

Slowing of Movements in Healthy Aging as a Rational Economic Response to an Elevated Effort Landscape

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Why do we move slower as we grow older? The reward circuits of the brain, which tend to invigorate movements, decline with aging, raising the possibility that reduced vigor is due to the diminishing value that our brain assigns to movements. However, as we grow older, it also becomes more effortful to make movements. Is age-related slowing principally a consequence of increased effort costs from the muscles, or reduced valuation of reward by the brain? Here, we first quantified the cost of reaching via metabolic energy expenditure in human participants (male and female), and found that older adults consumed more energy than the young at a given speed. Thus, movements are objectively more costly for older adults. Next, we observed that when reward increased, older adults, like the young, responded by initiating their movements earlier. Yet, unlike the young, they were unwilling to increase their movement speed. Was their reluctance to reach quicker for rewards due to the increased effort costs, or because they ascribed less value to the movement? Motivated by a mathematical model, we next made the young experience a component of aging by making their movements more effortful. Now the young responded to reward by reacting faster but chose not to increase their movement speed. This suggests that slower movements in older adults are partly driven by an adaptive response to an elevated effort landscape. Moving slower may be a rational economic response the brain is making to mitigate the elevated effort costs that accompany aging.

Key words: age; effort; metabolic cost; reaching movements; reward; utility; vigor

Significance Statement

Healthy aging coincides with a reduction in speed, or vigor, of walking, reaching, and eye movements. Here we tried to disentangle two potential causes of age-related slowing: reduced reward valuation due to loss of dopaminergic tone, or increased energy expenditure related to mitochondrial or muscular inefficiencies. Through a series of experiments and computational modeling, our results suggest that changes in the reaction time and movement speed together offer a quantifiable metric to differentiate between reward- and effort-based alterations in movement vigor. It appears that objective increases in the metabolic cost of moving, not reductions in reward valuation, are driving much of the movement slowing that accompanies healthy aging.

Introduction

Among healthy people there are stable inter-subject differences in movement speed: some individuals consistently move faster than others (Reppert et al., 2018). Indeed, a prominent factor that influences movement speed is aging. Older adults walk

(Waters et al., 1988; Laufer, 2005), reach (Ketcham et al., 2002; Kozak et al., 2003; Kitchen and Miall, 2018), and make saccadic eye movements (Irving et al., 2006; Dowiasch et al., 2015) at a slower speed than younger adults. Why do older people move slower?

In principle, a reduction in vigor may be due to changes in the reward system of the brain (Clark et al., 2019). In the healthy basal ganglia, dopamine is released when expecting a reward (Schultz et al., 1997; Bayer and Glimcher, 2005), which can subsequently facilitate faster movements (Kawagoe et al., 2004; da Silva et al., 2018; Summerside et al., 2018). However, the brain's ability to accurately predict the value of an upcoming reward depends in part on the integrity of these dopaminergic neurons, and individuals with dopamine deficits exhibit a diminished willingness to move faster toward (Mazzoni et al., 2007; Yang et al., 2023) or exert effort for (Schmidt et al., 2008; Chong et al., 2015)

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a reward. Because the integrity of the dopaminergic system declines with healthy aging (Dreher et al., 2008; Eppinger et al., 2011), a reduced sensitivity to reward may be one explanation for why older adults make slower movements (Shadmehr et al., 2010); in other words, older adults may be less motivated to perform quicker movements.

An alternative and perhaps complementary explanation is that as one grows older, it becomes more effortful to make movements. Moving at faster speeds, for example, often requires more metabolic energy (Ralston, 1958; Bruening et al., 2023; Courter et al., 2023). Older adults additionally require a greater rate of energetic expenditure to walk at a given speed (Waters et al., 1988; Martin et al., 1992; Ortega and Farley, 2015) and to produce a given power on a cycle ergometer (Neder et al., 2001; Conley et al., 2012). This elevated energetic expenditure is associated with a decrease in efficiency of the mitochondria and contractile elements of muscles (Conley et al., 2012), as well as an increase in the levels of co-activation of antagonist muscles (Seidler et al., 2002; Huang and Ahmed, 2013; Ortega and Farley, 2015), both of which occur during aging. Therefore, in addition to a decline in the reward system of the brain, aging coincides with an increase in the energetic requirements of movement. This raises the hypothesis that with aging, moving slower is a rational economic decision in response to a reduced expectation of reward and an increased expectation of effort.

Here, we attempted to quantify this economic landscape of movement as it changed with aging to decipher if either reduced reward sensitivity or heightened effort cost was a dominant mechanism causing slowness in older adults. We focused on a reaching task and, in a first experiment, measured the energy that the older adults expended as they moved their hand from one point to another. We found that the metabolic cost of reaching was indeed greater in the older adults than in the young. That is, the cost of performing a reach at a given speed was objectively larger. Next, we quantified sensitivity to reward in a second experiment and found that, like younger adults, the older participants responded to increased reward by reducing their reaction time. However, unlike the young, they were less able or willing to increase their movement speed. These data gave rise to another question: given the increased cost of movement in older adults, did the reduction in reaction time but not movement duration suggest that their valuation of reward was unimpaired?

To answer this question, we considered a normative model of behavior from foraging theory in which the objective of actions is to maximize a capture rate: reward minus effort, divided by time (Charnov, 1976; Richardson and Verbeek, 1986; Lemon, 1991; Bautista et al., 2001; Yoon et al., 2018). Model predictions suggested that, given their increased effort costs, when faced with the opportunity for greater reward, the older adults should respond not by increasing movement speed, but by primarily reducing their reaction times. In contrast, the young should do the opposite, primarily increase their movement speed rather than change reaction times.

To test these predictions, we performed a third experiment in which we tried to make the young subjects experience reaching as if they were older: we increased their reach effort costs (with respect to a baseline) and then measured how they responded to increased reward. When their effort costs were elevated, the young responded to reward like the older adults in that they reacted to increased reward not by increasing their movement speed but by reducing their reaction times. Thus, the slower movements in older adults may be a rational economic response to their elevated effort costs, not impaired reward valuation.

Materials and Methods

Participants

A total of 84 healthy subjects participated in our studies. For Experiment 1, we recruited 12 young adults (25 ± 2 years, six females, 66 ± 11 kg) and 12 older adults (75 ± 8 years, six females, 73 ± 18 kg). For Experiment 2, we recruited 20 young (26 ± 4 years, 10 females) and 20 older adults (72 ± 6 years, 10 females). For Experiment 3, we recruited 20 young adults (23 ± 4 years, 10 females). Participants were naive to the experiments and gave written informed consent approved by the University of Colorado Boulder Institutional Review Board before participating in this protocol.

All participants reported being primarily right-handed (Oldfield, 1971) and were screened to ensure all inclusion/exclusion criteria were met. Primary inclusion criteria included being within the specified age range (18–35 years for younger adults; >65 years for older adults) and physically active at least three times per week. Exclusion criteria included musculoskeletal impairments, injuries, or surgeries within the past year; neurological, vestibular, or ophthalmological disorders, diseases, or impairments; or other conditions, chronic illnesses, or medications that would have impaired ability to complete the tasks. Additionally, all older adults were deemed fully mobile as evident in earning the maximum score when performing a short physical performance battery (Guralnik et al., 1994). Young adult data for Experiment 2 have been reported previously by Summerside et al. (2018).

Task design

Experiment 1. The primary goal of Experiment 1 was to quantify the effect of reaching speed on the metabolic cost, or effort, of reaching. Participants sat in a chair designed to limit trunk movement and grasped the handle of a robotic arm using their right hand (shoulder–elbow robot, Interactive Motion Technologies). The robotic handle operated similarly to a computer mouse, where movements along the horizontal plane controlled the position of a cursor presented on a vertically positioned, 24 in LCD monitor ($1,920 \times 1,080$; 60 Hz refresh rate) located at eye level (Fig. 1A, see Results). For Experiment 1, and all experiments, the background color of the monitor was black.

We quantified effort by measuring metabolic cost as a function of movement distance and duration. Metabolic cost was estimated via expired gas analysis (TrueOne 2400, ParvoMedics). Participants wore a nose clip and breathed with their mouth through a two-way, nonrebreathable valve (Hans Rudolph) throughout all reaching bouts in Experiment 1. This allowed us to measure how the rates of oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) changed across conditions. To minimize the thermic effect of food on metabolic rate, all sessions were conducted in the morning with participants arriving having fasted overnight. The metabolic cart was calibrated at the start of each visit according to certified gas mixtures as well as a range of flow rates from a 3 L calibration syringe. The baseline, or resting, metabolic rate was measured while participants sat quietly in the chair holding the robotic handle. Baseline trials were taken at the start and end of the visit.

