



RESEARCH ARTICLE

Control of Movement

Age-related deficits in rapid visuomotor decision-making

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Abstract

Many goal-directed actions that require rapid visuomotor planning and perceptual decision-making are affected in older adults, causing difficulties in execution of many functional activities of daily living. Visuomotor planning and perceptual identification are mediated by the dorsal and ventral visual streams, respectively, but it is unclear how age-induced changes in sensory processing in these streams contribute to declines in visuomotor decision-making performance. Previously, we showed that in young adults, task demands influenced movement strategies during visuomotor decision-making, reflecting differential integration of sensory information between the two streams. Here, we asked the question if older adults would exhibit deficits in interactions between the two streams during demanding motor tasks. Older adults ($n = 15$) and young controls ($n = 26$) performed reaching or interception movements toward virtual objects. In some blocks of trials, participants also had to select an appropriate movement goal based on the shape of the object. Our results showed that older adults corrected fewer initial decision errors during both reaching and interception movements. During the interception decision task, older adults made more decision- and execution-related errors than young adults, which were related to early initiation of their movements. Together, these results suggest that older adults have a reduced ability to integrate new perceptual information to guide online action, which may reflect impaired ventral-dorsal stream interactions.

NEW & NOTEWORTHY Older adults show declines in vision, decision-making, and motor control, which can lead to functional limitations. We used a rapid visuomotor decision task to examine how these deficits may interact to affect task performance. Compared with healthy young adults, older adults made more errors in both decision-making and motor execution, especially when the task required intercepting moving targets. This suggests that age-related declines in integrating perceptual and motor information may contribute to functional deficits.

dorsal-ventral interactions; interception; object recognition; older adults; reaching

INTRODUCTION

Older adults exhibit functional deficits in many activities of daily living that require integration of sensory, cognitive, and motor processes. For example, driving requires rapid visuomotor integration to choose an appropriate motor response (e.g., judging a change in traffic lights to accelerate or brake). Age-related declines in vision, decision-making, or motor control are associated with deficits in many activities of daily living (1–3). These declines have been extensively

investigated in isolation, however, the underlying interactions that contribute to these deficits remain an open question.

Slower response times in older adults during perceptual decision-making are related to declines in sensory processes mediated in part by the ventral visual processing streams (4, 5). The ventral visual stream links the primary visual cortex to the inferior regions of the occipito-temporal cortex and is involved in perceptual aspects of visual sensory processing. Older adults show differences in performance on tasks that

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rely on ventral stream function, such as contrast discrimination (6–8), shape and object recognition (9–11), and color perception (12–14), which may be due to underlying changes in inhibitory neurotransmitters in the ventral visual stream (15).

The dorsal stream links the primary visual cortex to the superior regions of the occipito-parietal cortex. Cells in the dorsal visual stream are involved in visuomotor processing for eye and hand movements (16). This stream facilitates the visual control of movement, largely without conscious visual awareness (17). Compared with the ventral stream, it has been proposed that the dorsal stream exhibits earlier age-related decline in older adults (18, 19). In particular, processing of moving stimuli are impaired in older adults (20, 21). These changes accompany deficits in slow smooth pursuit eye movements used for tracking object motion (22, 23), but the relationship between these changes and visuomotor performance are not clear.

The differential age-related rates of decline in ventral and dorsal regions could affect many activities of daily living that require continuous and time-sensitive interactions between the two streams (24), but this has remained unexamined. Here, we hypothesized that older adults would exhibit impaired interactions between the dorsal and ventral streams during rapid visuomotor decision-making. To engage the ventral stream, we asked participants to select one of two alternative movements based on their judgment of an object's shape (25–27). We predicted that compared with young adults, older adults would make more decision errors and be less likely to make appropriate movement adjustments during decision-making.

Furthermore, we used manual reaching (toward static objects) and interception tasks (toward dynamic objects) to engage the dorsal visual stream in different ways. Dorsal frontoparietal areas are primarily engaged for planning and execution of reaching movements (28, 29). Interception movements also engage more ventral motion-sensitive areas, the middle temporal (MT) and medial superior temporal (MST) areas, for visual motion-processing (30, 31). How the engagement of additional neural areas affects performance is not clear, but our recent study has shown that under the same time constraints, interception movements tend to be less accurate than reaching movements (24). Motion-sensitive areas and eye movements associated with motion-processing also show early signs of decline in older adults (18, 21, 22, 32). Therefore, our second prediction was that older adults would make more decision- and execution-related errors in the interception task than the reaching task.

METHODS

Participants

Twenty-six younger participants (16 women; 23.7 ± 5.5 yr), and fifteen older participants (11 women; 69.2 ± 4.0 yr) completed the study. All participants were right-handed, had no known history of neurological disorders, had no current injuries or pain of the upper limbs and back, and had normal or corrected-to-normal vision. Participants gave verbal confirmation at the beginning of the task about being able to identify both objects (circle and

ellipse); one additional participant was excluded from the study before completion due to the inability to differentiate the shapes. All the participants provided written informed consent before participating and were compensated for their time. Experimental procedures were approved by the Institutional Review Board at the University of Georgia.

Apparatus

Participants were seated on a chair while their right hand grasped the handle of a robotic manipulandum that moved in a horizontal plane (KINARM End-Point Lab, KINARM, Kingston, Ontario, Canada). Visual stimuli (including the handle location) were projected at 60 Hz from a monitor above the workspace onto a semitransparent mirror, which occluded direct vision of the hand (Fig. 1A). The monitor displayed targets and a cursor representing the location of the right hand in a veridical horizontal plane. During the performance of the trials, the robot applied a constant background force (-3 N in the Y direction) to the handle and recorded movement position and velocity at 1,000 Hz (24, 33). Eye-tracking data were also recorded at 500 Hz using a video-based remote system (Eyelink 1000, SR Research, Ottawa, ON, Canada) and used to track fixations to begin each trial (see *Experimental Design and Procedure*), but not analyzed further for the current study.

Experimental Design and Procedure

Experimental procedures and the young adult dataset were described in a recent study (24). In brief, participants performed rapid reaching and interception movements with their right hand (see Fig. 1A). At the beginning of each trial, participants were instructed to move the hand cursor (1 cm diameter) into a yellow circle (2 cm diameter) that appeared at the starting position at the midline of the visual display. After reaching the starting position, participants were required to fixate at a fixation cross also positioned along the midline 22 cm away from the start position of the hand. After 500 ms of maintaining eye fixation (as determined from the eye-tracker) and hand position, both the fixation cross and start position disappeared. After the fixation cross disappeared, participants could move their eyes freely. After a 200 ms delay, a yellow object was presented inside a white rectangular box either on the left or right side, ± 16 cm along x-axis (see Fig. 1B). The location of the object along the y-axis could vary between 14.5 and 17 cm (uniform distribution). For the Reaching trials, the object stayed in its initial location. During Interception trials, the object traveled at a constant Euclidean velocity of ± 40 cm/s for Fast trials and ± 34 cm/s for Slow trials. The object could either be a circle (2 cm diameter) or an ellipse (minor axis = 2 cm, major axis = $1.15 \times$ minor axis) depending on the experimental block.

In the No Decision condition, the objects were always circles for every trial in the block. In the Decision condition, the object for each trial was randomly selected to be either a circle (50% of trials) or an ellipse. For each block of trials, the object could either stay in the same position (Reaching) or move horizontally across the screen (Interception). Hence, in the No Decision blocks, participants knew beforehand that all the objects would be circles, and for the Decision blocks they were told the object could either be a circle or an

