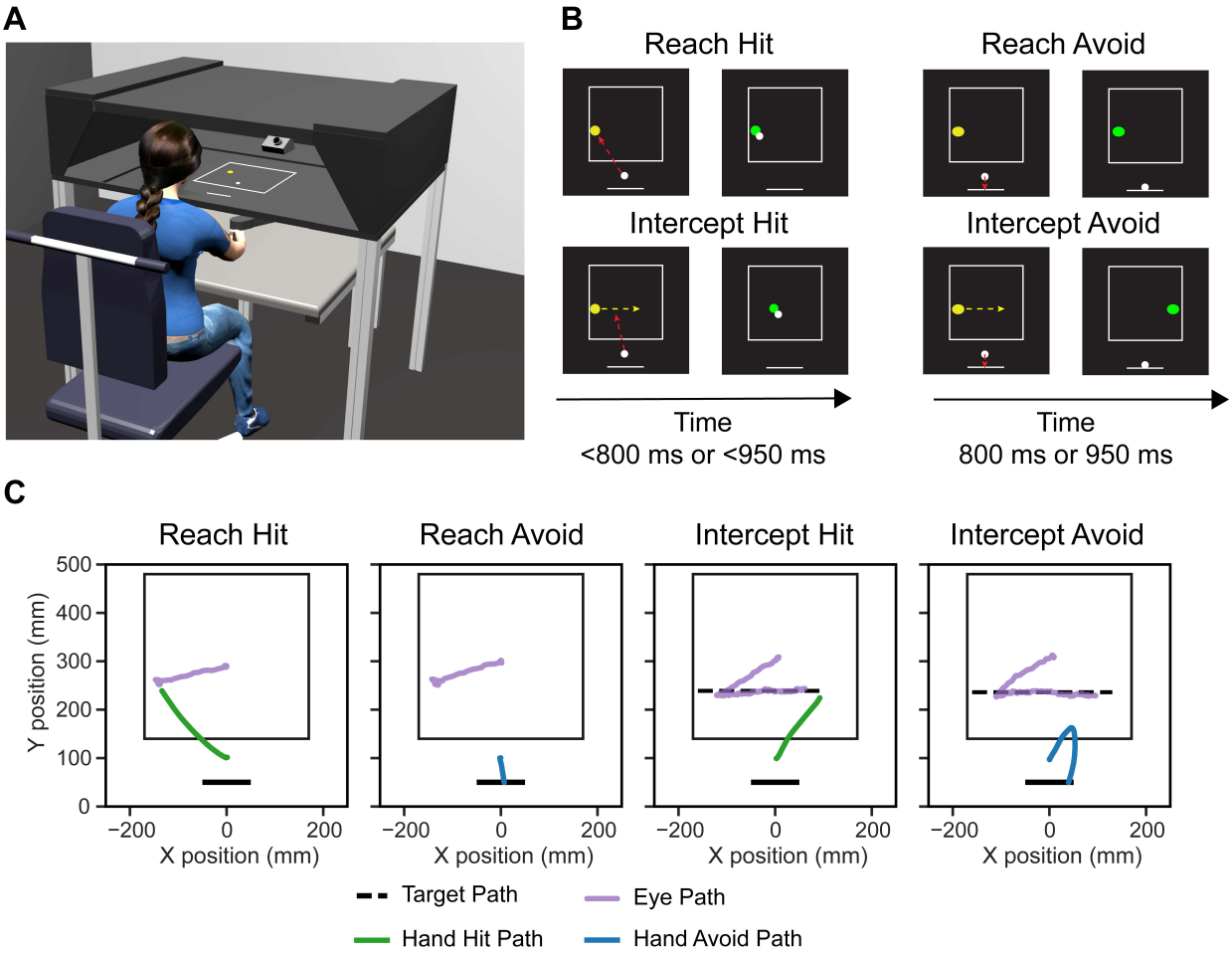

Figure 1. Experimental design and example trials. *A*: Experimental setup. Participants moved a robotic manipulandum with their right hand to control a cursor (white circle) in response to an object (yellow circle) on the visual display. A remote gaze-tracker at the back of the workspace recorded eye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

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Performance feedback was provided for 500 ms once the object was hit 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 after a 1500 - 2000 ms delay (see Fig. 1B).

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), object motion (Reach or Intercept), and maximum trial duration (Fast or Slow) (Table 1). Object shape (during Decision blocks) and the object start location were randomized across trials within each block.

Table 1. Experimental Blocks

	Reach	Intercept
No Decision	*Fast*	*Fast*
	Slow	*Slow*
Decision	*Fast*	*Fast*
	Slow	*Slow*

In No Decision blocks, the object to-be-hit is always a circle. In Decision blocks, the object is randomly selected to be either a circle or ellipse. The maximum trial duration (time object is viewable) is 800 ms for Fast trials and 950 ms for Slow trials, determined from the time it takes for the object to complete its path at Fast or Slow velocities in the Intercept condition.

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).

Arm Movements

Hand position and velocity data were first smoothed using a fourth-order Butterworth low-pass filter with a 5 Hz cutoff. Movement onset was defined as the time hand speed first

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exceeded 5% of the first local peak speed. Reaction time (RT) was calculated as the time from object onset to movement onset. Trials were excluded if there was no identifiable RT or if RT was less than 100 ms (1.4% of all trials). Movement time (MT) was calculated from movement onset to the time the cursor intersected the object (circle or ellipse). Because the “avoid” movements made towards the bar were kinematically different, they were not used for analyzing MT. The initial direction (ID) of the movement was calculated as the angle between the midline and the vector linking the hand position at the start to the hand position at peak acceleration. To assess the curvature of the trajectories, we calculated the normalized arc length, defined as the ratio between the arc length of the movement (summed absolute difference between every two points) and the arc length of the line connecting the start and end positions. A normalized arc length of 1 indicates an ideal straight-line path, whereas values greater than 1 indicate more curvature.

Each trial was classified based on the trial type and the hand positions during the movement. A trial was classified as attempting to hit the object if the hand position was closer to the object than to the bar at the end of the trial. Otherwise, the trial was classified as attempting to avoid the object. Trials were excluded if participants received correct feedback despite inaccurate motor performance; this was the case when the participant hit the circle only after missing the object on the initial attempt (2.3% of all trials) or when they attempted to hit an ellipse but missed (2.4% of Decision block trials).

The accuracy of trials in the No Decision blocks was based purely on motor performance. Trials were either classified as a “correct hit” if the circle was hit in the allotted time, or a “motor error” otherwise. Accuracy of the trials in the Decision block could be further classified based on signal detection theory nomenclature (Green and Swets 1966): “correct hit” if the circle was hit, “miss” if the circle was not hit, “correct avoid” if the ellipse was avoided, and “incorrect hit” if the ellipse was hit. The “misses” were subsequently divided into two subcategories based on presumed participant intent: if the participant initially aimed toward and attempted to hit the circle, the trial was classified as a “motor error”; otherwise the trial was classified as an “incorrect avoid”, implying the participant made an incorrect choice about the object shape. Decisional accuracy during the Decision blocks was calculated as the proportion of correct hits and correct avoids relative to all non-motor error trials.

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Finally, we were interested in how participants successfully planned their movements relative to the ongoing decision-making process during the Decision blocks. To this end, we examined the hand kinematics when the participant made “correct avoid” movements: on these trials, participants either moved directly to the bar (direct avoid), or first moved toward the object before re-directing to avoid the object and hit the bar (indirect avoid). We defined a trial as a direct avoid if the initial direction was aimed toward the bar (ID > 90° with respect to the midline) and an indirect avoid if initially aimed toward the object (ID < 90° with respect to the midline). The indirect avoid ratio was calculated as the proportion of indirect avoids over the overall number of correct avoids.

Eye Movements

Gaze data were low-pass filtered with a 20 Hz cutoff, and artifacts due to blinks, spikes, and gaze positions outside of the calibrated workspace. A previously validated geometric method was then used to transform gaze data from the eye-tracker onto the horizontal plane (Singh et al. 2017; Singh et al. 2016). Trials containing missing data or gaze angular velocities exceeding 3000°/s were manually inspected. If gaze events for the manually inspected trials could be reliably determined, then missing data and artifacts were corrected via interpolation; otherwise the gaze data were discarded for that trial. For Reach trials, saccades and fixations were identified using adaptive velocity-based thresholds for each participant. A similar procedure was used to separate saccades and smooth pursuit events during Intercept trials. Note that a gaze event was only classified as a fixation (in Reach trials) or smooth pursuit (in Intercept trials) if the target was foveated.

Individual saccades were discarded if the duration was <5 ms, and individual fixations and smooth pursuits were discarded if the duration was <40 ms. 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 initiated <100 ms after target onset and any initial saccade not directed to the object (>100 mm 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, gaze for a trial was not analyzed if the trial did not contain a valid saccade and a gaze event (fixation

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or pursuit) or if a gaze event (fixation or pursuit) occurred before any saccade. Overall, gaze data were included for 90.7% of Reach trials and 88.6% of Intercept trials.

Saccadic reaction time (SRT) was calculated as the onset of the initial saccade for a given trial. Likewise, gaze onset was determined as the time participants first fixated on the target (in Reach trials) or began smooth pursuit of the target (for Intercept trials). For each Intercept trial, we determined the number of saccades during the entire gaze period (catch-up saccades), normalized by the trial's gaze duration. For Intercept trials, we also determined the smooth pursuit lag as the horizontal distance (mm) between the moving object and the eye position during pursuit (excluding catch-up saccades). Smooth pursuit gain was calculated as the eye velocity relative to the object velocity for the open-loop (first 100 ms of pursuit), first 100 ms of the closed-loop (next 100 ms of pursuit), and full closed-loop (pursuit after first 100 ms) phases. Of note, smooth pursuit gains are typically computed using eye-trackers with chin rests (Brostek et al. 2017; Churchland and Lisberger 2002) or eye-trackers that are head-mounted (Spering et al. 2005). With these eye-trackers, gaze movements are computed as eye-in-head movements. In contrast, we used a remote eye-tracker which allowed small head movements to occur. Thus, our estimates of pursuit gains tend to be higher than the ones previously reported in the literature.