The experiment began with measurement of the baseline metabolic rate of energy expenditure while the subjects held the handle of the robot and maintained stillness at the home position of the cursor. After 5 min of stillness, they made alternating out and back movements along the anterior–posterior (y) axis. For odd numbered trials, the movement was away from the body, and on even numbered trials, the movement was back toward the body. A trial began by placing the cursor over a gray home circle. After a 150 ms delay, a white-outlined, black-filled circular target (diameter = 1.6 cm) appeared, and the participant was instructed to move the cursor to the newly projected target and stop. Participants executed their movements in this experiment according to two prescribed distances (10 and 20 cm), each with five prescribed durations. The five movement durations used at each distance are referred to as very slow (VS), slow (S), medium (M), fast (F), and very fast (VF). Across all distance-duration combinations, the metabolic cost of reaching was obtained for 10 conditions per participant. The number of trials for each condition depended on reach duration and distance, as well as age group (Table 1). The number of trials was selected to

Table 1. Number of trials and constrained movement duration by distance, age, and relative speed. Displayed as number of trials (movement duration)

Distance	Age	Very slow	Slow	Medium	Fast	Very fast
10 cm	Young	180 (1,000 ms)	200 (775 ms)	230 (500 ms)	260 (350 ms)	300 (125 ms)
	Older	180 (1,100 ms)	210 (800 ms)	230 (600 ms)	245 (500 ms)	260 (250 ms)
20 cm	Young	140 (2,050 ms)	160 (1,150 ms)	200 (800 ms)	230 (500 ms)	260 (250 ms)
	Older	130 (2,150 ms)	170 (1,250 ms)	210 (850 ms)	230 (550 ms)	250 (250 ms)

allow for ~6 min of reaching, with faster duration conditions requiring more trials.

Participants learned the desired duration for each condition based on two different feedback sources. The first was a blue training bar that would accompany the cursor along the left side of the movement path for the first four of every 20 trials. Upon movement initiation, this training bar would follow a minimum jerk trajectory toward the target indicating the prescribed reaching speed. The second source of feedback was an audiovisual stimulus once the cursor made contact with the target. If the cursor arrived within ± 50 ms of the desired duration, the target would flash yellow and deliver a pleasing tone (50 ms at 880 Hz followed by 50 ms at 3,520 Hz, played over two computer speakers located directly in front of participant). If the movement was too fast, the target would turn green and if the movement was too slow, it would turn gray.

Experiment 2. The purpose of Experiment 2 was to measure the effect of reward on reaching vigor. Participants were seated in a position identical to Experiment 1 (Fig. 1A, see Results) but no longer wore metabolic equipment. A trial began with a small green circular home target (diameter = 0.9 cm) appearing in the center of the screen. Participants moved the cursor (diameter = 0.6 cm) to overlap with the home target. After overlapping for a brief 150 ms, the home circle vanished, a quick audio stimulus was delivered (50 ms at 110 Hz followed by 50 ms at 220 Hz), and a larger red outer circle appeared (diameter = 14 cm) with its center the same as the home target. The outer ring included a small indicator located at one of four alternating locations (45°, 135°, 225°, or 315° from right horizontal). The goal of the task was to move the cursor through the outer ring while staying within the quadrant containing the indicator (Fig. 2A, see Results). Once a reach was initiated, visual feedback of the cursor was removed. When the now invisible cursor crossed the outer ring, the outer ring changed color from red to gray, signaling to the participant that they should return the cursor to the center. When the cursor returned within 9 cm of the center, the visual feedback of the cursor was restored, and the home target was re-illuminated to allow the next trial to begin.

In 25% of trials, a quadrant would be paired with a reward. The only requirement for receiving the reward was that the cursor crossed the 100° region centered on the quadrant indicator. This large region was intended to remove any differences in reach kinematics related to movement variability. The qualities of the reward stimulus consisted of a pleasing sound (50 ms at 880 Hz followed by 50 ms at 3,520 Hz) and a visual animation of the outer ring (ring flashed yellow for 50 ms and disappeared); both simultaneously delivered when the cursor crossed the outer ring. At the end of a rewarded trial, participants received an arbitrary four points, with the total accumulated points displayed on the upper right corner of the monitor. No feedback regarding points was delivered on nonrewarded trials. The presentation of quadrants was completely random within each experimental block. This means that there was at any time a 25% probability that the next trial would be in the rewarded quadrant. No participants were ever explicitly informed about when a new block began, the location of future rewards, or how rewards were distributed within or across blocks.

Importantly, participants were instructed only to reach in the direction of the indicated quadrant and were informed that nothing they did beyond that would change the quantity or quality of the reward. As long as they completed the trial in the indicated quadrant and that trial was rewarded, they would receive the full reward. If participants inquired about whether they needed to perform under any time or kinematic constraints, they were told that there was no wrong way to perform the movement and to simply reach in a manner that felt natural for them.

The participants were unaware of the number of trials they would be completing, only to expect the experiment to last 1 h. Each participant was compensated \$15 for their time with this amount being independent of any aspect of their performance in the task.

Experiment 3. The purpose of Experiment 3 was to directly assess the effect that added effort has on reward responsiveness of reaching vigor. The task was almost identical to the task from Experiment 2 outside of a few changes: (i) the distance from the central home circle to the edge of the target ring was also reduced to from 14 to 10 cm; (ii) participants had visual feedback of the cursor throughout the trial, though they were explicitly instructed that the only criterion for success was to cross the cursor anywhere along the 100° quadrant; and (iii) participants performed the protocol twice – once with low effort (0 kg added mass) and once with high effort (3.63 kg; 8 lbs) physical mass added to the robotic arm. The mass was affixed to the robot itself above the hand, such that participants did not have to support the mass against gravity but only had to overcome its inertia.

Experimental design

Experiment 1. Participants visited the laboratory on two separate days. Each visit began with the measurement of the baseline metabolic rate (holding the handle still while breathing through the mouthpiece and wearing the nose clip), then followed five reaching blocks at a single distance (Fig. 1B), and then concluded with another measurement of a baseline metabolic rate. Each reaching block consisted of 20 practice trials accompanied by the training bar, a short 1 min break, then an additional ~6 min of reaching while wearing the nose clip and mouthpiece required for gas exchange analysis. Five minute mandatory rest periods were included between blocks of reaching to allow an individual's metabolic rate to return to resting levels before the start of a new block. The constrained movement duration was consistent within each block, and the block order was randomized for each participant (Table 1). The distance reached on a given day (10 cm or 20 cm) was likewise randomized and counterbalanced across participants.

Experiment 2. Began with a familiarization protocol consisting of a single block of 40 trials (10 trials to each quadrant). During these trials, participants retained visual feedback of the cursor, were able to familiarize themselves with the task, and adjust the position of the chair to ensure all four quadrants could be comfortably accessed. All reaches during familiarization were unrewarded.

The experimental protocol came after familiarization and consisted of a baseline block of 40 trials (10 trials/quadrant) followed by four experimental blocks of 100 trials (25 trials/quadrant). At the start of the experimental protocol, the participants were informed that they would no longer be receiving visual feedback of the cursor when moving toward a quadrant. They were also told that quadrants would now be occasionally rewarded and that as long as they reached within the indicated 100° quadrant, they would receive the reward. There was no reward tied to any quadrant during the baseline block. In each of the experimental blocks, a single quadrant was consistently rewarded, with the location of the reward changing at the beginning of each new block. The order of rewarded quadrants was randomized across participants.

Experiment 3. To begin the protocol, participants performed 80, unrewarded baseline trials (20 reaches/quadrant) to familiarize themselves with the robotic arm. The baseline period immediately transitioned into the primary reward protocol, consisting of an additional 400 reaching trials. The 400 trials were separated into four blocks of

100 trials. Within each block, only one quadrant was associated with a reward and the experiment then progressed just as Experiment 2. The order of the rewarded quadrants was, again, randomized per subject, and there was a short 30 s break between blocks 1–2 and blocks 3–4. Participants were not informed of the location of the rewarded quadrant, how the reward location was distributed, nor when a new rewarded block began.

Participants performed the above protocol twice, with and without mass (~3.63 kg, 8 lbs) added to the handle of the robot (Fig. 4A). The order of the mass conditions was randomized and counterbalanced across participants. For six participants, the completion of the task with low and high effort occurred on two separate days; the remaining 14 participants performed both conditions on the same day with at least 10 min of rest between each condition. Each participant was compensated \$10 for their time, independent of task performance.

Data processing

Experiment 1. We calculated metabolic rate in watts (J/s) using the measured $\dot{V}O_2$ and $\dot{V}CO_2$ according to the Brockway equation (Brockway, 1987). We only included conditions where the respiratory exchange ratio was between 0.7 and 1.0, indicating aerobic respiration. The gross metabolic rate (\dot{e}_{gross}) was calculated as the average metabolic rate over the last 3 min of reaching in each condition. Baseline metabolic rate was calculated as the lower of the two average baseline metabolic rates measured during seated rest (\dot{e}_o) at the beginning and end of the visit.