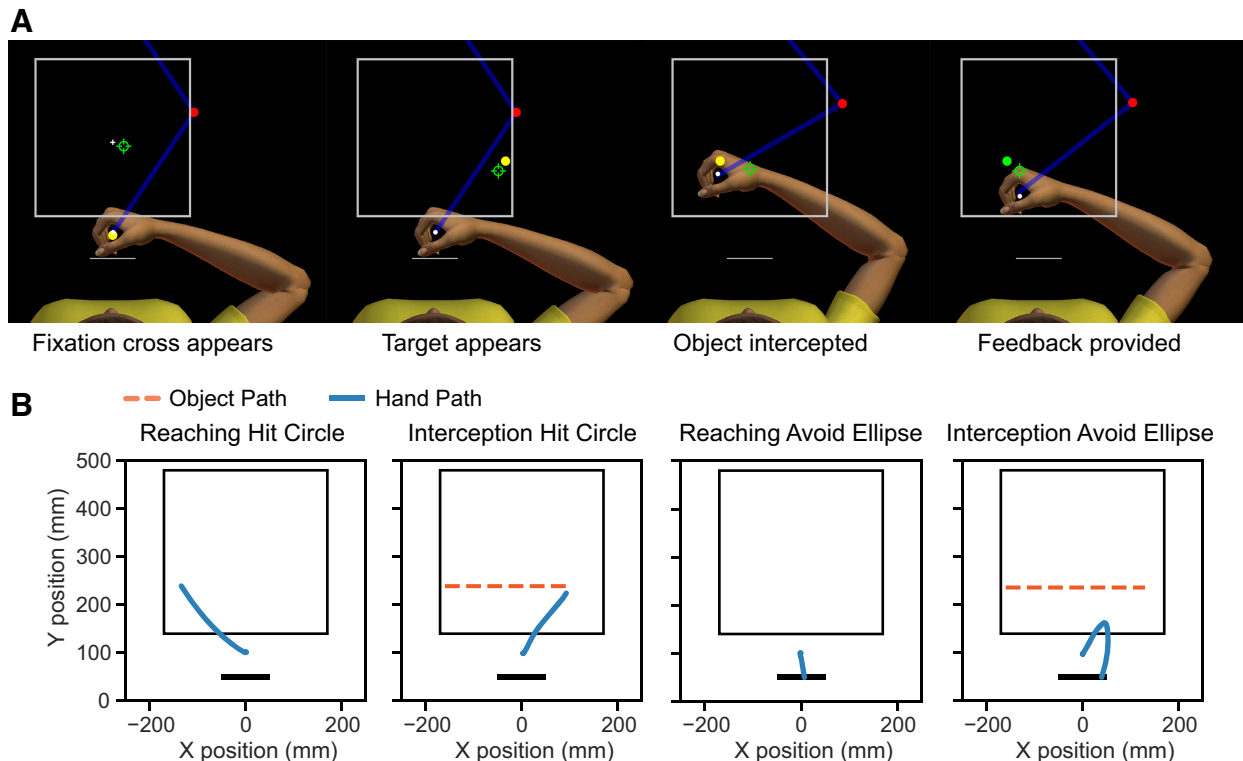


Figure 1. The experimental setup and an exemplar trial. **A:** sample trial for Interception task. The green crosshair represents the participant's gaze location, the white cursor represents the participant's hand location. After 500 ms of fixation on the fixation cross, a yellow target would appear on the left or right side of the screen and move toward the other end of the white box. Participants were provided with feedback when the target was intercepted or if the trial timed out. The target would turn red if the trial was unsuccessful or green if it was successful. **B:** example of hand paths and different trial scenarios from a representative participant.

ellipse. Participants were instructed to perform a reaching or interception movement as quickly and as accurately as possible when the object was a circle, and to avoid the object when it was an ellipse by moving the cursor in the opposite direction toward a bar drawn parallel to the frontal plane (Fig. 1B). For both Reaching and Interception trials, the object remained on the visual display until it was hit or the trial timed out. For the Interception trials, the maximum time on screen was determined by the object's constant Euclidean velocity: 800 ms for Fast trials and 950 ms for Slow trials. The maximum times for the Reaching trials were also 800 ms and 950 ms, to match the Interception condition.

After the hit or the trial timed out, participants received feedback of their performance for 500 ms. The object would change the color from yellow to green (successful) or red (unsuccessful). A trial was successful when a circle was hit (i.e., the cursor position overlapped with the circle) or when an ellipse was avoided when the trial timed out (i.e., the cursor position never overlapped with the ellipse). A trial was unsuccessful when an ellipse was hit or a circle was avoided. The intertrial delay was between 1,500 and 2,000 ms.

Each participant performed eight experimental blocks of 90 trials each (720 trials total). Rest breaks between blocks were provided to participants as needed. Blocks were randomized and consisted of a unique combination of conditions: decision type (No Decision or Decision), movement type (Reaching or Interception), and maximum trial

duration (Fast or Slow). To focus our analysis on the interaction of decision-making and movement type, trials from the Fast and Slow blocks were pooled; however, we report when results for Fast or Slow blocks significantly differed from the pooled results. During Decision blocks, object shape and location of the objects along the y-axis were randomized across trials within each block. During No Decision blocks, location of the circles along the y-axis was randomized.

Data Analysis

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

Hand movement data were filtered with a fourth-order Butterworth low-pass filter with a 5 Hz cutoff (34). Reaction time (RT) was calculated as the time between object onset and the time when hand speed exceeded 5% of the first local peak. Trials were excluded if RT was less than 100 ms. Peak speed (PS) was calculated as the hand's tangential velocity at the first local peak after movement onset. To allow for comparison of qualitatively similar movements across No Decision and Decision blocks, we excluded trials in which participants were not moving toward the object throughout the trial (i.e., moving toward the bar) in the PS analysis.

Initial decision errors were determined from the initial direction of movement, calculated as the angle between the midline and the vector formed between the starting hand position and hand position at peak acceleration. Trials in

which the initial direction was in the positive *Y* direction were classified as aimed toward the object, and trials in the negative *Y* direction were classified as aimed toward the bar. Initial decision errors occurred when there was a mismatch between the classified initial direction and the correct decision (i.e., aimed toward the object on ellipse trials or toward the bar on circle trials). Final decisions were based on the position of the cursor when the object was hit or the trial timed out. Trials in which the final cursor position was closer to the object on ellipse trials or closer to the bar on circle trials were classified as final decision errors. A corrected initial decision error was defined for trials in which an initial decision error occurred, but the final decision was correct.

Execution errors were identified on circle trials in which the final decision was correct, but the participant did not successfully hit the circle in the given time. Restricting the analysis to trials in which the circle was attempted to be hit allows for a comparison of No Decision blocks (in which all trials involved attempting to hit the circle), and Decision blocks (in which some trials involved an ellipse and/or a decision to avoid the object). The execution errors resulted from the cursor passing the *Y* position of the object without hitting it (i.e., poor trajectory), or from the hand failing to reach the *Y* position of the object (i.e., too slow).

Statistical Analysis

To compare performance and hand kinematic variables across conditions, we conducted two-way repeated measures ANOVAs using movement type (Reaching or Interception) as within-subject factor and age group (Young or Older) as between-subject factor. The α level for significance was set at 0.05 and effect sizes are reported using generalized η^2 . Post hoc pairwise comparisons were conducted using the Holm correction. Levene's test was used to evaluate the assumption of homogeneity of variance. If the Levene's test was significant, data were first normalized using a logarithmic transformation before the analysis. Linear regression was used for bivariate comparisons, with α level set to 0.05, and the statistical comparison of correlations between conditions was done using the Dunn and Clark's *z* for dependent groups with nonoverlapping variables (35). The statistical tests were conducted in R v.3.6.1, using the following packages: "afex," "emmeans," "car," and "cocoR" (36).

RESULTS

Older Adults Show Fewer Corrections of Initial Decision Errors

We first investigated decision-making performance of young and older adults based on their movement kinematics. Initial decision errors were identified on trials in which the initial hand movement direction did not match the expected movement direction (i.e., incorrectly trying to avoid a circle or hit an ellipse). Both young ($t = -11.10$, $P < 0.001$) and older adults ($t = -8.97$, $P < 0.001$) made more initial decision errors for Interception relative to Reaching [main effect of movement type: $F(1,39) = 191.91$, $P < 0.001$, $\eta^2 = 0.48$] (Fig. 2A). This suggests that compared with reaching movements, dorsal-ventral interactions are compromised during interception tasks.

Overall, older adults did not make significantly more initial decision errors than young adults [main effect of age: $F(1,39) = 3.63$, $P = 0.06$, $\eta^2 = 0.07$] (Fig. 2A). However, initial decision error rate depended on whether the trial was Fast (800 ms time out) or Slow (950 ms time out). In Fast trials, older adults made significantly more initial errors [main effect of age: $F(1,39) = 5.67$, $P = 0.02$, $\eta^2 = 0.09$], but made a similar number of errors as young adults in the Slow trials [main effect of age: $F(1,39) = 1.38$, $P = 0.25$, $\eta^2 = 0.03$]. This suggests that older adults make more initial decision errors under greater time constraints.