Statistical Analyses

To compare accuracy, hand and eye kinematic variables across conditions, we conducted repeated-measures ANOVAs using decision type (No Decision or Decision), movement type (Reach or Intercept), and trial duration (Fast or Slow) as within-subject factors. To evaluate the relative incidence of reaching and interception errors during Decision blocks, error type (motor error, incorrect avoid, incorrect hit) was used as a within-subject factor. Finally, avoid type (Indirect or Direct) was used as a within-subject factor when comparing reaction times of the correct avoid trials. For all ANOVA tests, the alpha level was set at 0.05 and effect sizes are reported using generalized η^2. Post hoc pairwise comparisons were conducted using the Holm correction (Holm 1979). Linear regression was used for bivariate comparisons, with alpha set to 0.05 and Holm's correction for multiple comparisons.

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Results

General performance characteristics

In the task, participants made rapid eye and arm movements in response to an object appearing on the visual display. On Reach trials, the object was located near the right or left edge of the display boundary. During Intercept trials, the object could be hit at any point as it moved horizontally at a constant Euclidean velocity from one boundary to the other. As illustrated in Figure 1C, after object onset participants typically made saccades directly to the object, followed by fixation on a stationary object (Reach trials) or smooth pursuit of a moving object (Intercept trials). On every trial, participants either attempted to hit the object by passing the cursor (representing hand position) through the object before the end of the trial or avoided the object by moving in the opposite direction toward a bar on the display.

Figure 2 shows the hand trajectories for two representative participants. Each line 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). Each trial's accuracy was classified based on the movement trajectory: for No Decision blocks, in which all movements were directed toward the object, accuracy was based solely on motor performance—a trial was a correct hit if the object was hit prior to the maximum duration or a motor error if not. In contrast, accuracy during Decision blocks relied on both making the correct decision about object shape and executing an accurate motor plan. Correct hits (hitting a circle) and correct avoids (moving toward the bar on ellipse trials) indicated accurate decisions and motor plans, whereas incorrect hits (hitting the ellipse) and incorrect avoids (moving toward the bar on circle trials) constituted errors in decision-making. Motor errors during the Decision blocks were identified as attempting to hit but missing the circle (Fig. 2).

More errors in perceptual decisions for interception than reaching

Figure 3A shows that movement type, decision type, and trial duration all influenced overall performance accuracy. The percentage of correct hits was lower for interceptions than for reaches [main effect of movement type: $F(1,25) = 88.64$, $p < 0.001$, $\eta^2 = 0.24$], and also lower for faster trial durations [main effect of trial duration: $F(1,25) = 151.42$, $p < 0.001$, $\eta^2 = 0.17$]. The decrease in correct hits at faster durations was larger for interceptions, [interaction of movement type and trial duration: $F(1,25) = 6.50$, $p = 0.02$, $\eta^2 = 0.01$], indicating that faster

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object velocity reduced interception performance beyond decreasing the time possible to hit the object.

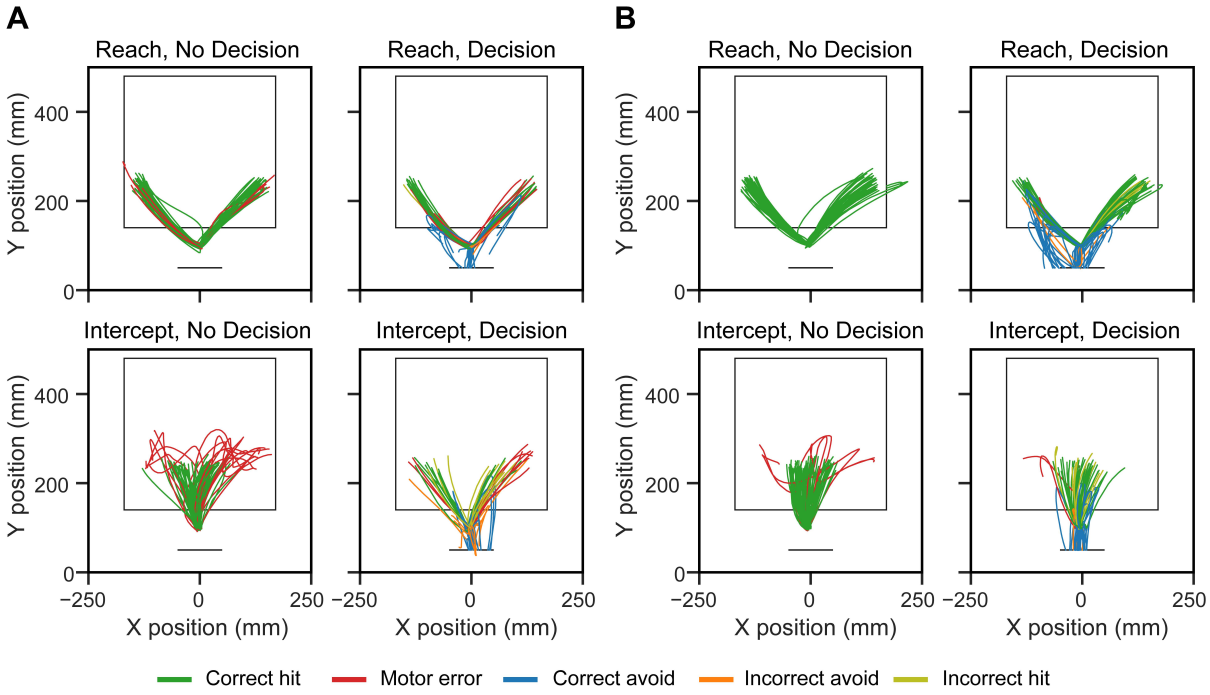

Figure 2. Example 2D trajectories from two representative participants. Each trajectory was classified as a correct hit of the circle, motor error (trying to hit circle but missing), correct avoid of the ellipse, incorrect avoid of the circle, or incorrect hit of the ellipse. *A*: This participant adjusted their interception trajectories during decision-making (see lower panels). *B*: This participant attempted to aim toward the midline for both Decision and No Decision Intercept blocks.

Overall, there was a direct decision cost on task performance, as the average percentage of correct hits decreased from 94.4 ± 0.5% for No Decision blocks to 83.7 ± 1.9% for Decision blocks [main effect of decision type: $F(1,25) = 50.39$, $p < 0.001$, $\eta^2 = 0.29$]. The decrease in accuracy for Decision blocks relative to No Decision blocks was larger for movements with faster trial durations [interaction of trial duration and decision type: $F(1,25) = 35.52$, $p < 0.001$, $\eta^2 = 0.06$], indicating that the participants were more affected by the imposed time constraints during decision-making.

Notably, the source of the errors (motor error, incorrect avoid, or incorrect hit) during Decision blocks differed depending on movement type and trial duration. During reaching movements, decision-making predominantly affected the motor error, but not decisional

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accuracy. For Reach trials at fast durations, there was a higher percentage of motor errors relative to incorrect avoids [$t(130) = 4.40$, $p < 0.001$] and incorrect hits [$t(130) = 4.08$, $p = 0.003$], whereas at slow durations, there were no differences in error percentage across the three error types (Fig. 3A). Motor errors for Reach trials at fast durations were higher for Decision blocks relative to No Decision blocks [$t(92.8) = 6.86$, $p < 0.001$], suggesting that under greater time constraints, participants tended to make correct decisions to hit the object but did not reach it in time.