Our goal was to calculate the metabolic cost of moving only (\dot{e}_r). The gross rate measured represents the combined cost of moving and the cost of not moving between each trial (\dot{e}_{ITI}), weighted by the time spent moving or not moving:

$$\dot{e}_{\text{gross}} = \frac{\dot{e}_r T_r - \dot{e}_{\text{ITI}} T_{\text{ITI}}}{T} \quad (1)$$

Here, T_{ITI} represents the average length of the inter-trial-interval, and T_r represents the average movement duration. T is the total movement duration:

$$T = T_r + T_{\text{ITI}} \quad (2)$$

If we assume that the cost of waiting is equal to the cost of rest, then the cost of waiting between trials \dot{e}_{ITI} can be represented by the baseline metabolic rate \dot{e}_o . We can then localize the metabolic cost of moving during each trial according to the equation:

$$\dot{e}_r = \dot{e}_{\text{gross}} \frac{T_r + T_{\text{ITI}}}{T_r} + \dot{e}_o \frac{T_{\text{ITI}}}{T_r} \quad (3)$$

For each age group, we parameterized this energy expenditure of reaching (\dot{e}_r) as a function of target distance (d) and reach duration (T_r), using previously described formulation (Ralston, 1958) and the data from Experiment 1:

$$\dot{e}_r = \dot{e}(T_r) = a + b \frac{d^i}{T_r^j} \quad (4)$$

By integrating Equation 4 as a function of time, we computed the total energy that was expended to reach a distance d (Eq. 5), or a “cost per movement” (CPM). The result was a concave-upward function of reach duration T_r (Fig. 1C):

$$e(T_r) = aT_r + b \frac{d^i}{T_r^{j-1}} \quad (5)$$

All parameter values (a , b , i , j) were obtained via bootstrapping (*nls* function and *boot* package available in R version 3.3.3). The young and older adult datasets were sampled over 10,000 replications with each

replication consisting of 120 points sampled with replacement (12 participants per age group, 10 conditions per participant).

All experiments. Mediolateral (x) and anteroposterior (y) positions of the handle were recorded at 200 Hz. With these signals we calculated radial position, which was then smoothed (fourth-order Butterworth filter with cutoff frequency of 10 Hz.). Instantaneous speed and acceleration were obtained through differentiating smoothed radial position. Accuracy was calculated as the variance of movement endpoints along the x - and y -axes. Jerk was calculated independently along the x - and y -axes by triple differentiating the position signals along those axes.

Reaction time was calculated as the difference in time between when the audiovisual start stimulus was delivered and the movement onset. The movement onset was identified using a threshold based on both radial speed of 0.05 m/s and radial acceleration of 0.05 m/s². In Experiment 1, the movement offset was determined as the last moment that the speed exceeded a threshold of 2.5 cm/s. In Experiments 2 and 3, offset was determined as the moment of maximal radial position from the home. Peak instantaneous outward speed was identified between the movement onset and movement offset.

Movement duration was calculated as the difference in time between the movement onset and movement offset. Total distance was measured as the difference in position between the movement onset and movement offset. Inter-trial interval (ITI) was measured between each trial as the time between the movement offset of the current trial and the movement onset of the subsequent trial. This meant that ITI represented the combined time spent repositioning the cursor for the next trial and the reaction time of that same trial.

Trials in Experiment 2 with reaction times greater than 700 ms or with crossing point distances outside of the 100° quadrant were removed from analysis. Across all young participants, this accounted for an exclusion of 0.46% of trials (43 for reaction time and 2 for crossing the ring in the incorrect quadrant). For the older participants, a total of 4.32% of trials were excluded (332 trials for reaction time and 14 trials for crossing the outer ring in the incorrect quadrant).

Trials in Experiment 3 were removed if reaction times were >700 ms or <100 ms, which excluded 0.98% of all trials (165/16,800) in total. Trials would have been excluded if the cursor did not cross the ring within the 100° arc; however, no trials were unsuccessful in this manner.

Statistical analysis

Experiment 1. All young adults were able to complete each of the five durations at each of the two distances. This resulted in a total of 120 metabolic measurements for the young adults. Two older adults were unable to complete one of the conditions resulting in a total of 118 metabolic measurements for the older adult group. To determine the effect of age on the metabolic rate of moving, we implemented a linear mixed effects regression predicting the log transform of gross rate of moving, \dot{e}_r , as a function of a binary age indicator (older = 1), an estimated arm mass (continuous, kg), a binary distance indicator (10 cm = 1), an average velocity (continuous, m/s), and a velocity–distance interaction. Due to expected differences in the body or arm mass between sexes (de Leva, 1996; Chambers et al., 2010), we also checked for an effect of sex using a binary indicator (female = 1); however, it returned insignificant and covaried with arm mass, so was excluded from the final model. Differences in baseline rate between the young and older adults were explored using an independent *t* test with each individual's baseline rates averaged across both visits.

We estimated the mass of the upper arm, lower arm, and hand using previously published estimates according to age, sex, and body mass (de Leva, 1996; Chambers et al., 2010). Differences in segment mass between the age and sex groups were directly compared using two-sample independent *t* tests. The total arm mass was included as a covariate in the aforementioned regression model.

We performed another linear mixed effects regression to predict the variance of movement endpoints in x - and y -axes and the sum of jerk squared ($\sum(\ddot{x}^2 + \ddot{y}^2)$) as a function of a binary age indicator (older = 1), a binary distance indicator (10 cm = 1), and average velocity (continuous, seconds).

Experiment 2. The effect of reward for every individual was quantified by comparing reaction time, peak speed, and movement duration of each reaching movement toward a quadrant when it was rewarded compared with when the movement to that same quadrant was not rewarded. Reaction time, peak speed, and movement duration were modeled using a linear mixed effects regression with age and reward, and as predictors. Fixed effects in each model were a binary reward predictor (rewarded = 1), a binary age predictor (older = 1), and a reward–age interaction. Between-subject variation was incorporated as a random intercept.

Experiment 3. Similar to Experiment 2, the primary kinematic measures of interest were reaction time, peak outward velocity, and movement duration. To describe both the individual and interacting effects of effort and reward, we constructed linear mixed effects regression models predicting each of the kinematic outcomes (reaction time, peak velocity, and movement duration). Fixed effects in each model were a binary reward predictor (rewarded = 1), a binary effort predictor (high effort = 1), and a reward–effort interaction. Between-subject variation was incorporated as a random intercept. All valid reaches were included when fitting the model.

All statistical tests were conducted at a significance level of $\alpha = 0.05$. Descriptive statistics are reported as mean \pm standard error. All p -values were adjusted for multiple comparisons using the Holm–Bonferroni’s method on a family-wise basis. When applicable, effect sizes were calculated using Cohen’s d for independent samples.

Computational model of movement time and reaction time

To investigate the idea that increases in movement effort should predispose individuals to emphasize reacting faster as opposed to moving faster, we developed a model using the utility of movement as a cost function:

$$J = \frac{k\alpha P(R = 1|T_r)P(R = 1|T_o) - e(T_o) - e(T_r)}{T_r + T_o}. \quad (6)$$

In the above expression, α is the value of reward, scaled by an arbitrary coefficient, k , $e(T_r)$ is the metabolic cost of reaching (Eq. 5), and $e(T_o)$ is the metabolic cost of waiting before starting the movement (i.e., the cost incurred by the reaction time) (Eq. 8; see Results). The term $P(R = 1|T_r)$ captures the speed–accuracy tradeoff, i.e., the probability of acquiring the reward given that the movement was of duration T_r (Eq. 9; see Results). To estimate $P(R = 1|T_r)$, we used the endpoint accuracy data that we had measured in our subjects for a 10 cm movement in Experiment 1 across the range of speeds and fit a logistic function with parameters b_0 and b_1 using a constrained search (*fmincon* in MATLAB). Separate pairs of parameters were fit for the young and older adults. We also incorporated a speed–accuracy tradeoff on reaction time, $P(R = 1|T_o)$, such that the probability of successfully moving in the correct direction increases with longer reaction times or longer times to adequately prepare the movement (Eq. 10; see Results) (Haith et al., 2016).

We lastly iterated over a series of reward values ($\alpha = \{20, 21, 22, \dots, 200\}$) and reward scaling coefficients ($k = \{0.8, 0.9, 1.0, 1.1, 1.2\}$) to perform a constrained search (*fmincon* in MATLAB) for the reaction times (T_o) and movement times (T_r) that maximized utility (J) for a given reward.

Data and software availability

All data used to draw the results presented in this report, including the R code necessary to analyze these data can be freely accessed at the following location: https://osf.io/cfm9v/?view_only=df7ccb37d27a4aeab01c1e2f83c40e98

Results

We sought to understand why healthy aging is accompanied by a reduction in movement speed. To answer this question, we measured the metabolic cost of reaching in groups of young (18–35 years) and older (66–87 years) adults as they reached at various

speeds. In our second and third experiments, we measured motor responses to varying amounts of reward when reaching with high and low effort costs.

Cost of reaching is greater in the older adults

We measured the rate of energy expenditure at rest and during reaching. In the baseline period, young and older subjects held the handle of a robotic arm and remained still (Fig. 1A). The resulting rate of energy expenditure \dot{e}_o was not significantly different between the two groups (t test, young = 77 ± 15 W, older = 69 ± 16 W, $p = 0.241$, $d = 0.49$). Thus, at baseline, energetic rates were comparable between the young and older adults.

As subjects reached, the rate of energy expenditure \dot{e}_r increased with average reach speed [main effect of speed, $\beta = 2.473$, 95% CI (2.200, 2.746), $p < 0.001$] (Fig. 1B). However, the older adults required a greater rate of energy expenditure to reach at a given speed [main effect of age: $\beta = 0.152$ W, 95% CI (0.041, 0.264), $p = 0.007$]. For example, the regression suggests older adults experience a 16.5% increase [95% CI (3.8%, 30.7%)] in the energetic rate of reaching at a given distance and velocity, on average (Fig. 1B).