Older adults had a higher percentage of final decision errors (i.e., final position closer to bar on circle trials or to the object on ellipse trials) than younger adults [main effect of age: $F(1,39) = 31.90$, $P < 0.001$, $\eta^2 = 0.41$], indicating that older adults were more likely to not correct an initially incorrect decision. Indeed, though the percentage of initial and final decision errors were positively correlated for both young (Reaching: $r = 0.44$, $P = 0.02$, Interception: $r = 0.46$, $P = 0.02$) and older (Reaching: $r = 0.88$, $P < 0.001$, Interception: $r = 0.92$, $P < 0.001$) adults, the association between initial and final decisions was significantly higher for older adults for both Reaching ($z = -2.53$, $P = 0.01$) and Interception ($z = -3.16$, $P = 0.002$) (Fig. 2B).

Why were older adults less likely to correct their initial decisions? One possibility is that older adults were more constrained by the motoric demands of the task. Supporting this idea, both young ($t = 8.30$, $P < 0.001$) and older adults ($t = 4.64$, $P = 0.001$) had more corrections during Reaching than Interception [main effect of movement type: $F(1,39) = 75.98$, $P < 0.001$, $\eta^2 = 0.26$], and young adults were much more likely to correct initial decision errors than older adults for both movement types [Reaching: $t = -5.43$, $P < 0.001$, Interception: $t = 4.77$, $P = 0.001$; main effect of age: $F(1,39) = 31.99$, $P < 0.001$, $\eta^2 = 0.40$] (Fig. 2C). Furthermore, older adults with more initial decision errors during Interception were also less likely to correct those errors ($r = -0.72$, $P = 0.002$), indicating that the initial decision errors were not simply a result of a strategy to "offload" the decision postinitiation (Fig. 2D). When further analyzing the speed of the trials, young adults showed a significant positive correlation for Interception for Slow trials ($r = 0.40$, $P = 0.04$), suggesting that at slower speeds, young adults could more easily correct initial errors. These results suggest that the capacity for online decision-making and movement correction is greater when the movement is easier to perform.

Older Adults Launch Interception Movements Earlier during Decision-Making

As expected, the added neural processing required for judging shapes led to a significant increase in reaction time (RT) during Decision blocks relative to No Decision blocks ($t = 22.92$, $P < 0.001$). The increase in RT for older adults ($t = -6.77$, $P < 0.001$) was larger for Reaching than for Interception trials [main effect of movement type: $F(1,38) = 42.64$, $P < 0.001$, $\eta^2 = 0.22$]. The interaction between age and movement type was also significant [$F(1,38) = 18.09$, $P < 0.001$, $\eta^2 = 0.11$] (Fig. 3A), implying that older adults chose to reduce decision time to initiate an earlier movement to

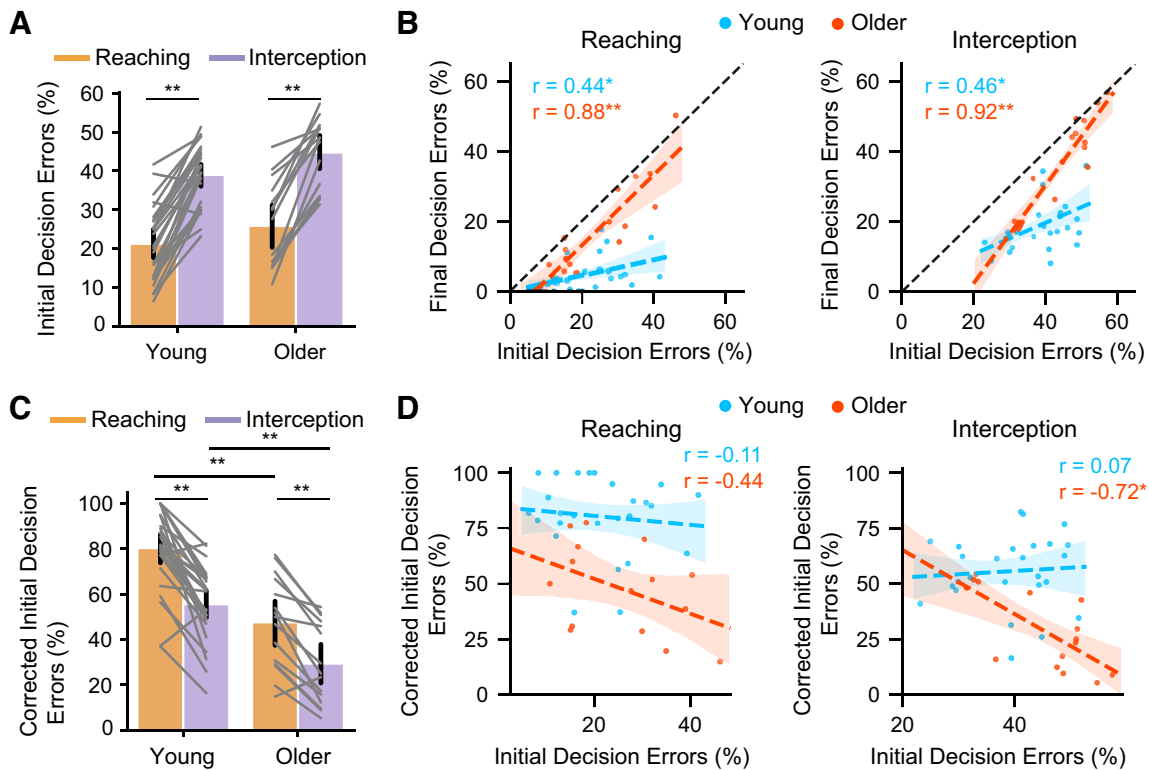


Figure 2. Older adults show fewer corrections of initial decision errors. **A:** initial decision errors were higher during Interception for both young and older adults. **B:** percentage of initial decision errors correlated more strongly with final decision errors for older adults in both Reaching and Interception. The dashed black line indicates no corrections were made during movements. **C:** corrected initial decision errors (change from initial decision to final decision) occurred more frequently during Reaching than Interception. Older adults corrected fewer initial decision errors. **D:** older adults with more initial decision errors were also less likely to correct initial errors in Interception. * $P < 0.05$, ** $P < 0.001$.

intercept the moving object. Descriptive statistics for reaction time (RT) and peak speed (PS) are reported in Table 1.

We first compared movement kinematics between Decision and No Decision to eliminate any confounds in the interpretation of our results. Overall, PS increased from No Decision to Decision, but there were no significant differences in the increase in PS between the two groups [main effect of age: $F(1,39) = 0.00$, $P = 0.95$, $\eta^2 < 0.001$] or between movement types [main effect of movement type: $F(1,39) = 3.40$, $P = 0.07$, $\eta^2 = 0.03$] (Fig. 3B). This suggests that when perceptual decision-making was added to the task, participants compensated for the longer reaction times with higher movement vigor (37).

We then looked at how the increase in RT during Decision blocks influenced initial decision errors. There was a strong

negative correlation between the increase in RT to Decision from No Decision with the initial decision errors for both Reaching ($r = -0.78$, $P < 0.001$) and Interception ($r = -0.81$, $P < 0.001$) for older adults (see Fig. 3C, top). Furthermore, among older adults, the difference in RT between Decision and No Decision predicted the final performance (see Fig. 3C, bottom) in the task for both Reaching ($r = -0.65$, $P = 0.01$) and Interception ($r = -0.81$, $P < 0.001$). Thus, older adults who adjusted their RTs to be longer during Decision blocks relative to No Decision had fewer initial and final decision errors whereas older adults who “rushed” their decisions (smaller difference between Decision RT and No Decision RT) exhibited a higher number of initial and final decision errors. When further analyzed between the speed of the trials, the correlation in Reaching was not significant for Slow trials ($r = -0.26$, $P = 0.37$).

For young adults, the correlation between RT adjustments and initial errors was only significant for Reaching ($r = -0.52$, $P = 0.01$) but not for Interception. Furthermore, the relationship between RT adjustments during decision-making and final decision errors was not significant in younger adults (Reaching: $r = 0.09$, $P = 0.66$; Interception: $r = 0.00$, $P = 0.99$) and significantly different from the correlations observed in older adults (Reaching: $z = 2.45$, $P = 0.01$; Interception: $z = 3.19$, $P = 0.001$). This suggests that, unlike older adults, the choice to initiate movement early was not associated with reduced decision accuracy as young adults could countermand their decision during the movement.