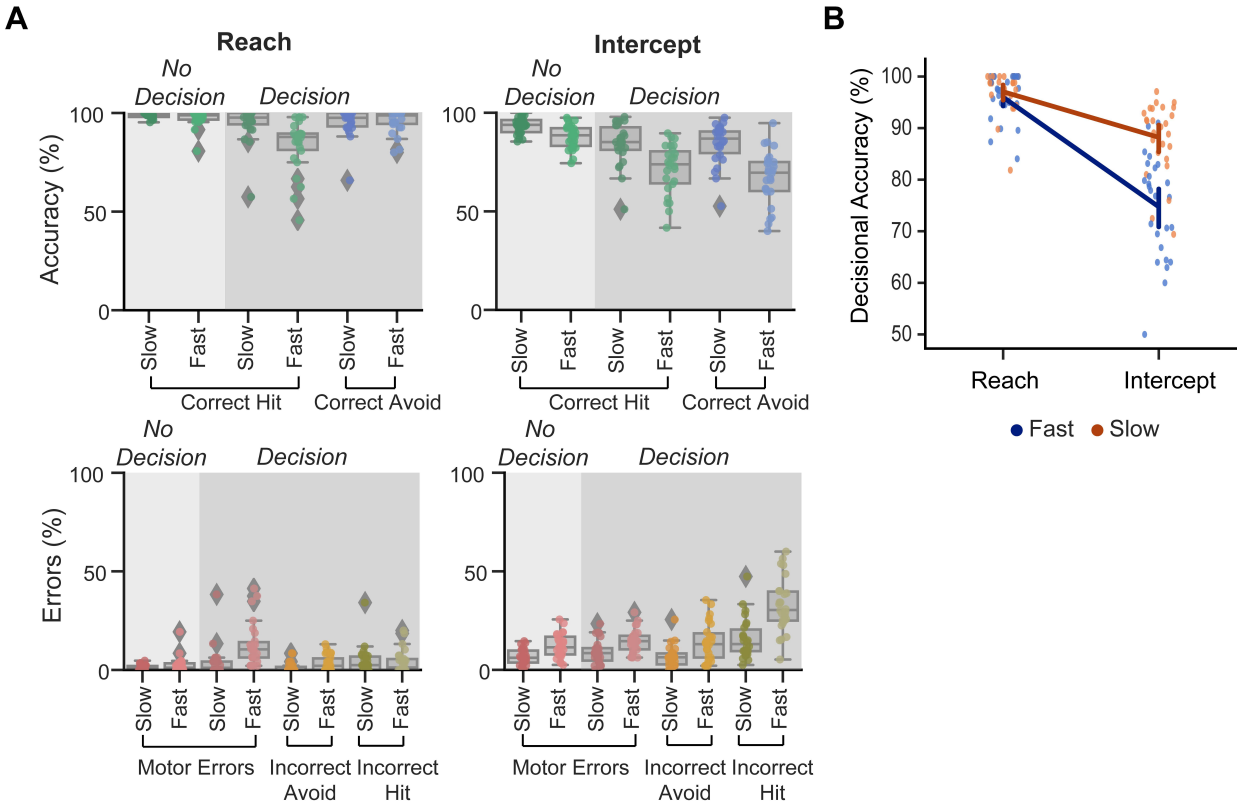

Figure 3. More errors in perceptual decisions for interception than reaching. A: Box plots of accuracy and errors across the different conditions. Each dot represents the mean for one participant for the given condition. Upper panels show the percentage of correct hits of the circle and correct avoids of the ellipse for reaching (left panel) and interception (right panel). Note that there were no correct avoids in No Decision blocks, as participants were instructed that the object would always be a circle. Lower panels show the percentage breakdown of the different types of errors (motor errors for No Decision blocks; motor errors, incorrect avoids, and incorrect hits for Decision blocks). For Decision blocks, the increase in errors was mainly due to motor errors for Fast reaches, and incorrect hits for Fast interceptions. B: Decisional accuracy percentage (correct hits and avoids relative to all non-motor error trials) for reaching and interception for fast (800 ms) and slow (950 ms) trial durations. Individual dots represent the mean for one participant. Error bars show the 95% confidence interval of the mean estimate.

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In contrast, during Intercept trials, the percentage of incorrect hits at fast trial durations was higher than the percentage of incorrect avoids and motor errors [all *t*'s > 8.84, all *p*'s < 0.001]. At slow trial durations, incorrect hit percentage was higher than incorrect avoid percentage [$t(130) = 4.42$, $p < 0.001$], but not motor error percentage [$t(130) = 3.32$, $p = 0.054$]. This provides evidence of a default strategy of trying to intercept the object, especially when the object was moving faster. This strategy led to a similar percentage of motor errors in No Decision and Decision [Fast: $t(92.8) = 1.41$, $p = 0.16$; Slow $t(92.8) = 1.84$, $p = 0.07$], but a large decrease in decisional accuracy relative to Reach trials [main effect of movement type: $F(1,25) = 113.55$, $p < 0.001$, $\eta^2 = 0.56$], especially at faster trial durations [interaction of trial duration and movement type: $F(1,25) = 70.95$, $p < 0.001$, $\eta^2 = 0.18$] (Fig. 3B). Overall, these results suggest that adding perceptual decision-making to a time-constrained task had an opposite effect on reaching and interception: during reaching, motor errors increased, whereas during interception, decision errors increased but motor accuracy was preserved.

Initial movement strategy predicts decisional accuracy during interception

In the current task, the object could be intercepted anywhere along the object's trajectory. To determine whether the decision about *where* to intercept might explain the decrease in decisional accuracy relative to reaching, we explored how participants initially aimed and landed their interceptive movements. Figure 4A shows the hit locations for all correct hit trials. In No Decision blocks, on average, participants tended to intercept the object slightly after it crossed the midline ($M = 28.7 \pm 2.9$ mm from midline). In contrast, there was a clear shift in object hit locations during Decision blocks ($M = 75.7 \pm 3.2$ mm from midline). Though interceptions were slightly more curved than reaches [main effect of movement type on normalized arc length: $F(1,25) = 10.63$, $p = 0.003$, $\eta^2 = 0.08$], interceptions were made along a relatively straight-line path that did not differ between No Decision and Decision blocks [main effect of decision type: $F(1,25) = 1.41$, $p = 0.25$, $\eta^2 = 0.01$] (see Fig. 4B). Furthermore, the final hit location was strongly correlated with the initial movement direction (No Decision: $r = 0.74$, $p < 0.001$; Decision: $r = 0.77$, $p < 0.001$), suggesting that participants were planning to intercept at a specific location rather than adjust their trajectory online (see Fig. 4C).

During Decision blocks, there were two main strategies for where to hit the object: participants either adjusted their movement trajectory to aim and hit the object away from the

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midline (as in Fig. 2A) or attempted to hit the object near the midline, similar to performance in No Decision blocks (as in Fig. 2B). To quantify the effects of these two strategies, we calculated the mean difference in initial direction between No Decision and Decision blocks for each participant—a larger difference in movement direction indicates the participant adjusted their initial movement strategy during decision-making. Interestingly, the change in initial movement direction was correlated with both reaction time (r = 0.53, p = 0.01) and incorrect hit rate (r = 0.42, p = 0.03), that is, participants who relied on a default motor plan to hit the object

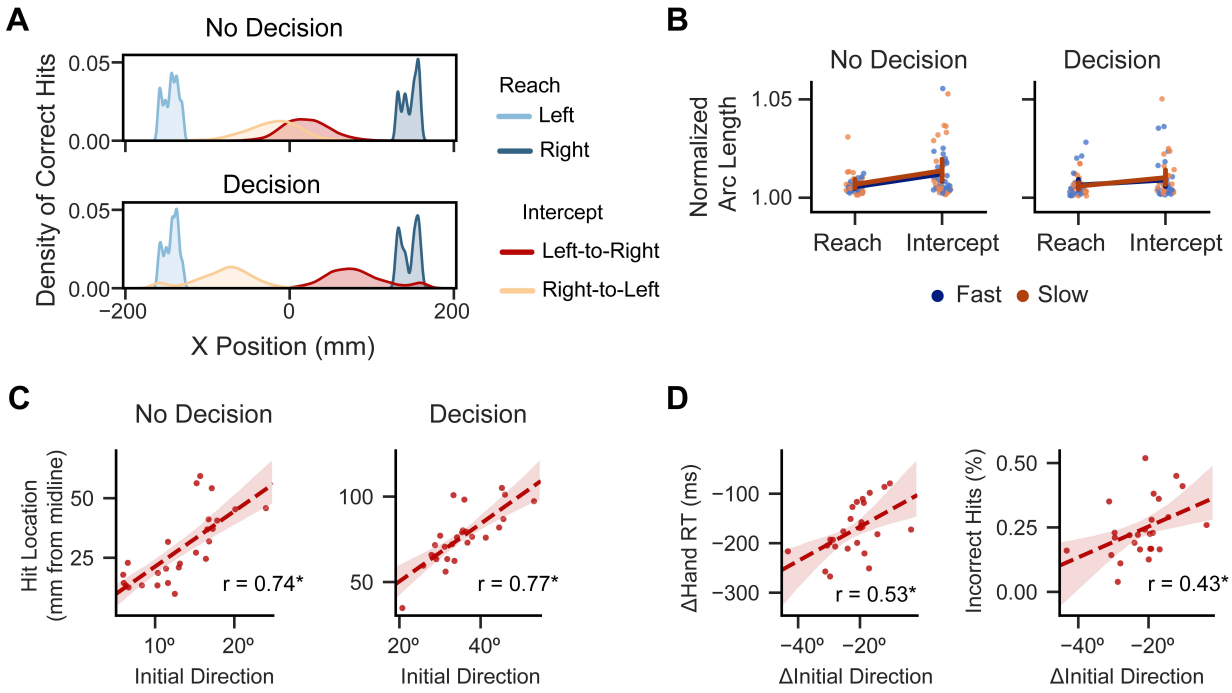

Figure 4. Initial movement strategy predicts decisional accuracy during interception. *A*: Univariate kernel density estimate of the horizontal hit position (0 mm = hit at the midline) for all correct hits of the circle. *B*: Arc length (summed absolute difference between every two points), normalized by the arc length of a straight-line path between start and hit positions. Both reach and interception movements were made along relatively straight paths (a normalized arc length of 1 indicates a perfectly straight-line path) and not different between decision blocks. Individual dots represent the mean for one participant. Error bars show the 95% confidence interval of the mean estimate. *C*: Initial movement direction of correct hits correlated with final hit location for No Decision (left panel) and Decision (right panel) interceptions, suggesting that participants planned to intercept objects at a specific location rather than make online adjustments to the trajectories. Shaded area represents the 95% confidence interval of the regression estimate. *D*: Participants who showed a larger mean change in initial movement direction from No Decision to Decision during interception showed a larger mean change in reaction time (left panel) and a lower percentage of incorrect hits (right panel). A negative change in initial movement direction indicates movements during Decision blocks were directed farther from the midline relative to No Decision blocks. For all regression plots, each dot represents the mean value for one participant. Shaded area represents the 95% confidence interval of the regression estimate. * indicates $p < 0.05$.

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independent of the perceptual decision were more likely to make decision errors (Fig. 4D). These results suggest that some participants used a default strategy of initiating similar movements for both No Decision and Decision conditions. Other participants who adjusted their initial movement strategy also exhibited improved decisional accuracy.