What might be the reason for this increased cost for the older adults? The simplest possibility is that the older adults were burdened by a heavier arm. To investigate this, we estimated the mass of the arm in each participant as a function of their total body mass, age, and sex using previously published observations (de Leva, 1996; Chambers et al., 2010). We found no significant differences in estimated upper arm mass between the two groups ($m_{\text{young}} = 1.75 \pm 0.33$ kg, $m_{\text{old}} = 1.77 \pm 0.39$, $p = 0.898$, $d = 0.05$), lower arm mass ($m_{\text{young}} = 1.00 \pm 0.23$ kg, $m_{\text{old}} = 1.16 \pm 0.35$, $p = 0.197$, $d = 0.54$), or hand mass ($m_{\text{young}} = 0.39 \pm 0.08$ kg, $m_{\text{old}} = 0.43 \pm 0.12$, $p = 0.331$, $d = 0.41$). Altogether, we could not attribute the elevated energetic cost of reaching in the older adults to a heavier limb.

Another possibility is that in the older adults, movements were jerkier, requiring costly corrections (Van Halewyck et al., 2015). Indeed, movements of the older adults were less accurate than the young adults, as illustrated by endpoint errors along the axes normal and tangential to the path to the target [normal, $\beta = 0.274$ mm, 95% CI (−0.19, 0.75), $p = 0.250$; tangential, $\beta = 3.559$ mm, 95% CI (1.38, 5.75), $p = 0.003$]. Perhaps these errors led to more corrective movements when approaching the target, subsequently resulting in greater effort costs. A way to probe the extent of corrective movements is to calculate the smoothness of the movement as the sum of squared jerk during the reach. We found that while the sum of squared jerk increased with faster movements [$\beta = 1,461,723.98$ (m/s³)², 95% CI (1,249,849.60, 1,673,330.76), $p < 0.001$], there was no effect of age [$\beta = -29,554.24$, 95% CI (−77,687.88, 18,792.92), $p = 0.224$]. In summary, reaching consumed a greater amount of energy in older adults and tended to be less accurate.

Like the young adults, older adults respond to reward by reducing reaction time, but they are less able or willing to increase their reach speed

In Experiment 2 we tested how the older and the young responded to reward. Young and older participants moved a cursor in an out-and-back motion toward a very large target, indicated by a 100° arc (Fig. 2A) (Summerside et al., 2018). Our design included very large targets because we wanted a task in which the reach endpoint accuracy did not play a significant role.

Subjects were free to select their reach speed. Within a given block, one of the quadrants was consistently paired with reward,

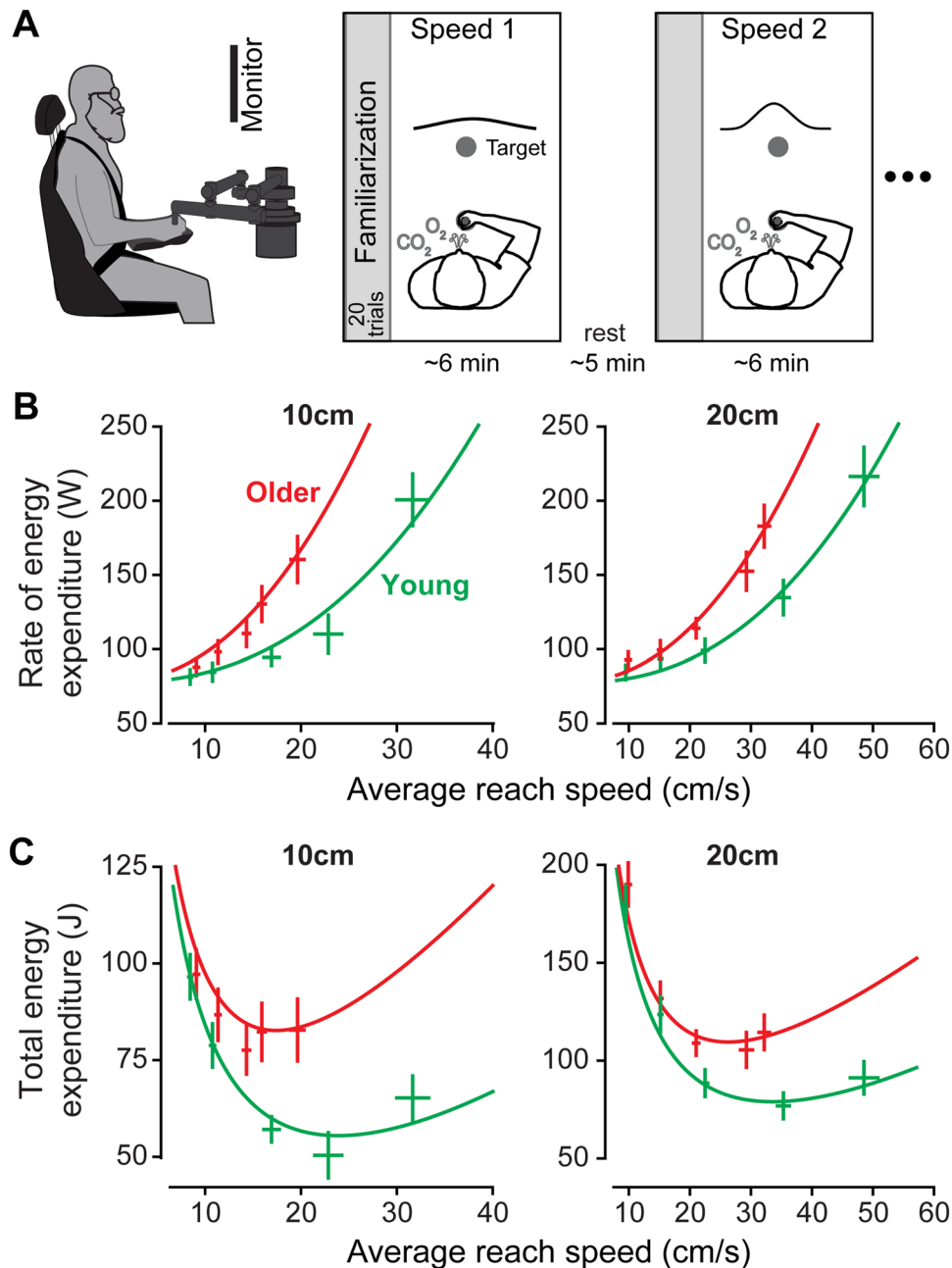


Figure 1. Reaching is energetically more costly in older adults (Experiment 1). **A**, Participants controlled a cursor presented on a monitor by moving a robotic manipulandum with their right hand in the horizontal plane at various prescribed speeds and distances. **B**, Rate of energy expenditure increased with reach speed at a given distance, but this cost was greater in the older adult group. Curves represent best fit from Equation 4: $a_{\text{young}} = 77.33$ (67.84 85.49)W, $a_{\text{older}} = 77.52$ (60.14 92.38)W; $b_{\text{young}} = 114.67$ (44.60 226.23), $b_{\text{older}} = 151.44$ (49.01 334.30), $i_{\text{young}} = 1.23$ (0.83 1.67), $i_{\text{older}} = 0.88$ (0.52 1.40); and $j_{\text{young}} = 2.44$ (1.85 3.15), $j_{\text{older}} = 2.17$ (1.39 3.55) [mean (95%CI)]. **C**, Total energy expenditure (cost of reaching). Vertical and horizontal error bars represent \pm SEM.

while the remaining three quadrants were always unrewarded. The reward consisted of a short, pleasant tone, a visual flashing of the outer ring, and four points. We had found previously that this feedback was a reasonable proxy for reward as it led participants to invigorate their reaching movements (Summerside et al., 2018). The only requirement for reward was that the cursor crossed anywhere along the 100° arc of the indicated quadrant.

Older adults took longer to initiate their movements. Their average reaction time was 401 ± 12 ms, significantly longer than the reaction times (292 ± 7 ms) observed in the young [$\beta = 109.6$ ms, 95% CI (81.5, 137.6), $p < 0.001$] (Fig. 2B). In trials toward the rewarded quadrant, both young and older adults

responded by reducing their reaction time [change in mean reaction time, $\Delta_{\text{young}} = -16 \pm 2$ ms, $\Delta_{\text{older}} = -17 \pm 4$ ms; main effect of reward, $\beta = -16.57$ ms, 95% CI (-21.1, -11.9), $p < 0.001$; reward by age interaction: $p = 0.863$] (Fig. 2D).