Table 1. Reaction time and peak speed

	Decision		No Decision	
	Reaching	Interception	Reaching	Interception
Reaction time, ms				
Young	464 ± 10	414 ± 11	273 ± 6	251 ± 8
Older	555 ± 14	404 ± 15	331 ± 8	290 ± 11
Peak speed, mm/s				
Young	1,029 ± 33	944 ± 30	935 ± 36	850 ± 32
Older	960 ± 43	837 ± 40	835 ± 48	777 ± 42

The values are shown as means ± SE. For Decision blocks, the reaction times and peak speeds were significantly longer and higher, respectively.

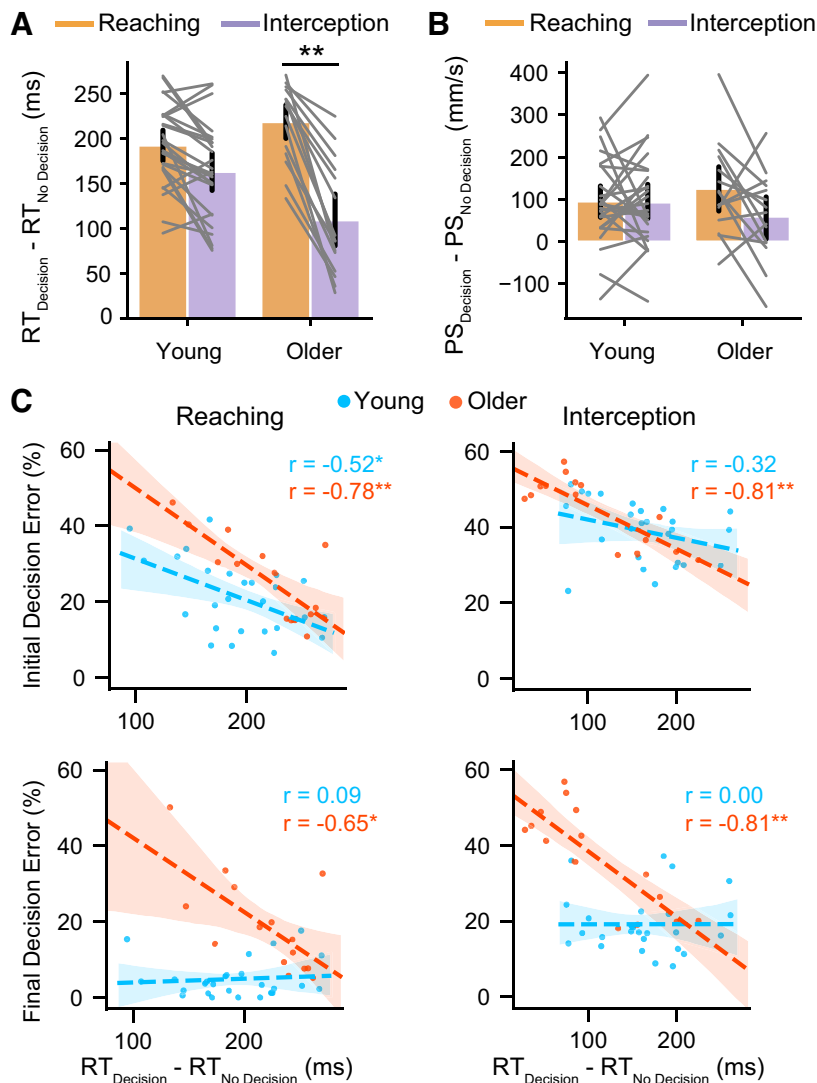


Figure 3. Older adults launch interception movements earlier during decision-making. **A:** the increase in reaction time (RT) from No Decision to Decision trials. Older adults showed a larger increase in RT during Reaching and a smaller increase in RT during Interception than young adults. **B:** The peak speed (PS) of the limb movement increased from the No Decision to Decision, but the increase in PS was similar across age group and movement type. **C:** The difference in reaction time from No Decision to Decision was negatively correlated with initial decision errors (top panel) and final decision errors (bottom panel) for older adults in both Reaching and Interception trials. * $P < 0.05$, ** $P < 0.001$.

Overall, the results for Reaching were consistent with expectations—older adults were slower to initiate movements during Decision trials, and individuals who took longer also made fewer initial and final decision errors. In other words, older adults favored decision accuracy during Reaching trials. In contrast, during Interception, older adults took 114 ± 15 ms longer in Decision blocks than the No Decision blocks, but this additional time was on average ~ 50 ms shorter than the additional time taken by the young adults (163 ± 11 ms). One explanation for this is that older adults were more likely to prematurely launch the movement before they had completed the decision during Interception, resulting in more erroneous decisions.

Decision to Move Early Is Associated with Poorer Movement Execution in Older Adults

In addition to decision errors, participants could also make errors specific to motor execution-related components of the task. Possible errors include either a poor estimate of the object's position or an inability to adjust to the imposed time constraints. These errors were identified only on circle

trials in which the final decision was correct, but participants did not successfully hit the circle in the given time.

In the No Decision condition, older adults made more execution errors in Interception ($t = 3.37$, $P = 0.003$) and Reaching trials ($t = 2.13$, $P = 0.04$) than young adults [main effect of age: $F(1,39) = 10.20$, $P = 0.003$, $\eta^2 = 0.14$; Fig. 4A, left]. Both young ($t = -10.39$, $P < 0.001$) and older adults ($t = -8.01$, $P < 0.001$) made more errors in Interception than Reaching trials [main effect of movement type: $F(1,39) = 160.47$, $P < 0.001$, $\eta^2 = 0.59$].

We correlated No Decision RT with the execution errors during No Decision and found no significant correlation for either young (Reaching: $r = 0.38$, $P = 0.06$; Interception: $r = 0.22$, $P = 0.28$) or older adults (Reaching: $r = 0.19$, $P = 0.51$; Interception: $r = 0.20$, $P = 0.46$). Thus, the reaction times alone were not predictive of accurate motor performance in the No Decision condition. However, the number of execution errors made during the No Decision conditions was predictive of the change in RT between Decision and No Decision conditions for both Reaching ($r = -0.52$, $P = 0.04$) and Interception ($r = -0.58$, $P = 0.02$) for older adults, but

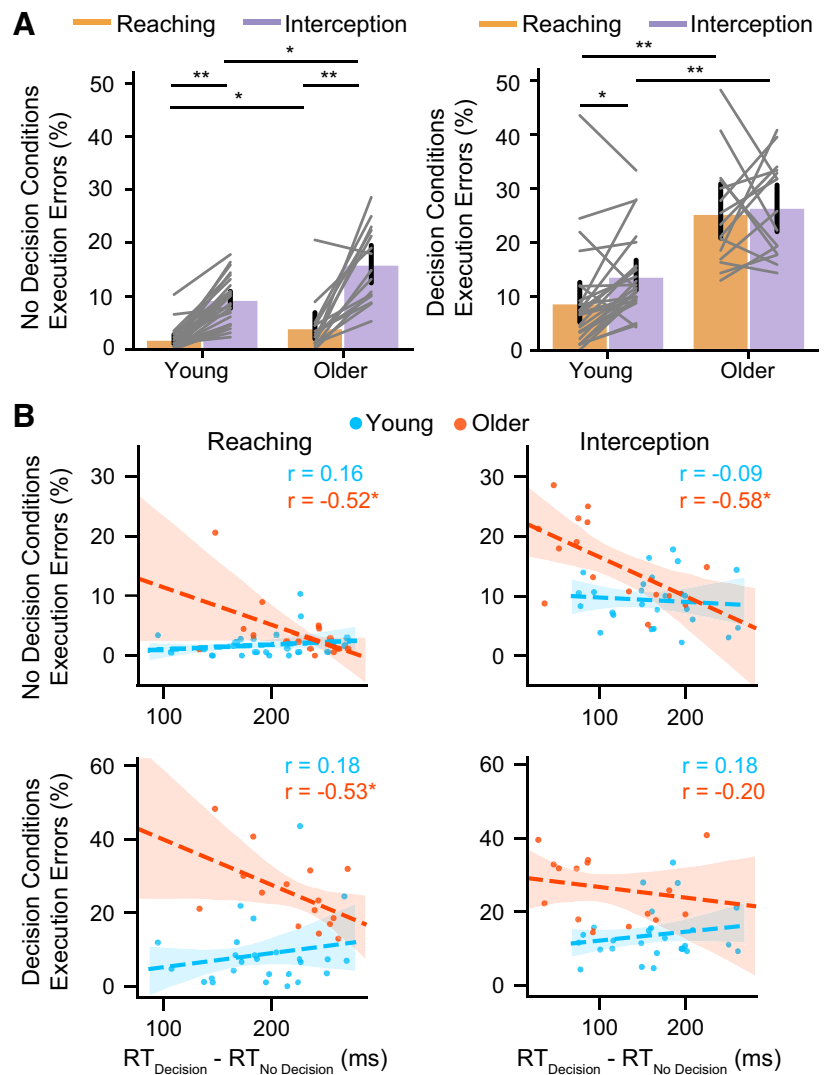


Figure 4. Decision to move early is associated with deficits in movement execution in older adults. **A:** older adults made more Interception and Reaching execution errors than young adults in the No Decision and Decision blocks. Older adults had a greater increase in execution errors during Decision blocks relative to No Decision. **B:** the difference in reaction time (RT) from No Decision to Decision was negatively correlated with execution errors for older adults in the No Decision blocks, for both Reaching and Interception. In Decision blocks, the difference in RT from No Decision to Decision was negatively correlated for older adults for Reaching. * $P < 0.05$, ** $P < 0.001$.