Interceptions and perceptual decisions differentially affect reaction and movement times

Figure 5 shows RTs and MTs for movements in which participants aimed toward and attempted to hit the circle: 94.1% of all No Decision trials, 48.7% of all Decision trials (Note that in Decision blocks, half of the trials were ellipses). Unexpectedly, in No Decision blocks, hand RTs were on average 22 ms faster for interceptions than for reaches, despite the higher difficulty associated with planning to intercept a moving target [main effect of movement type for No Decision: $F(1,25) = 13.02$, $p = 0.001$, $\eta^2 = 0.07$] (see Fig. 5A). Post-hoc tests showed that the difference was mainly due to shorter RTs for interception relative to reaching at Fast trial durations [Fast: $t(35) = 4.00$, $p = 0.002$; Slow: $t(35) = 2.56$, $p = 0.06$]. As shown in Figure 5B, movement time for Fast trial durations were shorter [main effect of trial duration for No Decision: $F(1,25) = 16.04$, $p < 0.001$, $\eta^2 = 0.02$], but were not different between reaching and interception [main effect of movement type for No Decision: $F(1,25) = 3.79$, $p = 0.06$, $\eta^2 = 0.05$].

As expected, perceptual decision-making led to a significant RT delay. Relative to No Decision blocks, RTs for Decision blocks were 173 ± 11 ms RT longer during Intercept trials, and 189 ± 10 ms longer during Reach trials [main effect of decision type: $F(1,25) = 483.5$, $p < 0.001$, $\eta^2 = 0.78$] (Fig. 5A). Thus, perceptual decisions involving the ventral stream clearly increased processing time for object identification (circle or ellipse) and motor response selection (hit or avoid). Similar to No Decision blocks, RTs during Decision blocks were also faster for Intercept trials and for Fast trial durations [main effect of movement type for Decision: $F(1,25) = 22.49$, $p < 0.001$, $\eta^2 = 0.11$); main effect of trial duration for Decision: $F(1,25) = 40.00$, $p < 0.001$, $\eta^2 = 0.05$]. The RT difference between Intercept and Reach trials was greater for Decision blocks (Intercept 38 ms faster) than No Decision blocks (22 ms faster) [$t(25) = 2.12$, $p = 0.04$]. Together, the RT results suggest that interceptive movements, shorter trial

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durations, and decision-making interact to encourage earlier movement initiation based on perceived time constraints.

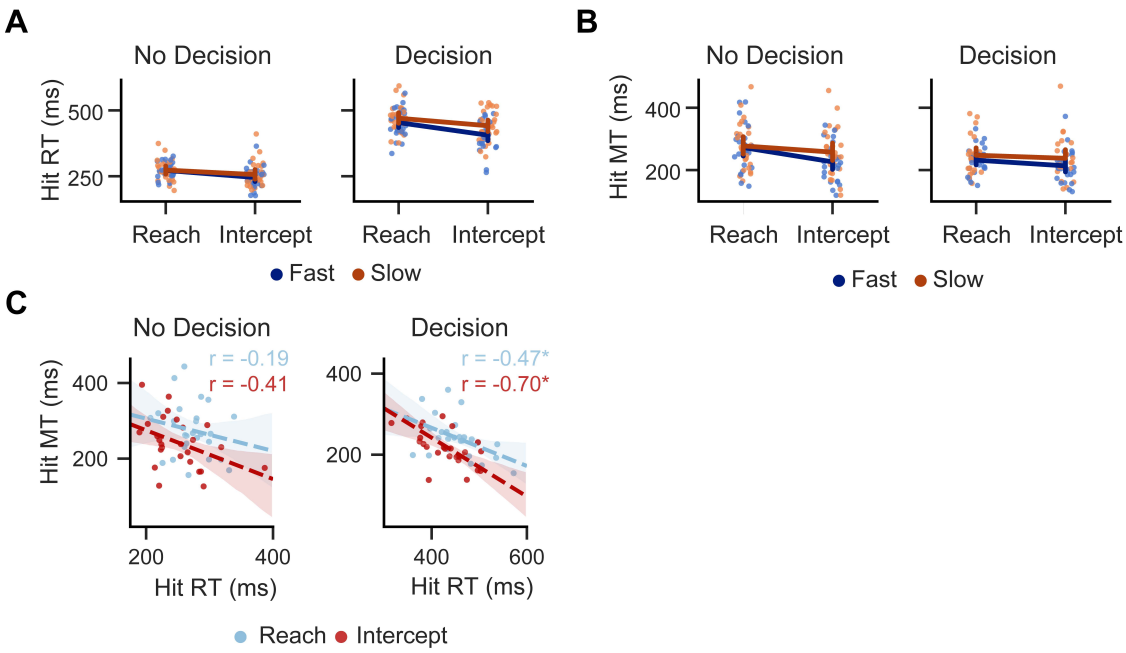

Figure 5. Interceptions and perceptual decisions differentially affect reaction and movement times. *A*: Reaction times of hits were longer in Decision blocks and shorter for interceptions in No Decision and Decision blocks. *B*: Movement times of hits were shorter for Decision blocks but no different between reaching and interception. Individual dots represent the mean for one participant. Error bars show the 95% confidence interval of the mean estimate. *C*: Reaction time and movement time are correlated during Decision (right panel), but not No Decision (left panel) blocks. Each dot represents the mean value for one participant. Shaded area represents the 95% confidence interval of the regression estimate. * indicates $p < 0.05$.

Though the large increase in RT during Decision blocks suggests additional time devoted to perceptual decision-making, there is evidence that the RT delay also benefited the efficiency of movement specification: MTs of the correct hits were faster during Decision blocks for both Reach and Intercept trials [main effect of decision type: $F(1,25) = 29.15$, $p < 0.001$, $\eta^2 = 0.04$] (Fig. 5B), likely a result of increased urgency (Thura and Cisek 2016) to hit the object following a prolonged RT period. The trade-off between the RTs and MTs of correct hits was most evident during decision-making: participants who had long RTs had faster MTs for Decision blocks (Reach: $r = -0.47$, $p = 0.01$; Intercept: $r = -0.70$, $p < 0.001$), but not for No Decision blocks (Reach: $r = -0.19$, $p = 0.34$; Intercept: $r = -0.41$, $p = 0.07$) (Fig. 5C). These results suggest that the RT delay for decisions was not solely for object identification and

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motor goal selection, but also for planning to hit the object faster under more restricted time limits.

Interception strategies favor ongoing decision-making after movement initiation

To further investigate how movements are planned relative to time-sensitive decision processing, we analyzed motor performance during movements to "avoid" the ellipse during Decision blocks. As can be seen in Figure 2A, on some trials participants adopted an "indirect avoid" strategy of first moving toward the object as if they would hit it, only to curve back around to hit the bar if an ellipse was identified during the movement. On other trials, participants made "direct avoids," moving in a straight-line path from the start position to the bar. Note that these indirect movements were predominantly observed for avoid decisions. The opposite pattern—moving toward the object after initially moving to avoid it, rarely occurred (<0.01% of Decision trials), highlighting the greater accuracy demands imposed by hitting the object vs. hitting the bar. To quantify participants' strategy use, we calculated the proportion of correct avoids that were indirect, i.e., involved a "change-of-mind" after movement initiation (Resulaj et al. 2009). All participants had both indirect and direct avoids, indicating a mixture of strategies used during the task. Overall, indirect avoids were more common during interception than reaching [main effect of movement type: $F(1,25) = 38.31$, $p < 0.001$, $\eta^2 = 0.21$) (Fig. 6A). This suggests that decisions about object shape were made (or refined) after movement initiation, and that the extent of this online processing depended on the computational complexity of the movement.

The advantage of this indirect launching strategy is participants could specify the more difficult motor command (hitting the object) early in the trial with enough time to complete the perceptual decision about shape and execute an easier movement (avoid and hit the bar) if necessary. If this is the case, indirect avoids should be associated with shorter RTs. Indeed, for both reaches and interceptions, indirect avoids had an average RT of 384 ± 9 ms, relative to 489 ± 11 ms for direct avoids [main effect of avoid type: $F(1,25) = 106.56$, $p < 0.001$, $\eta^2 = 0.47$] (Fig. 6B). Furthermore, as shown in Figure 6C, the initial direction of indirect avoids was similar to the initial direction of correct hits, indicating that even early movements were initiated with a specific motor plan to hit the circle. When trajectories of indirect avoids deviated from those of correct hits, they were directed farther from the midline than typical movements

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(longer tail for indirect avoids in Fig. 6C), suggesting an intermediate motor plan that incorporates uncertainty about ultimately hitting the circle or the bar.