However, in contrast to the consistent and robust effects of reward on reaction times of both older and young adults, we found a reduced effect of reward on reach speed in the older population as compared to young [main effect of reward, $\beta = 0.84$ cm/s, 95% CI (4.88, 12.0), $p = 3.43 \times 10^{-6}$; reward by age interaction, $\beta = -0.68$ cm/s, 95% CI (-11.8, -1.8), $p = 0.0081$]. Whereas young adults reached faster toward the rewarding target ($\Delta_{\text{young}} = 0.84 \pm 0.182$ cm/s), reward did not significantly increase

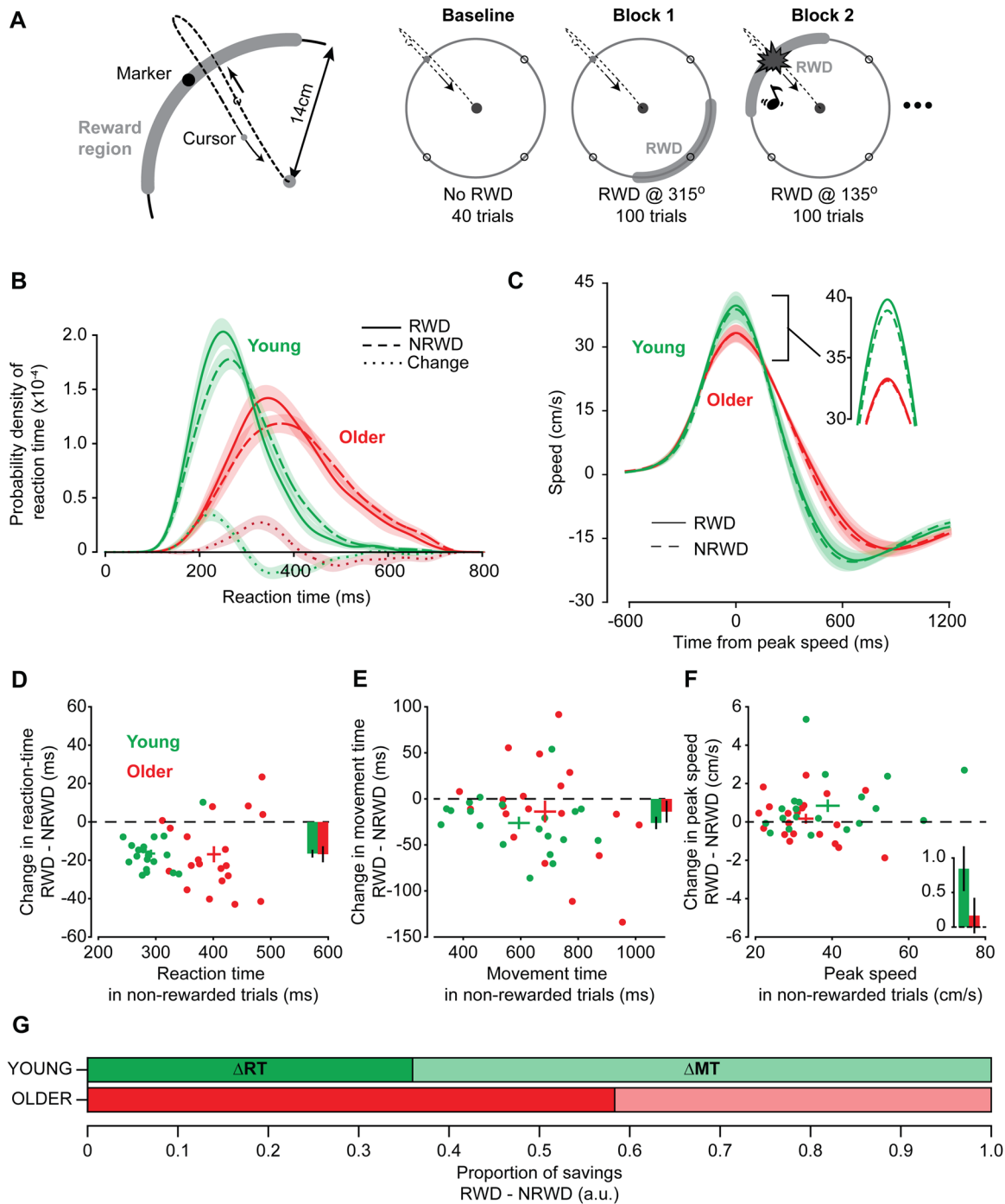


Figure 2. Reward quickens reaction time in both groups, but older adults are less willing to increase their movement speed (Experiment 2). **A**, Participants performed out-and-back reaches to alternating targets projected along a ring 14 cm from the home circle. The desired quadrant was indicated with a marker centered at the middle of the quadrant. Visual feedback of the cursor was removed during the outward portion of the movement and was re-displayed during the return portion of the reach once the hand was 9 cm from the home target. The protocol consisted of a baseline period with no reward followed by four experimental blocks. Each experimental block had one quadrant paired with a reward (RWD). Audiovisual reward stimulus was delivered upon crossing any region of the 100° target arc. The gray areas indicating reward were not visible to the participant, but are presented in the figure to convey which quadrant was paired with reward. **B**, We used a nonparametric kernel density estimation method to calculate the probability distribution for each individual when making movements to rewarded (RWD, solid curves) and nonrewarded (NRWD, dashed curves) quadrants as well as a difference (dotted curve) in these distributions at each bin (bin size = 5 ms). Younger adults (green curves) initiated movements earlier than older adults (red curves), but both groups responded to reward by reacting sooner. **C**, Effects of reward on movement execution in young (green) and older (red) adults. Young adults made movements toward quadrants paired with reward (RWD, solid curves) with greater peak speed when compared to that same quadrant when not rewarded (NRWD, dashed curves). Older adults reached with a peak speed that was independent of reward status. Inset graph depicts enlarged region highlighted peak speed. **D–F**, Scatter plot representing the relationship between rewarded (RWD, vertical axis) and nonrewarded (NRWD, horizontal axis) movements according to mean reaction time (**D**), movement duration (**E**), and peak speed (**F**). Dots represent individual participants. Crosses represent the mean for each age group, and the length of the bars represents \pm SEM. The mean effect of reward for each age group is indicated with the inset bar graph, reported as mean \pm SEM. **G**, Proportion of time savings due to reaction time (RT) and movement time (MT) in young vs. older adults. The proportion of time saved by reacting faster is larger in older adults.

reach speed in the older adults ($\Delta_{\text{older}} = 0.16 \pm 0.181$ cm/s) (Fig. 2C, F). Movement duration was affected similarly. Reward reduced movement durations in both groups [$\beta = -26.06$ ms, 95% CI ($-39.1, -13.0$), $p < 0.001$]. However, like peak velocity, reward-mediated changes in movement duration were numerically larger in the young ($\Delta_{\text{young}} = -26.06 \pm 6.649$ ms) compared with older adults ($\Delta_{\text{older}} = -13.89 \pm 6.619$ ms), although this trend did not reach statistical significance [Fig. 2E; reward by age interaction, $\beta = 12.16$ ms, 95% CI ($-6.22, 30.6$), $p = 0.1948$].

Both young and older adults got to the target on rewarded trials sooner; yet, they did so differently. The young reacted and moved faster, but relied primarily on faster movements, which accounted for approximately 65% of the total time savings on average. In contrast, older adults relied primarily on faster reaction times, which drove nearly 60% of the time savings (Fig. 2G).

In summary, both young and older adults reduced their reaction time when reaching toward a rewarding target. However, older adults were less willing to increase the speed of their movements in response to reward.

A greater effort cost should lead to slower movements and longer reaction times

To better understand these results, we tried to ask how older adults should alter their reaching movements in response to increased reward. Is their reluctance to increase speed but their willingness to reduce reaction time a rational response to age-related changes in effort costs?

If we assume that the reward promised at the end of the movement interacts with the effort that must be expended to make that movement, the result is a utility that can, in principle, specify the optimal movement. A normative form of this utility (Lemon, 1991) is employed in the field of optimal foraging: utility J is defined as the capture rate, i.e., the difference between the reward attained and effort expended, divided by time required to obtain that reward (Charnov, 1976; Shadmehr et al., 2016; Yoon et al., 2018). Earlier work has shown that this formulation makes testable predictions regarding how changes in the reward and effort landscape should affect patterns of movement (Yoon et al., 2018). Here, we used this idea to ask the following question: given that older adults are burdened by a greater energetic cost of reaching, and suffer from greater inaccuracy, how should they reach?

When a potentially rewarding target is presented to a subject, the duration of time that passes before acquisition of reward includes both the reaction time T_o , and the duration of the movement T_r . Let reward magnitude be specified by α , and use the capture rate to define the utility of the reach:

$$J = \frac{\alpha P(R = 1|T_r)P(R = 1|T_o) - e(T_o) - e(T_r)}{T_r + T_o}. \quad (7)$$

In this expression, $e(T_r)$ is the metabolic cost of reaching (Eq. 5), which was fit independently to young and older adult data from Experiment 1 and captured the measured data well [Fig. 1B; $r_{\text{young}} = 0.85$ (0.78–0.90), $r_{\text{old}} = 0.67$ (0.59–0.75)].