not for young adults (Reaching: $r = 0.16$, $P = 0.43$; Interception: $r = -0.09$, $P = 0.66$). These correlations were statistically different between young and older adults for Reaching ($z = 2.09$, $P = 0.04$) but not for Interception ($z = 1.62$, $P = 0.10$; Fig. 4B, top). The negative correlation between these variables suggests that older adults who made more execution errors during the No Decision condition were also more likely to initiate their movements early during Decision blocks.

In the Decision blocks, older adults made more execution errors than younger adults in both Interception ($t = 5.03$, $P < 0.001$) and Reaching ($t = 5.31$, $P < 0.001$) trials [main effect of age: $F(1,39) = 36.08$, $P < 0.001$, $\eta^2 = 0.41$; Fig. 4A, right]. Furthermore, the increase in execution errors during Decision (relative to No Decision) was larger for older adults [main effect of age: $F(1,39) = 32.05$, $P < 0.001$, $\eta^2 = 0.34$] for both Reaching ($t = 5.64$, $P < 0.001$) and Interception ($t = 3.07$, $P = 0.01$). Young adults made more errors in Interception than Reaching ($t = -2.79$, $P = 0.02$) [main effect of movement type: $F(1,39) = 4.31$, $P = 0.04$, $\eta^2 = 0.03$] but there were no differences for older adults.

The number of execution errors in the Decision blocks were correlated with the difference in RT between Decision and No Decision for older adults in Reaching trials ($r = -0.53$, $P = 0.04$, Fig. 4B, bottom), but not for young adults ($r = 0.18$, $P = 0.37$). These correlations were also significantly different ($z = 2.18$, $P = 0.03$). Execution errors during reaching in Decision blocks were predominantly due to not reaching the object in time (hand movement was too slow)—since there was no salient cue to indicate the time constraint during Reaching, older adults may have taken more time to make their decision and consequently did not have enough time to hit the object. For Interception, the correlation between the difference in RT and execution errors was not significant for young or older adults and there was no difference between the correlations ($z = 1.08$, $P = 0.28$).

Finally, we also performed secondary analyses to investigate possible sex-related differences. Among older adults, we had a higher proportion of females (11 of 15) and that could have skewed the results. To test for possible sex-related differences, we performed t tests comparing male and female performance, separately for young and older adults. We

found no significant differences between the two sexes for all our variables of interest (all t values <1.94 , all P values >0.05).

DISCUSSION

This study examined how aging impacts decision-making and motion-processing for visuomotor performance. To that end, young and older adults judged the shape of objects and made manual reaching and interception movements based on those decisions. We found that compared with young controls, older adults corrected a smaller percentage of their initial decision errors, resulting in a lower final decision accuracy. Final decision errors were more strongly correlated with a smaller reaction time increase during decision-making in older adults than young adults, and execution errors increased more during decision-making relative to young adults. Together, these results confirm our first prediction and suggest that older adults had a greater difficulty with the online adjustments necessary to successfully decide on and execute the appropriate movement. Furthermore, consistent with our second prediction, these differences were exacerbated when the task required intercepting a moving object rather than reaching a stationary object, suggesting that the capacity for online decision-making and movement corrections depends on task demands.

Initial Decisions Made by Older Adults Reflect a Stronger Commitment to an Action Plan

Final decision errors were typically lower than the initial decisions errors for all the participants (Fig. 2). This suggests that participants changed their mind on the initial decision during the movement. Decision-making involves accumulation of noisy evidence to produce a decision (38, 39). Previous work has shown that in a two-alternative forced choice task, participants sometimes initiate limb movements before decision-making is complete and then change their mind during the ongoing movement (40, 41). Resulaj et al. (40) proposed a model showing that the change in the initial decision may reflect that the sensorimotor system exploits information that is still in the “processing pipeline” when the initial decision is made to subsequently either reverse or reaffirm the initial decision.

We found similar results in our study. Older adults made slightly more initial errors than young controls, but this difference did not reach significance ($P = 0.06$). Importantly, older adults corrected a smaller percentage of those initial errors (Fig. 2C). This pattern of results suggests that: 1) older adults may be less able to exploit sensory information in the “processing pipeline” once the limb movement is underway; and 2) this capability is further diminished when they intercept moving objects. A simple interpretation of these results is that online processing of visuomotor information during movements may leave limited “bandwidth” for perceptual decision-making in older adults, minimizing the likelihood of online corrections to initial decision errors. In other words, the initial decision made by older adults is a stronger commitment to a plan of action, whereas younger adults are not fully committed to their initial decision. The additional visual motion-processing and continuous movement control required during interception movements, especially for

older adults, may further reduce the likelihood for adjusting decisions postinitiation (42).

Early Age-Induced Declines in Dorsal Stream Processing May Underlie Execution Errors

In our study, participants had to make limb movements toward static (Reaching) and dynamic (Interception) objects. The frontoparietal areas along the dorsal visual stream are involved in the control of reaching movements (28, 30, 43) through facilitation of visual attention, eye movements, motion-processing, and eye-hand coordination (44–46). The different eye-hand coordination strategies required for interception movements engage additional neural areas along the dorsal stream, such as area MT+ that is involved in smooth pursuit eye movements (47–50). In the No Decision condition, older adults made more movement execution errors than young adults while performing interception movements (Fig. 4A). These deficits may be due to the early age-induced declines in dorsal stream-mediated pursuit eye movements (22) as well as motion-processing (18, 19).

Humans produce different movement trajectories for interception movements compared with reaching movements (51). This has been attributed to a more pronounced reliance on online feedback control for interception where limb movements are regulated through continuous processing of sensory information (52–54). Online feedback control is facilitated by dorsal stream areas in the posterior parietal cortex (55, 56). Not surprisingly, reaching studies using the target-jump paradigm have shown deficits in online feedback control in older adults (57, 58). We only measured one aspect of kinematic performance, hand peak speed (PS), and found no differences between the groups or between movement type conditions. However, the fact that older adults made more execution errors does support the notion that online feedback control may be compromised in older adults.

Visuomotor Decision Errors Suggest Impaired Ventral-Dorsal Stream Processing in Older Adults

Shape recognition is primarily facilitated by the ventral visual stream (25–27, 59). Accordingly, the Decision condition was assumed to engage additional areas along the ventral visual stream to differentiate the circular targets from the ellipses. We found only small, nonsignificant differences in initial decision errors between older and young adults. This suggests that neural processing in the ventral stream may not deteriorate to the same extent as the dorsal stream, resulting in somewhat intact cognitive processing relative to deficits in motor control in older adults (60, 61).

One interesting result in our study was that initial decision errors were higher during the interception movements for both groups (Fig. 2A). As the total trial time was fixed and limited to 800–950 ms, participants in both groups may have initiated interception movements prematurely, before the decision-making process was complete to secure enough time to complete the movement (24). The reaction time adjustments during Decision blocks were indeed shorter for interception movements than reaching movements for both groups, but even more pronounced among older adults (Fig. 3A). This resulted in more initial and final decision errors

during interception, supporting recent evidence that decision-making is impaired when the movement required is more demanding to perform (62, 63). The dorsal and ventral streams are driven predominantly by magnocellular and parvocellular inputs, respectively, and axons of parvocellular cells have slower conduction velocity than magnocellular cells (64). Consequently, information-processing tends to be slower in the ventral stream (65). The relative sluggishness of this pathway and the additional burden of online sensory feedback processing during interception movements may have resulted in the limb motor system initiating movements before the decisions signals in the ventral networks reached the threshold for an overt decision.