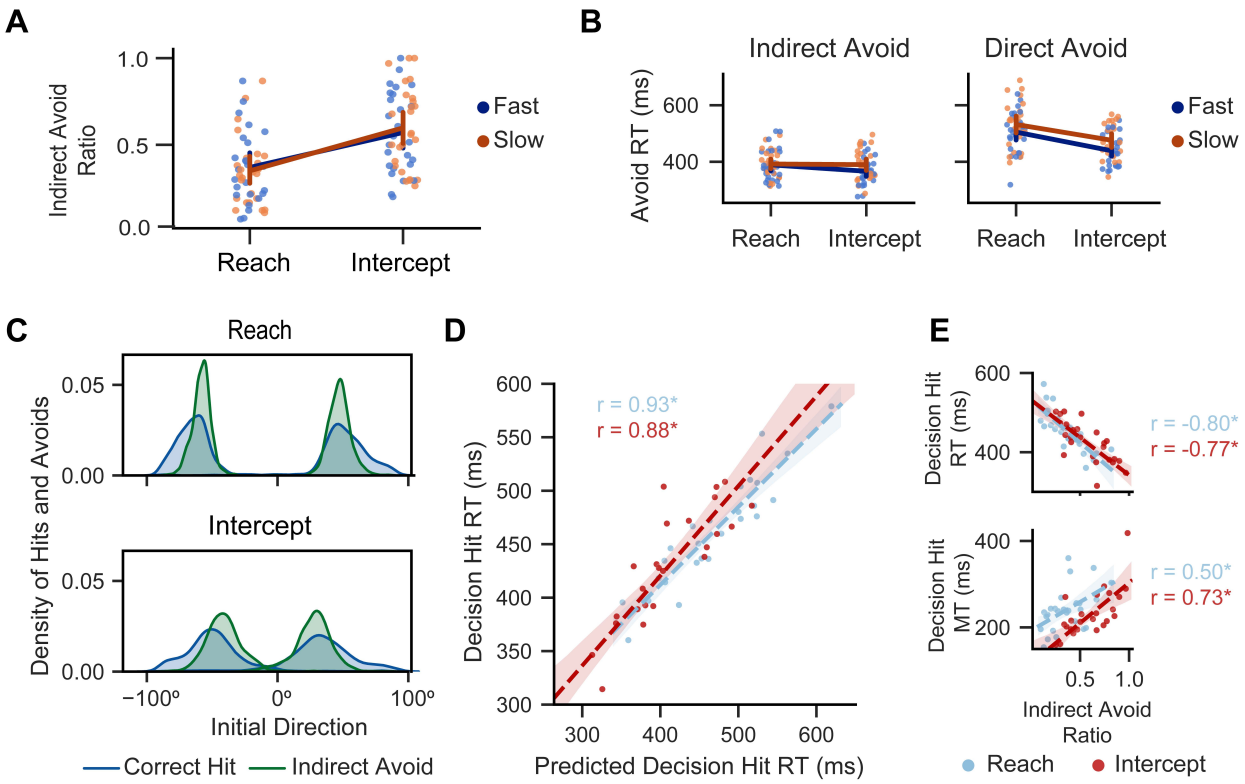

Figure 6. Interception strategies favor ongoing decision-making after movement initiation. *A*: Indirect avoid ratio (proportion of correct avoid movements initially aimed toward the ellipse over all correct avoids) during Decision blocks were higher for interception, suggesting more online adjustments after movement initiation. *B*: Mean reaction times for indirect (initially aimed toward ellipse) were shorter than direct (initially aimed toward bar) correct avoids. Individual dots represent the mean for one participant. Error bars show the 95% confidence interval of the mean estimate. *C*: Kernel density estimate of the initial movement direction (0° = aimed at midline) for indirect avoids of the ellipse showed a similar distribution to correct hits of the circle during Decision blocks for reaching (upper panel) and interception (lower panel). *D*: Reaction times of correct hits during Decision blocks could be predicted from the sum of a participant's mean reaction times for indirect and direct avoids, weighted by the relative proportion of indirect and direct avoids for that participant. *E*: Participant's with higher indirect avoid ratios exhibited lower reaction times (upper panel) and higher movement times (lower panel) times for correct hits. Each dot represents the mean value for one participant. The shaded area represents the 95% confidence interval of the regression estimate. * indicates $p < 0.05$.

Across participants, there was large variability in "avoid strategy" (indirect vs. direct) and RTs. To test if a participant's avoid strategy could explain their reaction time across all decision trials, we developed a simple model of RT for correct hits during decision-making:

$$\widehat{RT}_{Hit} = Prop_{indirect} * RT_{indirect} + (1 - Prop_{indirect}) * RT_{direct}$$

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where $Prop_{indirect}$ is the proportion of indirect hits for a participant, and $RT_{indirect}$ (RT_{direct}) is the participant's mean RT for indirect (direct) avoids. This model strongly predicted a participant's observed RT for correct hits during Decision blocks [Reach: $r = 0.93$, $p < 0.001$; Intercept: $r = 0.88$, $p < 0.001$], which suggests that participants initiated their movement based on a perceived sense of urgency (see Fig. 6D). Furthermore, participants with a higher proportion of indirect avoids exhibited shorter hit RTs [Reach: $r = -0.80$, $p < 0.001$; Intercept: $r = -0.77$, $p < 0.001$] and longer MTs [Reach: $r = 0.50$, $p = 0.03$; Intercept: $r = 0.73$, $p < 0.001$]. This suggests that participants with earlier RTs during Decision blocks relied more on online adjustments and decision-making post-movement initiation (Fig. 6E).

Saccadic reaction times are faster and decoupled from hand reaction time during perceptual decisions

Saccades, fixations (for Reach trials), and smooth pursuits (for Intercept trials) were identified using a geometric method to transform gaze data to the horizontal plane and adaptive velocity-based thresholds (Singh et al. 2016) for each participant (see Fig. 7A). Since standard task performance consisted of an initial saccade followed by onset of gaze (fixation or smooth pursuit), we restricted our eye movement analysis to the trials that followed that structure (see Methods for details).

Figure 7B plots the distribution of saccadic reaction times (SRTs), gaze onsets, and hand RTs relative to object onset. In No Decision blocks, gaze onset and hand RT were near-simultaneous, with hand RT occurring 13.6 ± 7.6 ms after gaze onset for Reach trials and 11.3 ± 9.2 ms after gaze onset for Intercept trials. In contrast, there was a large delay between gaze onset and hand RT in Decision blocks (Reach gaze-to-RT: 216.5 ± 10.5 ms; Intercept gaze-to-RT: 189.7 ± 11.6 ms), indicating a de-coupling of eye and arm movement during perceptual decision-making. Interestingly, compared to No Decision blocks, SRTs were on average 14 ms faster during Decision blocks for reaches and 14 ms faster for interceptions [main effect of decision type: $F(1,25) = 28.06$, $p < 0.001$, $\eta^2 = 0.11$]. Fixation onset was also faster during Decision blocks for Reach trials, but there was no effect of decision on onset of smooth pursuit [Reach: $t(43.6) = -4.31$, $p < 0.001$; Intercept: $t(43.6) = 0.94$, $p = 0.35$].

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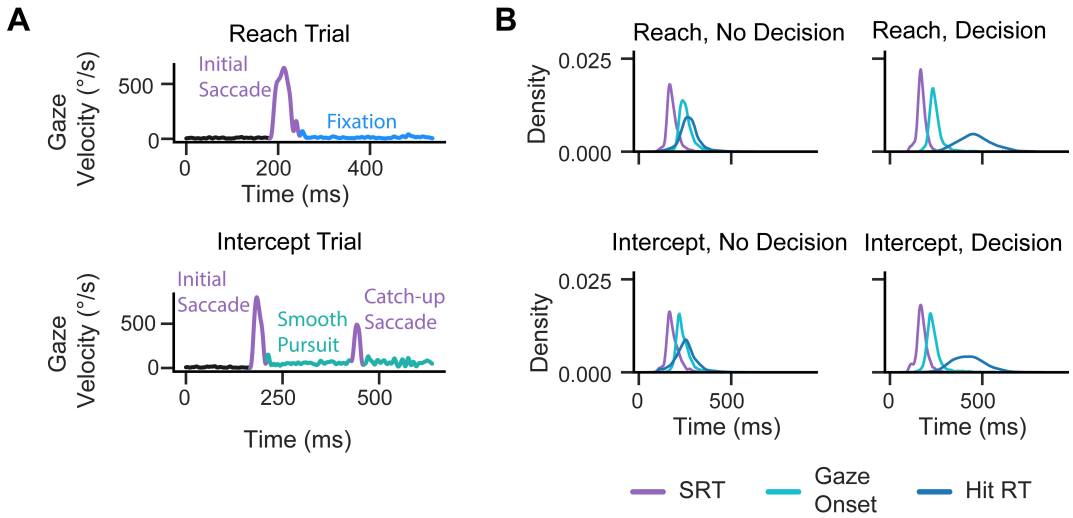

Figure 7. Saccadic reaction times are faster and decoupled from hand reaction time during perceptual decisions. *A*: Two representative trials showing classification of gaze events using adaptive velocity-based thresholds. In reaches to stationary objects, saccades are differentiated from fixations; in interceptions of moving objects, saccades are differentiated from smooth pursuit movements. *B*: Kernel density estimate showing the close distribution of saccadic reaction times, gaze onsets, and reaction times for circle hits across participants during No Decision, which become more spread out in Decision blocks. Mean saccadic reaction times were faster in Decision blocks.

Higher smooth pursuit gains occur in interception movements during perceptual decisions

During interception, the initial saccade landed behind the object and continued to lag during smooth pursuit (see Fig. 8A). As expected, initial saccade and smooth pursuit lag was larger for Fast trial durations (i.e., when the object was moving at faster velocities) [initial saccade main effect of trial duration: $F(1,25) = 41.91$, $p < 0.001$, $\eta^2 = 0.06$); smooth pursuit main effect of trial duration: $F(1,25) = 136.18$, $p < 0.001$, $\eta^2 = 0.34$]. In addition, the mean lag amplitude was larger during Decision blocks for both the initial saccade [main effect of decision type: $F(1,25) = 18.02$, $p < 0.001$, $\eta^2 = 0.04$] and smooth pursuit [main effect of decision type: $F(1,25) = 22.33$, $p < 0.001$, $\eta^2 = 0.16$]. This result suggests that participants made larger oculomotor errors when perceptual decision-making was required.

As shown in Figure 8A, by around 300 ms, there was no longer a difference in object lag between No Decision and Decision blocks. This effect is also evident by analyzing the smooth pursuit gain: while there is no effect of decision type on gain during the open-loop period (first 100 ms) [main effect of decision type: $F(1,25) = 3.71$, $p = 0.07$, $\eta^2 = 0.01$], gain is increased for Decision blocks relative to No Decision blocks during the closed-loop period [main effect of decision type: $F(1,25) = 39.01$, $p < 0.001$, $\eta^2 = 0.13$] (Fig. 8 B,C). This effect is

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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 type: $F(1,25) = 10.83$, $p = 0.003$, $\eta^2 = 0.03$]. This suggests that the negative closed feedback loop that minimizes retinal error between gaze and target is engaged differently when perceptual decision-making occurs during pursuit eye movements. Finally, the normalized number of catch-up saccades occurring during pursuit, was slightly higher during Decision blocks [main effect of decision type: $F(1,25) = 10.58$, $p = 0.003$, $\eta^2 = 0.09$] (Fig. 8D). Together, these results suggest that ocular movements are altered when object shape must be identified in addition to the object's spatial location.