We made an important assumption that effort was also spent, or wasted, while waiting to move during the reaction time period, $e(T_o)$. To approximate this cost, we assumed this energy expenditure of waiting was that of holding still, or the baseline metabolic rate \dot{e}_o , which we found did not differ between age groups. The total amount of energy spent prior to beginning a movement, $e(T_o)$, was then proportional to the reaction time T_o :

$$e(T_o) = \dot{e}_o T_o. \quad (8)$$

For each age group and movement duration, we also used the mean and standard deviation of subject endpoint error from the 10 cm movements in Experiment 1 to calculate the probability that the endpoint was within the target radius (0.8 cm). This accuracy, which would affect the probability of successfully receiving a reward akin to a speed–accuracy tradeoff (Fitts, 1954), was then described as a function of reach duration according to the following equation, where b_0 and b_1 were parameters fit to independently to young and older adult data (Fig. 3B):

$$P(R = 1|T_r) = \frac{1}{1 + e^{-b_0 - b_1 T_r}}. \quad (9)$$

We used the term $\Pr(R = 1|T_o)$ to represent the fact that reaction times also affect accuracy of the chosen movement direction, with the probability of success increasing with longer reaction times (Eq. 10; Fig. 3A) (Haith et al., 2016; Hardwick et al., 2019). It was described with a similar logistic equation to movement time:

$$P(R = 1|T_o) = \frac{q}{1 + e^{-c_0 - c_1 T_o}} + p, \quad (10a)$$

$$p = \frac{1}{n \text{ targets}}; \quad q = 1 - p. \quad (10b)$$

Without data to fit for reaction time probability of reward, the parameters c_0 and c_1 were determined assuming a nonzero, chance probability of reward (p) when the reaction time was near zero (<150 ms), and a 100% probability of reward at reaction times of approximately 400 ms (Haith et al., 2016). We considered a scenario where there are $n = 40$ potential targets (i.e., the maximum number of nonoverlapping 0.8 cm radius targets that can fit around a 10 cm radius circle), and thus an early reaction time would result in a chance probability (p) of a reach toward the correct target (Eq. 10b). Theory predictions remained conceptually the same across a range of parameter (c_0 and c_1) values.

Next, we were equipped to compute the reaction times (T_o^*) and movement durations (T_r^*) that maximize this utility for young and older adults:

$$\left. \frac{d[\alpha \Pr(R = 1|T_r) \Pr(R = 1|T_o) - e(T_o)]}{dT_o} \right|_{T_o^*} = J|_{T_r^*, T_o^*}, \quad (11a)$$

$$\left. \frac{d[\alpha \Pr(R = 1|T_r) \Pr(R = 1|T_o) - e(T_r)]}{dT_r} \right|_{T_r^*} = J|_{T_r^*, T_o^*}. \quad (11b)$$

These equations made sensible predictions: in the face of an increased metabolic cost of reaching, and increased inaccuracy, the best policy for the older adults is to reduce reach speed, and increase reaction time (Fig. 3C). Importantly, these results were maintained even when using equivalent speed–accuracy tradeoffs between the young and older adults, as well as across a range of parameter values. Thus, an increased cost of reaching alone is sufficient to slow movements.

Next, we used the equations to examine the results of Experiment 2. Under Hypothesis 1, older adults move slower than the young adults primarily because of their increased effort costs. Under Hypothesis 2, older adults move slower than the young adults primarily because they value reward less.

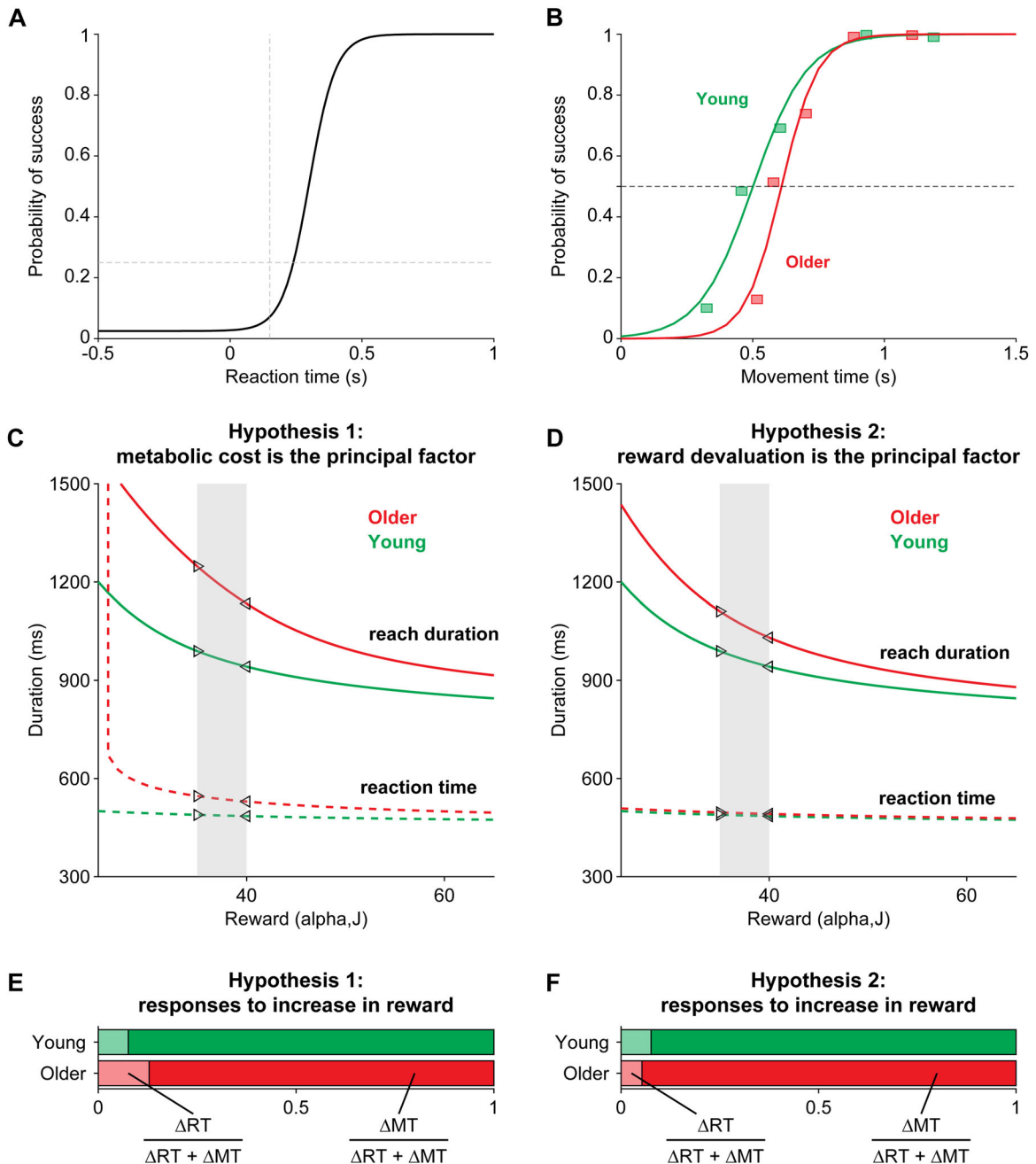


Figure 3. A rational response to increased effort costs is to slow movements and reaction times. **A**, Logistic function representing the speed–accuracy tradeoff for reaction times. **B**, Logistic curves fit to endpoint data of older (red) and young (green) adults representing the speed–accuracy tradeoff for movement times. For a given reach duration, older adults saw a lower probability of success than the young. **C**, Effect of effort costs on optimal reaction times (dotted lines) and movement times (solid lines) across arbitrary reward values, using (Eq. 7). Fitted metabolic parameters (Fig. 1B) and associated speed–accuracy curves were used for the young and older curves. **D**, Effect of reward devaluation on optimal reaction times and movement times. Green curves represent optimal solutions based on the younger adult metabolic fits, accuracy, and nominal reward valuation ($k = 1$). Red curves are optimal solutions with the same effort costs, but older adult accuracy and reduced reward valuation ($k = 0.8$). **E**, **F**, The proportions of time saved ($\Delta RT / (\Delta RT + \Delta MT)$) due to reducing reaction time or movement time for an arbitrarily selected increase in reward from 45 J to 50 J (gray region in **C**, **D**). Compared to young, older adults should allocate a larger proportion of time savings to reducing reaction times due to higher metabolic costs (**E**). If older adults were instead valuing reward less, their proportion of time savings from reaction time should instead be lower (**F**).

Can the results of Experiment 2 help us dissociate between the predictions of these two alternatives?

In older adults, energetic costs were greater than the young, and movements suffered from greater inaccuracy. However, the energetic cost of reaction time was the same (because in our two groups, the baseline metabolic costs were not different). To compute the predictions of Hypothesis 1, we inserted the measured metabolic costs and accuracy into Equation 11 and computed how reaction time and movement duration should

change in response to a given change in reward via the following

$$\text{ratios: } \frac{\Delta RT}{\Delta RT + \Delta MT} \text{ and } \frac{\Delta MT}{\Delta RT + \Delta MT}.$$

We found that according to Hypothesis 1 (increased effort cost), in response to increased reward both older adults and the young should reduce their movement duration and reaction times, but because moving faster costs more for older adults, they should focus more of the change in their reaction times (Fig. 3E). That is, if the increased effort costs are the main issue for older

adults, then they should respond to reward by reducing their reaction time, not movement time.