There could be other factors that could have also contributed to decision and execution errors. A recent study has shown that GABA levels decline along the ventral stream in older adults and this decline likely also contributes to less distinct neural activation patterns for recognizing faces and houses (15). This would suggest that shape processing should also be deficient in older adults. Indeed, many older adults reacted more slowly than younger adults during Decision blocks of reaching movements. Those older adults who launched movements early made more decision errors. In addition, age-induced proprioceptive deficits (66, 67) could have also contributed to higher number of execution errors made by older adults. However, quantifying the contributions of these deficits is beyond the scope of this work.

Subcortical Areas May Trigger Shorter Reaction Times during Interception Movements in Older Adults

The frontoparietal areas for reaching movements are well delineated and have been previously described (28, 29, 68). These neural areas are involved in sensorimotor transformations associated with motor planning and execution. In addition to these areas, interception movements also involve the middle temporal (MT) and medial superior temporal (MST) areas for motion-processing (for review, see Refs. 31 and 69). These two areas are reciprocally connected with both premotor (70) and parietal areas (69) and process motion for continuous visual control of interception. These areas are also involved in generation of smooth pursuit eye movements that play a significant role in the control of interception movements (71). The engagement of additional neural areas for motion-processing would suggest longer processing times and delayed reactions for interception movements. However, our data do not support that. Reaction times are comparable for reaching and interception movements (Table 1). This suggests that motion-processing areas may play an important role in the online control of interception movements.

The reaction time (RT) adjustments made by older adults during Decision blocks of interception movements were shorter than during reaching movements. Thus, older adults launched limb movements more rapidly during Decision Interception trials. Though this seems surprising, other studies have also shown similar results where older adults made more ballistic interception movements than young adults (32, 72). These results suggest that older adults may have experienced an elevated sense of perceived urgency during interception movements.

Though we did not observe any differences in limb kinematics (peak speed; PS) between the two groups, the shorter reaction times support this interpretation.

Another possibility is that rapidly moving stimuli may preferentially release in older adults the manual following response (73), a short-latency and stereotyped motor response generated by direct retinotectal and tecto-reticulospinal pathways that target proximal arm muscles (74, 75). The manual following response is a primitive protective reflex that is elicited without sufficient preparation and does not have the sophistication of voluntary motor responses. Hyperactivation of the manual following response pathway may cause an early release of these motor responses in older adults. The unsophisticated spatiotemporal characteristics of these movements may be responsible for more erroneous motor performance (Fig. 4, A and C). Hyperactivation of this pathway in older adults might be caused by two factors: 1) maladaptive slowing of neural processing downstream of MT+ in the parietal cortex (76); and 2) dopamine depletion in the basal ganglia (77) and consequent disinhibition of the superior colliculus. This would leave reflex pathways for the manual following response hyperexcitable in older adults (78) and cause faster and more ballistic movements, especially when the visual stimuli are moving.

Prefrontal processing is also known to exhibit age-induced decline and could have affected response inhibition, i.e., prevented an early release of movement without complete preparation (79–81). But impaired response inhibition would have affected both reaching and interception movements similarly. However, older adults initiated early movements only during interception trials of Decision blocks. This supports our view that alternative factors may explain shorter reaction times for interception movements.

Limitations

There are well-characterized age-related declines in cognitive processing, especially in tasks that involve a high degree of cognitive control (82). These declines correspond with structural and functional differences in prefrontal cortex. Prefrontal cortex has direct reciprocal connections with both dorsal and ventral stream areas, and may facilitate interactions between the two streams (83, 84). Therefore, given the cognitive components of the present task, including demands related to task switching, goal maintenance, and response inhibition, it is possible that our observed visuomotor impairments in older adults may arise from declines in prefrontal function. We aim to test the specific contributions of prefrontal areas and its role in ventral-dorsal stream processing in future work.

Second, we did not have a sex-balanced design—there were a greater proportion of males in the young adult group (10 of 26) than the older adult group (4 of 15). Previous studies have shown sex-based differences in brain activity in sensorimotor areas, particularly the dorsal stream during movement preparation (85, 86). Thus, though we did not find any significant differences in task performance between male and female participants in either the young or older adult group, we cannot exclude the possibility that our observed deficits in visuomotor performance in older adults may in part be related to sex differences between the two groups.

Conclusions

In summary, our results showed that compared with young adults, older adults were less effective in correcting initial decision errors made during both reaching and interception movements. Older adults also made more decision errors and movement execution errors during interception movements than reaching movements, reflecting the role of differential task demands in online decision-making and visuomotor control. Overall, these results suggest that early age-induced declines in dorsal stream processing and the ability to incorporate ventral stream information during movement may have a strong effect on visuomotor function in older adults.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

A.G.-G., D.A.B., M.S., I.L.K., C.T.B., and T.S. conceived and designed research; A.G.-G. and D.A.B. performed experiments; A.G.-G. and D.A.B. analyzed data; A.G.-G., D.A.B., and T.S. interpreted results of experiments; A.G.-G., D.A.B., and T.S. prepared figures; A.G.-G., D.A.B., and T.S. drafted manuscript; A.G.-G., D.A.B., M.S., I.L.K., C.T.B., and T.S. edited and revised manuscript; A.G.-G., D.A.B., M.S., I.L.K., C.T.B., and T.S. approved final version of manuscript.