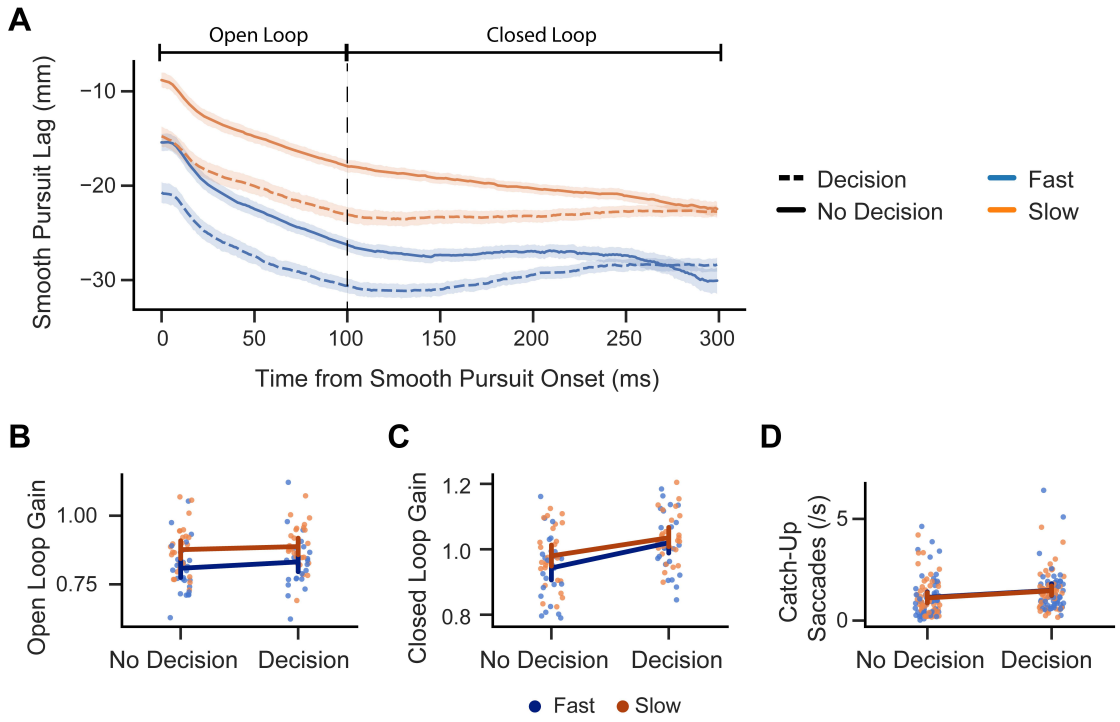

Figure 8. Higher smooth pursuit gains occur in interception movements during perceptual decisions. *A*: Smooth pursuit lag across interception trials as a function of time from smooth pursuit onset. Positive values indicate that the pursuit led the object, whereas negative values indicate lag. Participants lagged more during Decision blocks and in Fast trial durations (higher object velocity). The shaded area represents the 95% confidence interval of the mean estimate at each time point. *B*: Open-loop gain (first 100 ms) during interception was higher at Fast trial durations but did not differ between decision blocks, whereas *C*: closed-loop gain and *D*: the number of catch-up saccades per second were higher in Decision blocks. Individual dots represent the mean for one participant. Error bars show the 95% confidence interval of the mean estimate.

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Discussion

In the current study, we asked the question: how does perceptual decision-making involving the two visual streams affect visuomotor coordination in reaching and interception movements? To address this question, we developed a novel visuomotor task where participants either made reaching or interception movements to stationary or moving targets, respectively. In one condition, based on the shape of the object, participants had to decide whether to make a reaching or interception movement. If the object were a circle, they were instructed to reach towards (or intercept) the target. If the object were an ellipse, they were asked to make a movement away from the ellipse towards a horizontal bar.

We proposed three hypotheses in this study. First, we hypothesized that the interception movements would require additional computations associated with rapid coordinate transformations from the real-world to the retinotopic reference frame, and as a result, interception movements would show longer reaction times and reduced accuracy. Though interception movements were less accurate, reaction times for interception movements were in fact shorter than reaching movements. Thus, our first hypothesis was not supported. Our second hypothesis was that under time pressure, neural processing involving both the ventral and dorsal visual streams should become more parallel. In support of this hypothesis, we found faster reaction times and more subsequent movement adjustments that reflected online decision-making after movement initiation. Our third and final hypothesis was that in the interception task, the smooth pursuit gains will be higher to pursue moving objects more closely and compensate for the impaired and slower object identification that occurs during pursuit eye movements. This hypothesis was supported.

Shorter reaction times for interceptions suggest reflexive arm initiation to moving targets

Interception movements refer to a broad category of movements (catch the object, hit or kick it away, or redirect its trajectory) directed towards moving objects (reviewed in Brenner and Smeets 2018). One of the most well-studied interception movements are projectile catching movements (Cesqui et al. 2012; Lacquaniti et al. 1993; Tombini et al. 2009; Zago et al. 2009). Visuomotor coordination in these interceptive movements is constrained by the spatiotemporal kinematics of the target under gravity like conditions. The target travels along a

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rectilinear or curvilinear path and interception movement involves getting the arm into the path of the projectile.

In contrast, the interception movements in our study involved chasing a moving target before it disappeared from the workspace. We found that interception movements were less accurate than reaching movements (see Fig. 3) and less accurate when objects moved faster. Furthermore, participants committed more motor errors for fast interceptions than fast reaches (Fast and Reach blocks). The movement times were similar for both the Reach and Intercept conditions, but were shorter for the Fast condition (see Fig. 5). Neural noise that causes a trade-off between movement speed and accuracy (Fitts 1954) partially explains why participants made a higher number of motor errors during the Fast Condition (for both Reach and Intercept movements), but it doesn't quite explain why movements were less accurate when targets were moving.

One prominent hypothesis is that goal-directed arm movements are controlled by the visuomotor system based on a difference vector between the positions of the hand and the target (Shadmehr and Wise 2005). Targets are localized in space through coordinate transformation from an extrinsic to an egocentric frame of reference through neural processing in networks spanning the parietal and premotor cortices (Bernier and Grafton 2010; Beurze et al. 2010; Pesaran et al. 2006). For moving targets, the dynamic location of the target in extrinsic space will need to be continuously transformed to a retinotopic reference frame, imposing a significant computational burden on the nervous system (Dimitriou et al. 2013). Thus, delays associated with neural processing of moving targets during online feedback control may result in a sluggish update of motor plans and erroneous outcomes. These delays in neural processing should also affect the planning phase of the movement and cause delayed initiation of movement. For example, a potential strategy during interception would be to project the current location of the target into the future, and then execute a linear arm trajectory towards the future location of the target. Computing the kinematic trajectory to the future target location requires both sensory processing and prediction and should add additional computational costs and slow down the initiation of the arm movement.

However, this oversimplified explanation is not empirically supported when we look at the reaction times for reach and interception movements; the reaction times for interception movements were shorter than the reaching movements. This result is difficult to reconcile with

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the vector difference hypothesis because this hypothesis would predict that the planning of the interception movement vector should be at least as difficult as the planning of the reach movement vector. However, the shorter reaction times suggests a relatively automatic process associated with control of interception movements to moving targets. This is consistent with recent reports that propose that moving targets may impose a sense of perceived urgency and more reflexive control of interception movements than reaching movements (Cisek et al. 2009; Lara et al. 2018; Perfiliev et al. 2010; Reichenbach 2016). In other words, the automatic reflexive limb response may be initiated by the neural nodes involved in motion detection (areas MT/MST) while gating subsequent sensorimotor transformations in the parietal-premotor cortical loops that facilitate initiation of reaching movements to stationary targets (Pisella et al. 2000).

One limitation in our study is that reaching movements were made to the left or right edge of the workspace, whereas participants tended to intercept the object close to the midline (Fig. 4A). Thus, higher reaction times during reaching may be partially due to performing higher amplitude movements (Munro et al. 2007). However, movement times did not differ between movement types and shortening the maximum trial duration (Fast versus Slow) influenced reaction times in interceptions more than reaches. This provides support for the role of automatic limb responses to moving targets in explaining reaction times.

Greater online integration of ventral stream and decision processing during interception

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 and dorsal streams, respectively (Goodale and Milner 1992; Goodale and Westwood 2004). While much work has concerned how the two visual streams serve unique functional roles 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 order to perform the correct action (hit the object or avoid it), participants must first accurately identify the object's shape (circle or ellipse). We found that even under time constraints (800 ms to hit the object in the Fast condition), participants could perform object recognition and formulate a decision prior to movement initiation. Relative to No Decision blocks, in which participants only needed to process object information to facilitate movement, there was an

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average RT delay of 189 ms (during reaching) and 173 ms (during interception) in Decision blocks, which is within the processing delays associated with a ventral-prefrontal-motor pathway or ventral-basal ganglia-motor pathway for shape 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 across participants that perceptual processing engaging the ventral stream can fully precede dorsal stream involvement supporting sensorimotor transformations of the visual information for action.