In Hypothesis 2 (reduced valuation of reward), we imagined the counterfactual condition that the older and the young had the same effort costs of reaching. Thus, under this hypothesis older adults moved slower because they valued the reward less. In this case, the two groups differed not in terms of their effort costs, but because of differences in evaluation of reward and differences in accuracy (Fig. 3D). We imagined that in older adults, reward α was devalued (represented by $k\alpha$, where $k < 1$; Eq. 7), reach accuracy was as measured, but the cost of reaching was the same as in the young adults. Reward devaluation was sufficient to produce the reduced reach speeds and longer reaction times in older adults (Fig. 3D). Importantly, Hypothesis 2 predicted that in response to increased reward, both older adults and the young adults should reduce their movement duration and reaction times, but because increasing movement speed now costs the same in the two groups, older adults should focus more of the change in their reach speed, not reaction time (Fig. 3F). Thus, according to Hypothesis 2, if the slower movements in older adults were primarily a consequence of diminished reward valuation, then compared to the young, they should shorten their reach duration to a greater extent. This was the opposite of what we observed in Experiment 2.

In summary, our normative model suggests that the results of Experiment 2 are consistent with Hypothesis 1 and not Hypothesis 2. That is, when effort costs of a reach are increased, it is rational to respond to increased reward by primarily reducing reaction times, not movement times.

Increasing the effort cost of reaching in the young makes them respond to reward like older adults

The inference that arises from the model is that older adults may be reaching slower principally because they are burdened with increased effort costs. But to make a causal link between the increased effort costs and their response to reward, we thought of a third experiment: make the young experience the effort costs of older adults and see if they would now behave like older adults in responding to reward.

In Experiment 3, we explicitly manipulated the effort cost of reaching in the young. A new group of young participants completed a protocol like the one detailed in Experiment 2. However, they completed the paradigm twice – once with low effort (0 kg), and once with high effort (~3.63 kg/8 lbs physical mass added to the robotic arm) (Fig. 4A).

Reward had a robust main effect on all kinematic parameters, demonstrating a generalized “speeding-up” of movement. Under constant effort conditions, reward reduced reaction time [$\beta = -5.94$ ms, 95% CI (-8.71, -3.16), $p = 2.72 \times 10^{-5}$], increased peak velocity [$\beta = 2.50$ cm/s, 95% CI (2.14, 2.86), $p < 2 \times 10^{-16}$], and reduced movement duration [$\beta = -18.92$ ms, 95% CI (-24.80, -13.04), $p = 5.73 \times 10^{-10}$] (Fig. 4B–F).

Effort also had a significant main effect on all movement characteristics, tending to slow down reaches (Fig. 4B–F). For a given reward state, on average, effort increased reaction time ($\beta = 7.44$ ms, 95% CI (5.48, 9.40), $p = 1.08 \times 10^{-13}$), decreased peak velocity ($\beta = -5.00$ cm/s, 95% CI (-5.26, -4.75), $p < 2 \times 10^{-16}$), and increased movement duration ($\beta = 48.96$ ms, 95% CI (44.80, 53.12), $p < 2 \times 10^{-16}$) (Fig. 4B–F).

When responding to rewarded targets, subjects reduced their reaction time by $\Delta_{\text{low}} = 5.94 \pm 1.413$ ms in the low effort condition, less than the $\Delta_{\text{high}} = 8.22 \pm 1.413$ ms reduction that was present in the high effort condition. In the high effort condition, compared to

the low effort conditions, subjects quickened reaction times just as much, if not more to reward [reward by effort interaction, $\beta = -2.28$ ms, 95% CI (-6.20, 1.64), $p = 0.254$] (Fig. 4B,D).

In contrast, a significant interaction modulated the peak velocity's response to reward in the presence of effort [reward by effort interaction, $\beta = -1.29$ cm/s, 95% CI (-1.80, -0.78), $p = 3.16 \times 10^{-6}$]. This suggests that the increase in reach speed when responding to reward was mitigated by effort. In the low effort condition, the peak velocity increased by $\Delta_{\text{low}} = 2.50 \pm 0.184$ cm/s toward a rewarded target as compared to its nonrewarded counterpart (38.51 cm/s nonrewarded compared to 41.01 cm/s rewarded). In the high effort condition, the increase in the peak velocity was smaller, at $\Delta_{\text{high}} = 1.21 \pm 0.184$ cm/s, when compared to its nonrewarded counterpart (33.507 cm/s nonrewarded compared to 34.72 cm/s rewarded) (Fig. 4C,F). Similarly, in response to reward, movement duration reduced to a greater extent in the low effort ($\Delta_{\text{low}} = 18.92 \pm 2.998$ ms) compared to the high effort condition ($\Delta_{\text{high}} = 14.62 \pm 2.996$ ms), although the interaction did not reach significance (Fig. 4E; reward by effort interaction, $\beta = 4.30$ ms, 95% CI (-4.01, 12.61), $p = 0.311$). Thus, the increase in movement speed when responding to reward was mitigated by effort.

In summary, when we made the movements of the young adults more effortful, they seemingly shift reward sensitivity toward reaction time responsiveness, possibly because reducing reaction time incurs a lower energetic cost than reducing movement duration. These results mirror what was seen with older adults and our theoretical predictions, suggesting that, to obtain reward when movement is effortful, increases in vigor begin to favor faster reaction times over faster movement times (Fig. 4G).

Discussion

We found that the metabolic cost of reaching was elevated in older adults, implying that it was energetically advantageous for them to move slower. But is this increased effort cost a causal factor in the slowing of movements in the older adults? To explore this question, we presented young and older adults an opportunity to acquire reward. Both groups responded by decreasing their reaction times. However, only the young adults increased their reach speed. To ask whether this was a rational economic response, we used a computational model of reaching in which the objective was to maximize the total rewards acquired, minus the efforts expended, divided by time. According to this model, when effort costs were increased, it was rational to respond by primarily reducing reaction times, not movement times. To test the predictions of the model, we tried to make the young experience the effort costs of the older population – we added a mass to their hand – and again measured their response to reward. Now the young adults responded to reward like the older adults, principally through reduced reaction times, not movement times. Thus, the reduced movement speed in the older adults, as well as their reluctance to increase this speed in response to reward, may be a rational economic response to an increased metabolic cost of reaching.

Metabolic rate of reaching is elevated in older adults

We found that like the young adults (Shadmehr et al., 2016), in the older adults the energetic expenditure of reaching grew larger with distance and speed. However, for a given speed and distance, older adults expend greater amounts of energy to reach than the young. Similar age-dependent findings have been observed in walking. As we age, we adopt slower walking velocities which are correlated with overall greater energetic costs (Martin et al., 1992; Waters et al., 1988; Jones et al., 2009).