REFERENCES

- McGwin G Jr, Brown DB. Characteristics of traffic crashes among young, middle-aged, and older drivers. *Accid Anal Prev* 31: 181–198, 1999. doi:10.1016/S0001-4575(98)00061-X.
- Anstey KJ, Wood J, Lord S, Walker JG. Cognitive, sensory and physical factors enabling driving safety in older adults. *Clin Psychol Rev* 25: 45–65, 2005. doi:10.1016/j.cpr.2004.07.008.
- Christou EA. Aging and variability of voluntary contractions. *Exerc Sport Sci Rev* 39: 77–84, 2011. doi:10.1097/JES.0b013e31820b85ab.
- Dully J, McGovern DP, O'Connell RG. The impact of natural aging on computational and neural indices of perceptual decision making: a review. *Behav Brain Res* 355: 48–55, 2018. doi:10.1016/j.bbr.2018.02.001.
- Goodale MA, Milner AD. Separate visual pathways for perception and action. *Trends Neurosci* 15: 20–25, 1992. doi:10.1016/0166-2236(92)90344-8.
- Delahunt PB, Hardy JL, Werner JS. The effect of senescence on orientation discrimination and mechanism tuning. *J Vis* 8: 5–5, 2008. doi:10.1167/8.3.5.
- McGovern DP, Hayes A, Kelly SP, O'Connell RG. Reconciling age-related changes in behavioural and neural indices of human perceptual decision-making. *Nat Hum Behav* 2: 955–966, 2018. doi:10.1038/s41562-018-0465-6.
- Tulunay-Keesey U, Ver Hoeve JN, Terkla-McGrane C. Threshold and suprathreshold spatiotemporal response throughout adulthood. *J Opt Soc Am A* 5: 2191–2200, 1988. doi:10.1364/josaa.5.002191.
- Lehky SR, Tanaka K. Neural representation for object recognition in inferotemporal cortex. *Curr Opin Neurobiol* 37: 23–35, 2016. doi:10.1016/j.conb.2015.12.001.
- Grill-Spector K, Kourtzi Z, Kanwisher N. The lateral occipital complex and its role in object recognition. *Vision Res* 41: 1409–1422, 2001. doi:10.1016/S0042-6989(01)00073-6.
- Corbetta M, Miezin FM, Dobmeyer S, Shulman GL, Petersen SE. Selective and divided attention during visual discriminations of shape, color, and speed: functional anatomy by positron emission tomography. *J Neurosci* 11: 2383–2402, 1991. doi:10.1523/JNEUROSCI.11-08-02383.1991.
- Delahunt PB, Hardy JL, Okajima K, Werner JS. Senescence of spatial chromatic contrast sensitivity. II. Matching under natural viewing conditions. *J Opt Soc Am A Opt Image Sci Vis* 22: 60–67, 2005. doi:10.1364/josaa.22.000060.
- Elliott SL, Hardy JL, Webster MA, Werner JS. Aging and blur adaptation. *J Vis* 7: 8, 2007. doi:10.1167/7.6.8.
- Jung GH, Kline DW. Resolution of blur in the older eye: neural compensation in addition to optics? *J Vis* 10: 7, 2010. doi:10.1167/10.5.7.
- Chamberlain JD, Gagnon H, Lalwani P, Cassady KE, Simmonite M, Seidler RD, Taylor SF, Weissman DH, Park DC, Polk TA. GABA levels in ventral visual cortex decline with age and are associated with neural distinctiveness. *Neurobiol Aging* 102: 170–177, 2021. doi:10.1016/j.neurobiolaging.2021.02.013.
- Snyder LH, Batista AP, Andersen RA. Coding of intention in the posterior parietal cortex. *Nature* 386: 167–170, 1997. doi:10.1038/386167a0.
- Milner A. Is visual processing in the dorsal stream accessible to consciousness? *Proc Biol Sci* 279: 2289–2298, 2012. doi:10.1098/rspb.2011.2663.
- Langrová J, Kuba M, Kremláček J, Kubová Z, Vít F. Motion-onset VEPs reflect long maturation and early aging of visual motion-processing system. *Vision Res* 46: 536–544, 2006. doi:10.1016/j.visres.2005.06.024.
- Sciberras-Lim ET, Lambert AJ. Attentional orienting and dorsal visual stream decline: review of behavioral and EEG studies. *Front Aging Neurosci* 9: 246, 2017. doi:10.3389/fnagi.2017.00246.
- Kavcic V, Martin T, Zalar B. Aging effects on visual evoked potentials (VEPs) for motion direction discrimination. *Int J Psychophysiol* 89: 78–87, 2013. doi:10.1016/j.jpsycho.2013.05.012.
- Billino J, Pilz KS. Motion perception as a model for perceptual aging. *J Vis* 19: 3, 2019. doi:10.1167/19.4.3.
- Sharpe JA, Sylvester TO. Effect of aging on horizontal smooth pursuit. *Invest Ophthalmol Vis Sci* 17: 465–468, 1978.
- Knox PC, Davidson JH, Anderson D. Age-related changes in smooth pursuit initiation. *Exp Brain Res* 165: 1–7, 2005. doi:10.1007/s00221-005-2265-2.
- Barany DA, Gómez-Granados A, Schrayner M, Cutts SA, Singh T. Perceptual decisions about object shape bias visuomotor coordination during rapid interception movements. *J Neurophysiol* 123: 2235–2248, 2020. doi:10.1152/jn.00098.2020.
- Lehky SR, Sereno AB. Comparison of shape encoding in primate dorsal and ventral visual pathways. *J Neurophysiol* 97: 307–319, 2007. doi:10.1152/jn.00168.2006.
- Pasupathy A. Neural basis of shape representation in the primate brain. In: *Visual Perception. Fundamentals of Vision: Low and Mid-Level Processes in Perception*, edited by Martinez-Conde S, Macknik SL, Martinez LM, Alonso JM, Tse PU. Amsterdam: Elsevier, 2006, p. 293–313. Progress in Brain Research 154.
- Konkle T, Caramazza A. Tripartite organization of the ventral stream by animacy and object size. *J Neurosci* 33: 10235–10242, 2013. doi:10.1523/JNEUROSCI.0983-13.2013.
- Vesia M, Crawford JD. Specialization of reach function in human posterior parietal cortex. *Exp Brain Res* 221: 1–18, 2012. doi:10.1007/s00221-012-3158-9.
- Battaglia-Mayer A, Caminiti R. Corticocortical systems underlying high-order motor control. *J Neurosci* 39: 4404–4421, 2019. doi:10.1523/JNEUROSCI.2094-18.2019.
- Bosco G, Carrozzo M, Lacquaniti F. Contributions of the human temporoparietal junction and MT/V5+ to the timing of interception