However, closer investigation of the movement trajectories and corresponding RTs during “avoid” trials provides evidence that additional processing of object information and decision-making could occur after movement initiation. During both reaching and interception blocks, we observed that participants would occasionally initiate their movements toward the circle only to curve around past the original start location and hit the bar. The presence of these “indirect avoids” provide evidence of an evolving decision given accumulating stimulus information (Resulaj et al. 2009; Selen et al. 2012). In contrast to previous studies investigating sensorimotor decisions of the limb that vary the motion or spatial location of the target under different task demands (Burk et al. 2014; Gallivan et al. 2016; van den Berg et al. 2016), here we show that sensorimotor transformations computed in the dorsal stream can seamlessly integrate incoming information about object shape that originates in the ventral stream (Davare et al. 2007; Konen and Kastner 2008; Lehky and Tanaka 2016; Sereno and Maunsell 1998). The distribution of initial movement directions of indirect avoids overlapped with the initial directions of correct hits and skewed toward the direction of the bar, which supports previous work suggesting that movements are purposefully planned to optimize task success given uncertainty about the impending decision (Haith et al. 2015; Nashed et al. 2017; Wong and Haith 2017). Thus, even though the imposed time constraints still allow for sequential stimulus identification, decision-making, and movement execution, participants often favored an alternative strategy in which both ventral and dorsal stream processes co-occur during preparation and execution (Haith et al. 2016; Orban de Xivry et al. 2017).

What determines the magnitude of the bias towards simultaneous processing in the ventral and dorsal streams during decision-making? One likely driving factor is the subjective urgency of the upcoming response. Saccadic reaction times were faster in Decision blocks, reflecting a greater perceptual urgency to foveate on the peripheral object to allow more time

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to identify its shape (Montagnini and Chelazzi 2005; Trottier and Pratt 2005). The increased urgency to initiate a saccade was associated with reduced positional accuracy of initial gaze and may have contributed to a dissociation between saccadic and hand RTs during Decision blocks. This trade-off emphasizes the dual role of the oculomotor system in decision formation and motor control (Fooken and Spering 2019; Joo et al. 2016), in which the use of eye movements for perceptual decision-making could interfere with its role in facilitating sensorimotor transformations for accurate limb movement.

The perceived urgency during task performance depended on the complexity of the motor response (Thura and Cisek 2016). Interceptions had lower accuracy than reaches during decision-making, largely due to participants incorrectly hitting a higher proportion of moving ellipses. In addition, the proportion of indirect avoids was higher for interception, indicating a stronger bias toward initiating a hit movement prior to making a perceptual decision about object shape. A higher proportion of indirect avoids was associated with shorter RTs, which indicates 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). Notably, the higher incorrect hit rate during interception was associated with the inability to adjust initial movement trajectories that account for decisional demands but was otherwise unrelated to motor performance (see Fig. 4). This suggests that the motor system, involving the dorsal stream, may initiate a control policy that can flexibly incorporate prolonged processing of sensory information in the ventral stream for online movement corrections. Our study does not address how the dorsal stream receives ventral stream information about object shape, but recent work has identified pathways between the two streams that could facilitate direct communication during ongoing sensorimotor control (Budisavljevic et al. 2018; Hutchison and Gallivan 2018; Takemura et al. 2016).

Modulation of smooth pursuit gains during perceptual decision-making implicate the frontal eye fields in online interactions between the two visual streams

Smooth pursuit gains have been conventionally defined as the ratio of target and gaze velocity in angular coordinates in head-fixed conditions. The first 100 ms of the smooth pursuit movement is referred to as the open-loop phase (Barnes 2008; Tychsen and Lisberger 1986). This is followed by the onset of closed-loop pursuit, which is mainly controlled by a negative

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feedback loop to ensure that the eye velocity closely matches the target velocity. We compared both open-loop and closed-loop gains for the Interception blocks for the No-Decision and Decision conditions. As expected, our results show no differences in open-loop gains between the two conditions (see Fig. 8).

We are aware of only one study in which investigators studied how object recognition is affected during pursuit eye movements. Schütz and colleagues (Schütz et al. 2009) superimposed an English alphabet letter on a gray noisy patch and either moved it across the workspace at a fixed speed of 10.6°/sec (pursuit condition) or kept it stationary (fixation condition). At the end of each trial, participants were instructed to select a letter from a pool of 20 letters to indicate which letter appeared on the patch. They showed that on average participants identified fewer targets correctly during the pursuit condition than the fixation condition, suggesting an impaired ability to recognize letters during pursuit eye movements. Though letter perception primarily involves Wernicke's area in the superior temporal gyrus, there are neural areas in the ventral visual stream that are involved in letter recognition. This suggests that recognition of object shapes should be harder while intercepting moving objects in Decision blocks.

In contrast to the slow speed of 10.6°/sec used by Schütz and colleagues, the objects in our experiment moved at approximately 80-90°/sec. This speed approaches the limit of smooth pursuit in humans (Meyer et al. 1985) and 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. We found that participants increased the closed-loop gain of the pursuit to foveate the objects during the Decision condition. This result suggests that the visual perceptual decision-making network, that includes the ventral visual stream, dorsolateral prefrontal regions and frontal eye fields (Heekeren et al. 2004; Heekeren et al. 2008; Sakagami and Pan 2007), may provide either a predictive or urgency signal to the smooth pursuit system to increase the gain and minimize the retinal error between the target and the gaze. Indeed, stimulation and lesion studies have implicated the frontal eye fields with the modulation of smooth pursuit gain during object tracking (Gagnon et al. 2006; Keating 1991; Morrow and Sharpe 1995; Shi et al. 1998). Furthermore, anatomical tracer studies in primates have shown that the dorsal and ventral processing streams converge in the lateral frontal eye fields (Schall et al. 1995). Taken together with our data, this suggests that in tasks where

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perceptual decision-making is necessary during pursuit eye movements, the frontal eye fields may modulate pursuit gains to meet task demands.

Conclusions

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 the ventral and dorsal streams. We found lower accuracy and hand RTs for interception movements relative to reaching movements, effects that were amplified when a decision about object shape was required for accurate movement specification. During decision-making, participants had faster saccadic RTs and adopted online arm movement strategies that incorporated an evolving decision about object shape. Participants exhibited higher smooth pursuit gains to compensate for initial eye movements focused on the perceptual decision. These results suggest that the extent of simultaneous ventral-dorsal stream interactions during ongoing movement depends on the perceived urgency to act, which is greater when intercepting a moving target.

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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.

Andersen RA, and Buneo CA. Intentional maps in posterior parietal cortex. *Annual Review of Neuroscience* 25: 189-220, 2002.

Andersen RA, Essick GK, and Siegel RM. Encoding of spatial location by posterior parietal neurons. *Science* 230: 456-458, 1985.

Archambault PS, Ferrari-Toniolo S, Caminiti R, and Battaglia-Mayer A. Visually-guided correction of hand reaching movements: The neurophysiological bases in the cerebral cortex. *Vision Research* 110, Part B: 244-256, 2015.

Barnes GR. Cognitive processes involved in smooth pursuit eye movements. *Brain and Cognition* 68: 309-326, 2008.

Bernier P-M, and Grafton ST. Human posterior parietal cortex flexibly determines reference frames for reaching based on sensory context. *Neuron* 68: 776-788, 2010.

Beurze SM, Pelt SV, and Medendorp WP. Behavioral reference frames for planning human reaching movements. *Journal of Neurophysiology* 96: 352-362, 2006.

Beurze SM, Toni I, Pisella L, and Medendorp WP. Reference frames for reach planning in human parietofrontal cortex. *Journal of Neurophysiology* 104: 1736-1745, 2010.

Biguer B, Jeannerod M, and Prablanc C. The coordination of eye, head, and arm movements during reaching at a single visual target. *Experimental Brain Research* 46: 301-304, 1982.

Boussaoud D, and Bremmer F. Gaze effects in the cerebral cortex: reference frames for space coding and action. *Experimental Brain Research* 128: 170-180, 1999.

Brenner E, and Smeets JB. Continuous visual control of interception. *Human Movement Science* 30: 475-494, 2011.

Brenner E, and Smeets JBJ. Continuously updating one's predictions underlies successful interception. *Journal of Neurophysiology* 120: 3257-3274, 2018.

Brenner E, Smeets JBJ, and van den Berg AV. Smooth eye movements and spatial localisation. *Vision Research* 41: 2253-2259, 2001.

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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.

Caminiti R, Ferraina S, and Mayer AB. Visuomotor transformations: early cortical mechanisms of reaching. *Current Opinion in Neurobiology* 8: 753-761, 1998.

Cesqui B, d'Avella A, Portone A, and Lacquaniti F. Catching a ball at the right time and place: Individual factors matter. *PLoS One* 7: e31770, 2012.

Churchland AK, and Lisberger SG. Gain control in human smooth-pursuit eye movements. *Journal of Neurophysiology* 87: 2936-2945, 2002.

Cisek P, and Kalaska JF. Neural mechanisms for interacting with a world full of action choices. *Annual Review of Neuroscience* 33: 269-298, 2010.

Cisek P, Puskas GA, and El-Murr S. Decisions in changing conditions: the urgency-gating model. *Journal of Neuroscience* 29: 11560-11571, 2009.

Clower DM, Hoffman JM, Votaw JR, Faber TL, Woods RP, and Alexander GE. Role of posterior parietal cortex in the recalibration of visually guided reaching. *Nature* 383: 618, 1996.

Colby C, and Goldberg M. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* 255: 90-92, 1992.

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.

Dekleva BM, Kording KP, and Miller LE. Single reach plans in dorsal premotor cortex during a two-target task. *Nature Communications* 9: 3556, 2018.

Delorme A, Richard G, and Fabre-Thorpe M. Ultra-rapid categorisation of natural scenes does not rely on colour cues: a study in monkeys and humans. *Vision Research* 40: 2187-2200, 2000.

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Desmurget M, and Grafton S. Forward modeling allows feedback control for fast reaching movements. *Trends in Cognitive Sciences* 4: 423-431, 2000.

Dessing JC, Crawford JD, and Medendorp WP. Spatial updating across saccades during manual interception. *Journal of Vision* 11: 4-4, 2011.

Dimitriou M, Wolpert DM, and Franklin DW. The temporal evolution of feedback gains rapidly update to task demands. *Journal of Neuroscience* 33: 10898-10909, 2013.