- revealed by transcranial magnetic stimulation. *J Neurosci* 28: 12071–12084, 2008. doi:10.1523/JNEUROSCI.2869-08.2008.
31. Zago M, McIntyre J, Senot P, Lacquaniti F. Visuo-motor coordination and internal models for object interception. *Exp Brain Res* 192: 571–604, 2009. doi:10.1007/s00221-008-1691-3.
32. De Dieuleveult AL, Brouwer A-M, Siemonsma PC, Van Erp JB, Brenner E. Aging and sensitivity to illusory target motion with or without secondary tasks. *Multisens Res* 31: 227–249, 2018. doi:10.1163/22134808-00002596.
33. Singh T, Fridriksson J, Perry C, Tryon SC, Ross A, Fritz S, Herter TM. A novel computational model to probe visual search deficits during motor performance. *J Neurophysiol* 117: 79–92, 2017. doi:10.1152/jn.00561.2016.
34. Winter DA. *Biomechanics and Motor Control of Human Movement*. Hoboken, NJ: Wiley, 2009.
35. Dunn OJ, Clark V. Correlation coefficients measured on the same individuals. *J Am Stat Assoc* 64: 366–377, 1969. doi:10.1080/01621459.1969.10500981.
36. Diedenhofen B, Musch J. cocor: a comprehensive solution for the statistical comparison of correlations. *PLoS One* 10: e0121945, 2015 [Erratum in *PLoS One* 10: e0131499, 2015]. doi:10.1371/journal.pone.0121945.
37. Summerside EM, Shadmehr R, Ahmed AA. Vigor of reaching movements: reward discounts the cost of effort. *J Neurophysiol* 119: 2347–2357, 2018. doi:10.1152/jn.00872.2017.
38. Ratcliff R, Smith PL. A comparison of sequential sampling models for two-choice reaction time. *Psychol Rev* 111: 333–367, 2004. doi:10.1037/0033-295X.111.2.333.
39. Gold JI, Shadlen MN. The neural basis of decision making. *Annu Rev Neurosci* 30: 535–574, 2007. doi:10.1146/annurev.neuro.29.051605.113038.
40. Resulaj A, Kiani R, Wolpert DM, Shadlen MN. Changes of mind in decision-making. *Nature* 461: 263–266, 2009. doi:10.1038/nature08275.
41. Friedman J, Brown S, Finkbeiner M. Linking cognitive and reaching trajectories via intermittent movement control. *J Math Psychol* 57: 140–151, 2013. doi:10.1016/j.jmp.2013.06.005.
42. Burk D, Ingram JN, Franklin DW, Shadlen MN, Wolpert DM, Kiebel S. Motor effort alters changes of mind in sensorimotor decision making. *PLoS One* 9: e92681, 2014. doi:10.1371/journal.pone.0092681.
43. Senot P, Baillet S, Renault B, Berthoz A. Cortical dynamics of anticipatory mechanisms in interception: a neuromagnetic study. *J Cogn Neurosci* 20: 1827–1838, 2008. doi:10.1162/jocn.2008.20129.
44. Corbetta M. Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural systems? *Proc Natl Acad Sci USA* 95: 831–838, 1998. doi:10.1073/pnas.95.3.831.
45. Medendorp WP, Buchholz VN, Van Der Werf J, Leoné F. Parietofrontal circuits in goal-oriented behaviour. *Eur J Neurosci* 33: 2017–2027, 2011. doi:10.1111/j.1460-9568.2011.07701.x.
46. Battaglia-Mayer A, Caminiti R. Parieto-frontal networks for eye-hand coordination and movements. *Handb Clin Neurol* 151: 499–524, 2018. doi:10.1016/B978-0-444-63622-5.00026-7.
47. Mrotek LA, Soechting JF. Target interception: hand-eye coordination and strategies. *J Neurosci* 27: 7297–7309, 2007. doi:10.1523/JNEUROSCI.2046-07.2007.
48. Spering M, Schütz AC, Braun DI, Gegenfurtner KR. Keep your eyes on the ball: smooth pursuit eye movements enhance prediction of visual motion. *J Neurophysiol* 105: 1756–1767, 2011. doi:10.1152/jn.00344.2010.
49. Delle Monache S, Lacquaniti F, Bosco G. Eye movements and manual interception of ballistic trajectories: effects of law of motion perturbations and oclusions. *Exp Brain Res* 233: 359–374, 2015. doi:10.1007/s00221-014-4120-9.
50. Dukelow SP, DeSouza JF, Culham JC, van den Berg AV, Menon RS, Vilis T. Distinguishing subregions of the human MT+ complex using visual fields and pursuit eye movements. *J Neurophysiol* 86: 1991–2000, 2001. doi:10.1152/jn.2001.86.4.1991.
51. Smeets JBJ, Brenner E. Perception and action are based on the same visual information: distinction between position and velocity. *J Exp Psychol Hum Percept Perform* 21: 19–31, 1995. doi:10.1037//0096-1523.21.1.19.
52. Van Donkelaar P, Lee R, Gellman R. Control strategies in directing the hand to moving targets. *Exp Brain Res* 91: 151–161, 1992. doi:10.1007/BF00230023.
53. Lee D, Port NL, Georgopoulos AP. Manual interception of moving targets II. On-line control of overlapping submovements. *Exp Brain Res* 116: 421–433, 1997. doi:10.1007/pl00005770.
54. Montagne G, Laurent M, Durey A, Bootsma R. Movement reversals in ball catching. *Exp Brain Res* 129: 87–92, 1999. doi:10.1007/s002210050939.
55. Day B, Lyon I. Voluntary modification of automatic arm movements evoked by motion of a visual target. *Exp Brain Res* 130: 159–168, 2000. doi:10.1007/s002219900218.
56. Pisella L, Grea H, Tilikete C, Vighetto A, Desmurget M, Rode G, Boisson D, Rossetti Y. An 'automatic pilot' for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nat Neurosci* 3: 729–736, 2000. doi:10.1038/76694.
57. Sarlegna FR. Impairment of online control of reaching movements with aging: a double-step study. *Neurosci Lett* 403: 309–314, 2006. doi:10.1016/j.neulet.2006.05.003.
58. O'Rielly JL, Ma-Wyatt A. The effect of age and perturbation time on online control during rapid pointing. *PLoS One* 14: e0222219, 2019. doi:10.1371/journal.pone.0222219.
59. Breitmeyer BG. Contributions of magno-and parvocellular channels to conscious and non-conscious vision. *Philos Trans R Soc Lond B Biol Sci* 369: 20130213, 2014. doi:10.1098/rstb.2013.0213.
60. Kuba M, Kremláček J, Langrová J, Kubová Z, Szanyi J, Vít F. Aging effect in pattern, motion and cognitive visual evoked potentials. *Vision Res* 62: 9–16, 2012. doi:10.1016/j.visres.2012.03.014.
61. Ruitenberg MFL, Koppelmans V. Cognition in motion: evidence for intact action control with healthy aging. *J Gerontol B* 76: 252–261, 2021. doi:10.1093/geronb/gbaa184.
62. Reynaud AJ, Saleri Lunazzi C, Thura D. Humans sacrifice decision-making for action execution when a demanding control of movement is required. *J Neurophysiol* 124: 497–509, 2020. doi:10.1152/jn.00220.2020.
63. Hesse C, Kangur K, Hunt AR. Decision making in slow and rapid reaching: Sacrificing success to minimize effort. *Cognition* 205: 104426, 2020. doi:10.1016/j.cognition.2020.104426.
64. Maunsell JH, Ghose GM, Assad JA, Mcadams CJ, Boudreau CE, Noerager BD. Visual response latencies of magnocellular and parvocellular LGN neurons in macaque monkeys. *Vis Neurosci* 16: 1–14, 1999. doi:10.1017/s0952523899156177.
65. Chen C-M, Lakatos P, Shah AS, Mehta AD, Givre SJ, Javitt DC, Schroeder CE. Functional anatomy and interaction of fast and slow visual pathways in macaque monkeys. *Cereb Cortex* 17: 1561–1569, 2007. doi:10.1093/cercor/bhl067.
66. Verschueren SMP, Brumagne S, Swinnen SP, Cordo PJ. The effect of aging on dynamic position sense at the ankle. *Behav Brain Res* 136: 593–603, 2002. doi:10.1016/S0166-4328(02)00224-3.
67. Shaffer SW, Harrison AL. Aging of the somatosensory system: a translational perspective. *Phys Ther* 87: 193–207, 2007. doi:10.2522/ptj.20060083.
68. Gallivan JP, Culham JC. Neural coding within human brain areas involved in actions. *Curr Opin Neurobiol* 33: 141–149, 2015. doi:10.1016/j.conb.2015.03.012.
69. Merchant H, Zarco W, Prado L, Perez O. Behavioral and neurophysiological aspects of target interception. *Adv Exp Med Biol* 629: 201–220, 2009. doi:10.1007/978-0-387-77064-2_10.
70. Gilaie-Dotan S. Visual motion serves but is not under the purview of the dorsal pathway. *Neuropsychologia* 89: 378–392, 2016. doi:10.1016/j.neuropsychologia.2016.07.018.
71. van Donkelaar P, Lee RG. The role of vision and eye motion during reaching to intercept moving targets. *Hum Mov Sci* 13: 765–783, 1994. doi:10.1016/0167-9457(94)90017-5.
72. DeGoede KM, Ashton-Miller JA, Liao JM, Alexander NB. How quickly can healthy adults move their hands to intercept an approaching object? Age and gender effects. *J Gerontol A Biol Sci Med Sci* 56: M584–M588, 2001. doi:10.1093/gerona/56.9.M584.
73. Whitney D, Ellison A, Rice NJ, Arnold D, Goodale M, Walsh V, Milner D. Visually guided reaching depends on motion area MT+. *Cereb Cortex* 17: 2644–2649, 2007. doi:10.1093/cercor/bhl172.
74. Boehnke SE, Munoz DP. On the importance of the transient visual response in the superior colliculus. *Curr Opin Neurobiol* 18: 544–551, 2008. doi:10.1016/j.conb.2008.11.004.
75. Pruszynski JA, King GL, Boisse L, Scott SH, Flanagan JR, Munoz DP. Stimulus-locked responses on human arm muscles reveal a

- rapid neural pathway linking visual input to arm motor output. *Eur J Neurosci* 32: 1049–1057, 2010. doi:10.1111/j.1460-9568.2010.07380.x.
76. **Justino L, Kergoat H, Kergoat MJ.** Changes in the retinocortical evoked potentials in subjects 75 years of age and older. *Clin Neurophysiol* 112: 1343–1348, 2001. doi:10.1016/s1388-2457(01)00551-x.
 77. **Seidler RD, Bernard JA, Burutolu TB, Fling BW, Gordon MT, Gwin JT, Kwak Y, Lipps DB.** Motor control and aging: Links to age-related brain structural, functional, and biochemical effects. *Neurosci Biobehav Rev* 34: 721–733, 2010. doi:10.1016/j.neubiorev.2009.10.005.
 78. **Basso MA, Powers AS, Evinger C.** An explanation for reflex blink hyperexcitability in Parkinson's disease. I. Superior colliculus. *J Neurosci* 16: 7308–7317, 1996. doi:10.1523/JNEUROSCI.16-22-07308.1996.
 79. **Rajah MN, Languay R, Valiquette L.** Age-related changes in prefrontal cortex activity are associated with behavioural deficits in both temporal and spatial context memory retrieval in older adults. *Cortex* 46: 535–549, 2010. doi:10.1016/j.cortex.2009.07.006.
 80. **Peters A, Sethares C, Luebke J.** Synapses are lost during aging in the primate prefrontal cortex. *Neuroscience* 152: 970–981, 2008. doi:10.1016/j.neuroscience.2007.07.014.
 81. **Hermans L, Leunissen I, Pauwels L, Cuypers K, Peeters R, Puts NA, Edden RA, Swinnen SP.** Brain GABA levels are associated with inhibitory control deficits in older adults. *J Neurosci* 38: 7844–7851, 2018. doi:10.1523/JNEUROSCI.0760-18.2018.
 82. **Paxton JL, Barch DM, Racine CA, Braver TS.** Cognitive control, goal maintenance, and prefrontal function in healthy aging. *Cereb Cortex* 18: 1010–1028, 2008. doi:10.1093/cercor/bhm135.
 83. **Cloutman LL.** Interaction between dorsal and ventral processing streams: where, when and how? *Brain Lang* 127: 251–263, 2013. doi:10.1016/j.bandl.2012.08.003.
 84. **Thorpe SJ, Fabre-Thorpe M.** Seeking categories in the brain. *Science* 291: 260–263, 2001. doi:10.1126/science.1058249.
 85. **Gorbet DJ, Sergio LE.** Preliminary sex differences in human cortical BOLD fMRI activity during the preparation of increasingly complex visually guided movements. *Eur J Neurosci* 25: 1228–1239, 2007. doi:10.1111/j.1460-9568.2007.05358.x.
 86. **Rogojin A, Gorbet DJ, Hawkins KM, Sergio LE.** Cognitive-motor integration performance is affected by sex, APOE status, and family history of dementia. *J Alzheimers Dis* 71: 685–701, 2019. doi:10.3233/JAD-190403.