Donders FC. On the speed of mental processes. *Acta Psychologica* 30: 412-431, 1969.

Doniger GM, Foxe JJ, Murray MM, Higgins BA, Snodgrass JG, Schroeder CE, and Javitt DC. Activation timecourse of ventral visual stream object-recognition areas: high density electrical mapping of perceptual closure processes. *Journal of Cognitive Neuroscience* 12: 615-621, 2000.

Fitts PM. The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology* 47: 381-391, 1954.

Fooken J, and Spering M. Decoding go/no-go decisions from eye movements. *J Vis* 19: 5, 2019.

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. *Nature Reviews Neuroscience* 19: 519-534, 2018.

Gallivan JP, Logan L, Wolpert DM, and Flanagan JR. Parallel specification of competing sensorimotor control policies for alternative action options. *Nature Neuroscience* 19: 320-326, 2016.

Goodale MA, and Milner AD. Separate visual pathways for perception and action. *Trends in Neurosciences* 15: 20-25, 1992.

Goodale MA, Pelisson D, and Prablanc C. Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature* 320: 748-750, 1986.

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.

Grafton S, Fagg A, and Arbib M. Dorsal premotor cortex and conditional movement selection: A PET functional mapping study. *Journal of Neurophysiology* 79: 1092-1097, 1998.

Green DM, and Swets JA. *Signal detection theory and psychophysics*. Wiley New York, 1966.

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Grill-Spector K, Kourtzi Z, and Kanwisher N. The lateral occipital complex and its role in object recognition. *Vision Research* 41: 1409-1422, 2001.

Haith AM, Huberdeau DM, and Krakauer JW. Hedging your bets: Intermediate movements as optimal behavior in the context of an incomplete decision. *PLoS Computational Biology* 11: e1004171, 2015.

Haith AM, Pakpoor J, and Krakauer JW. Independence of movement preparation and movement initiation. *Journal of Neuroscience* 36: 3007-3015, 2016.

Hecht D, Reiner M, and Karni A. Multisensory enhancement: gains in choice and in simple response times. *Experimental Brain Research* 189: 133, 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.

Hegdé J. Time course of visual perception: coarse-to-fine processing and beyond. *Progress in Neurobiology* 84: 405-439, 2008.

Holm S. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6: 65-70, 1979.

Honda H. The extraretinal signal from the pursuit-eye-movement system: Its role in the perceptual and the egocentric localization systems. *Perception & Psychophysics* 48: 509-515, 1990.

Hutchison RM, and Gallivan JP. Functional coupling between frontoparietal and occipitotemporal pathways during action and perception. *Cortex* 98: 8-27, 2018.

Jax SA, and Rosenbaum DA. Hand path priming in manual obstacle avoidance: rapid decay of dorsal stream information. *Neuropsychologia* 47: 1573-1577, 2009.

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.

Kalaska JF, and Crammond DJ. Deciding not to GO: neuronal correlates of response selection in a GO/NOGO task in primate premotor and parietal cortex. *Cerebral Cortex* 5: 410-428, 1995.

Keating E. Frontal eye field lesions impair predictive and visually-guided pursuit eye movements. *Experimental Brain Research* 86: 311-323, 1991.

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Konen CS, and Kastner S. Two hierarchically organized neural systems for object information in human visual cortex. *Nature Neuroscience* 11: 224-231, 2008.

Lacquaniti F, Carrozzo M, and Borghese NA. Time-varying mechanical behavior of multijointed arm in man. *Journal of Neurophysiology* 69: 1443-1464, 1993.

Lara AH, Elsayed GF, Zimnik AJ, Cunningham JP, and Churchland MM. Conservation of preparatory neural events in monkey motor cortex regardless of how movement is initiated. *Elife* 7: 2018.

Lehky SR, and Sereno AB. Comparison of shape encoding in primate dorsal and ventral visual pathways. *Journal of Neurophysiology* 97: 307-319, 2007.

Lehky SR, and Tanaka K. Neural representation for object recognition in inferotemporal cortex. *Current Opinion in Neurobiology* 37: 23-35, 2016.

Meyer CH, Lasker AG, and Robinson DA. The upper limit of human smooth pursuit velocity. *Vision Research* 25: 561-563, 1985.

Mishkin M, Ungerleider LG, and Macko KA. Object vision and spatial vision: two cortical pathways. *Trends in Neurosciences* 6: 414-417, 1983.

Montagnini A, and Chelazzi L. The urgency to look: prompt saccades to the benefit of perception. *Vision Res* 45: 3391-3401, 2005.

Morrow MJ, and Sharpe JA. Deficits of smooth-pursuit eye movement after unilateral frontal lobe lesions. *Annals of Neurology* 37: 443-451, 1995.

Munoz DP, and Corneil BD. Evidence for interactions between target selection and visual fixation for saccade generation in humans. *Experimental Brain Research* 103: 168-173, 1995.

Munro H, Plumb MS, Wilson AD, Williams JH, and Mon-Williams M. The effect of distance on reaction time in aiming movements. *Exp Brain Res* 183: 249-257, 2007.

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.

Pélisson D, Prablanc C, Goodale MA, and Jeannerod M. Visual control of reaching movements without vision of the limb. II. Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of a double-step stimulus. *Experimental Brain Research* 62: 303-311, 1986.

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Perfiliev S, Isa T, Johnels B, Steg G, and Wessberg J. Reflexive limb selection and control of reach direction to moving targets in cats, monkeys, and humans. *Journal of Neurophysiology* 104: 2423-2432, 2010.

Pesaran B, Nelson MJ, and Andersen RA. Dorsal premotor neurons encode the relative position of the hand, eye, and goal during reach planning. *Neuron* 51: 125-134, 2006.

Pisella L, Grea H, Tilikete C, Vighetto A, Desmurget M, Rode G, Boisson D, and Rossetti Y. An 'automatic pilot'for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nature Neuroscience* 3: 729-736, 2000.

Prablanc C, Desmurget M, and Gréa H. Neural control of on-line guidance of hand reaching movements. In: *Progress in Brain Research*Elsevier, 2003, p. 155-170.

Prablanc C, Echallier J, Komilis E, and Jeannerod M. Optimal response of eye and hand motor systems in pointing at a visual target. *Biological Cybernetics* 35: 113-124, 1979.

Prablanc C, Pélisson D, and Goodale M. Visual control of reaching movements without vision of the limb. I. Role of retinal feedback of target position in guiding the hand. *Experimental Brain Research* 62: 293-302, 1986.

Reichenbach A. The detection continuum for motor control comprises preparation and adjustments. *Motor Control* 20: 177-181, 2016.

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. *Current Opinion in Neurobiology* 12: 149-154, 2002.

Rizzolatti G, and Matelli M. Two different streams form the dorsal visual system: anatomy and functions. *Experimental Brain Research* 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.

Rushworth M, Johansen-Berg H, Göbel SM, and Devlin J. The left parietal and premotor cortices: motor attention and selection. *NeuroImage* 20: S89-S100, 2003.

Sakagami M, and Pan X. Functional role of the ventrolateral prefrontal cortex in decision making. *Current Opinion in Neurobiology* 17: 228-233, 2007.

bioRxiv preprint doi: https://doi.org/10.1101/821074; this version posted October 29, 2019. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Saunders JA, and Knill DC. Humans use continuous visual feedback from the hand to control fast reaching movements. *Experimental Brain Research* 152: 341-352, 2003.

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.

Schlag J, and Schlag-Rey M. Through the eye, slowly; Delays and localization errors in the visual system. *Nature Reviews Neuroscience* 3: 191-200, 2002.

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. *Proceedings of the National Academy of Sciences* 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.

Shadmehr R, and Wise SP. *The Computational Neurobiology of Reaching and Pointing: A Foundation for Motor Learning*. The MIT press, 2005.

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 C, Tryon SC, Ross A, Fritz S, and Herter TM. A novel computational model to probe visual search deficits during motor performance. *Journal of Neurophysiology* 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.

Smeets JB, Oostwoud WL, and Brenner E. Movement adjustments have short latencies because there is no need to detect anything. *Motor Control* 20: 137-148, 2016.

Song J-H, and Nakayama K. Target selection in visual search as revealed by movement trajectories. *Vision Research* 48: 853-861, 2008.

bioRxiv preprint doi: https://doi.org/10.1101/821074; this version posted October 29, 2019. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Spering M, Kerzel D, Braun DI, Hawken MJ, and Gegenfurtner KR. Effects of contrast on smooth pursuit eye movements. *Journal of Vision* 5: 6-6, 2005.

Sternberg S. The discovery of processing stages: Extensions of Donders' method. *Acta Psychologica* 30: 276-315, 1969.

Stevenson SA, Elsley JK, and Corneil BD. A “gap effect” on stop signal reaction times in a human saccadic countermanding task. *Journal of Neurophysiology* 101: 580-590, 2009.

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. Seeking categories in the brain. *Science* 291: 260-263, 2001.

Thura D, and Cisek P. Modulation of premotor and primary motor cortical activity during volitional adjustments of speed-accuracy trade-offs. *Journal of Neuroscience* 36: 938-956, 2016.

Tombini M, Zappasodi F, Zollo L, Pellegrino G, Cavallo G, Tecchio F, Guglielmelli E, and Rossini PM. Brain activity preceding a 2D manual catching task. *NeuroImage* 47: 1735-1746, 2009.

Trottier L, and Pratt J. Visual processing of targets can reduce saccadic latencies. *Vision Research* 45: 1349-1354, 2005.

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.

Ulrich R, Mattes S, and Miller J. Donders's assumption of pure insertion: an evaluation on the basis of response dynamics. *Acta Psychologica* 102: 43-76, 1999.

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.

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.

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. *Experimental Brain Research* 192: 571-604, 2009.