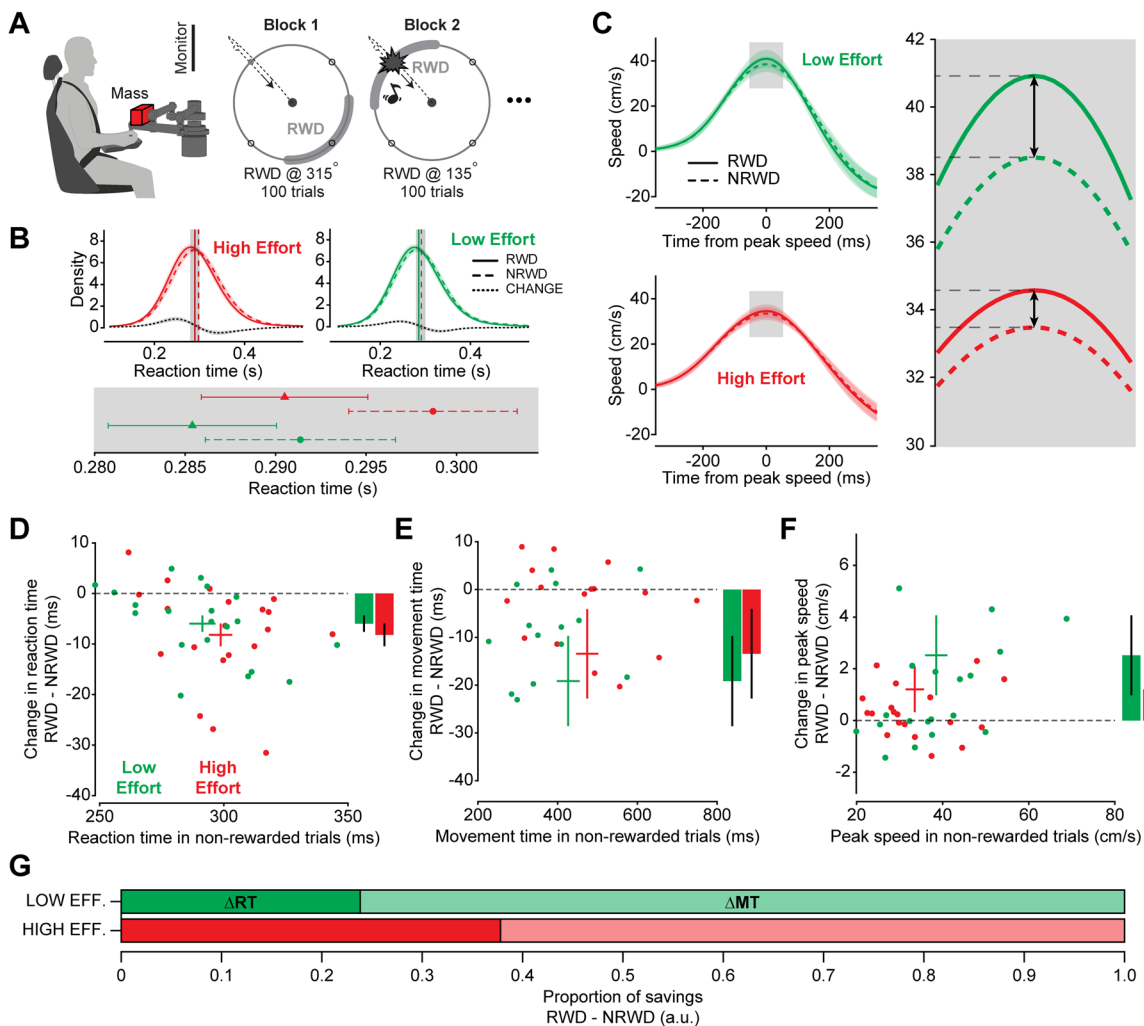


Figure 4. Increased effort slows movement and reaction times in young adults, and mitigates effect of reward on movement speed (Experiment 3). **A**, Design for Experiment 3. Participants performed out-and-back reaches to alternating targets projected along a ring 10 cm from the home circle. The paradigm was like that of Experiment 2, except visual feedback of the cursor was maintained for the duration. Participants performed this protocol twice, once with no added mass (0 kg) to the handle of the robot, and once with 3.63 kg/8 lbs added mass. **B**, Nonparametric kernel density estimation for the probability distribution reaction times when making movements to rewarded (RWD, solid curves) and nonrewarded (NRWD, dashed curves) quadrants as well as a difference (dotted curve) in these distributions at each bin (bin size = 5 ms). Low effort (green curves) movements were initiated earlier than high effort (red curves), reward reduced reaction times in both groups. **C**, Effects of reward on peak speed in low (green) and high (red) effort conditions. Speeds requiring low effort were overall faster than high effort. Rewarded movements had higher peak speeds regardless of effort (RWD, solid curves) compared to nonrewarded (NRWD, dashed curves). **D–F**, Scatter plot representing the relationship between nonrewarded (NRWD, horizontal axis) and the difference between rewarded and nonrewarded (RWD–NRWD, vertical axis) reaction time (**D**), movement duration (**E**), and peak speed (**F**). Dots represent individual participants. The intersection at each cross represents the mean for each age group and the length of the bars represents \pm SEM. The mean effect of reward for each age group is indicated with the inset bar graph, reported as mean \pm SEM. **G**, Proportion of time savings due to reaction time (RT) and movement time (MT) in low versus high effort (Experiment 3). The proportion of time saved by reacting faster is larger when effort is higher.

The elevated cost of reaching in older adults may arise from several factors. The skeletal muscle mitochondria may experience a reduction in their capacity to generate the needed ATP and a reduction in the efficiency with which they convert oxygen to ATP. Coen et al. (Coen et al., 2013) showed that both mitochondrial capacity and efficiency are reduced with age and correlate with preferred walking speed; reduced mitochondrial function predicted slower preferred walking speeds. Older adults may have also made reaches with greater levels of muscle coactivation, despite extensive familiarization with the task. Increased coactivation may also lead to greater energetic costs (Huang et al., 2012; Huang and Ahmed, 2014).

Here, we considered absolute energetic costs, but it is possible that individuals consider costs relative to their aerobic capacity. Similar to absolute energetic expenditure, aerobic capacity has also been demonstrated to be lower in older adults (Fiser et al.,

2010; Coen et al., 2013). Thus, irrespective of both the demonstrated age-related increases in absolute energy cost and the possible reduced aerobic capacity, we would predict slower movements and a reduced willingness to respond to reward.

We did not consider the possibility that there is a subjective, age-dependent inflation in the cost of effort, providing an additional explanation as to why older adults were not willing to adjust their movement speed. While the dopaminergic midbrain has long been a target for the coding of reward value (Schultz et al., 1997; Tobler et al., 2005), there is more recent evidence suggesting that dopamine release rises in anticipation of higher task effort (Varazzani et al., 2015). Wardle et al. (2011) were able to identify a positive association between an individual's level of activity in dopaminergic regions and their willingness to exert effort for a given reward. Similarly, individuals with decreased dopaminergic tone, such as those with Parkinson's disease

(PD), show a heightened sensitivity to effort (Mazzoni et al., 2007; Schmidt et al., 2008; Chong et al., 2015). Dopamine release in the moments before movement onset increases speed of the ensuing movement (da Silva et al., 2018), and greater amounts of dopamine are released during movements that require greater effort (Varazzani et al., 2015). This dopaminergic response declines as a function of aging (Dreher et al., 2008; Chowdhury et al., 2013), suggesting that both reward valuation and the willingness to invest effort may be impaired, ultimately leading to reduced movement speed. Overall, our results implicate effort costs but cannot dismiss contributions from heightened effort sensitivity.

Individuals relied on reaction time to obtain the more effortful reward sooner

When reaching costs increased – either through higher metabolic cost in the older adults or through increased mass on the arm of the younger group – we observed a change in the strategy to obtain reward. Though reaction times and movement speeds were on average slower in the higher effort condition (Nagasaki et al., 1983; Stelmach and Worringham, 1988; Reppert et al., 2018), in response to increased reward people decreased reaction times to a greater extent than movement speed. To understand this, we considered a model (Eq. 6) in which both standing still, and moving, expended energy, but at different rates (baseline metabolic rates during standing still and elevated rates during moving). The model demonstrated that when the cost of moving increased, it was a good policy to respond to reward by reduced reaction times, as compared to movement times, consistent with our observations in both groups of subjects.

These results shed light on a recent PD study from Kojovic et al. (2014), in which they investigated performance in a rewarded reaction time task for patients on and off dopaminergic medication. When successful performance was monetarily rewarded, PD patients and healthy controls quickened reaction time irrespective of medication state. However, only PD patients in the on-state quickened movement time in response to reward (those in the off-state did not). The PD patients, in whom metabolic costs of movement tend to be higher (Christiansen et al., 2009), reacted more quickly to obtain reward, but only moved more quickly for the same reward when supplemented with additional dopamine. However, others have found that modulation of vigor with reward was maintained in both healthy older adults and individuals with PD (Tecilla et al., 2023). Movement times were measured as the average inter-key press interval, and were faster in both groups to greater expected reward. Here, we focus on movement peak velocity, a metric we have confirmed correlated with greater energetic expenditure. Thus, it is possible that shorter inter-key press intervals do not exact the same increase in energetic cost that would bias older adults to avoid faster movement times.

Reducing reaction time carries a cost of accuracy

While reducing reaction time, rather than increasing movement speed, emerges as an optimal strategy to respond to increased reward in high effort environments, it nevertheless carries a risk. In our model of utility (Eq. 7), we included a speed–accuracy tradeoff on reaction time (Eq. 10). Previous work has suggested that the time before a movement can be separated into two independent phases: a preparation and an initiation phase (Haith et al., 2016; Hardwick et al., 2019). While movements can be prepared rapidly, likely in the primary and premotor cortices, there

is often a delay in their initiation. In the rewarded reaching task, if individuals were to initiate movements before they were adequately prepared, the odds of accurate target selection are near chance (Fig. 3A); but if individuals delay movement initiation, the probability of moving to the correct quadrant rapidly increases toward certainty (Haith et al., 2016).

Increased effort cost of a planned movement has a robust effect on increasing the reaction time of that movement (Sheridan, 1984; Ivry, 1986; Shadmehr et al., 2016; Yoon et al., 2018). If we take the reaction time measured here as a sum of the preparation and initiation times, then reaction times could be lengthened by slowing either or both processes. Aging accompanies a degeneration of the nigrostriatal dopamine system, and accordingly reduced striatal dopamine transporter availability has been correlated with the slowing of reaction time in older adults (van Dyck et al., 2008). Additionally, older adults see decrements in neuromuscular properties of muscle, synaptic integrity, and a number of motor units, which have been linked to reaction time slowness (Lewis and Brown, 1994). Thus, in older adults, evidence points to slowing in both higher-level preparation and peripheral initiation contributing to their slowed reaction times.

Younger adults, when faced with increased mass and higher effort movements, may also experience slower reaction times because of changes in preparation and initiation. With higher force movements, Nagasaki et al. (Nagasaki et al., 1983) found that both “premotor” (i.e., preparation) and “motor” (i.e., initiation) reaction times increased, suggesting that higher forces demand increased central processing time for movement organization alongside increased time for developing the appropriate muscle tension to begin moving.

Lastly, the possibility remains that movements could have been prepared with the same rate in our experiment, but a delay in initiation reflected a more risk-averse strategy. For example, PD patients are often more impulsive and may compensate for slower velocity saccades by a reduction in latency; however, these shorter latency saccades result in higher rates of inaccuracy and error (Fookien et al., 2022). In other words, PD patients may be engaging with riskier, more impulsive, reaction times to compensate for slowness. Neurologically healthy individuals who do not exhibit impulsivity may be increasing the delay between preparation and initiation, especially if the effort required is higher, to ensure that the movement will be successfully executed toward the correct target, avoiding unnecessarily wasted energy (Symmonds et al., 2010; Haith et al., 2016).

Learning of stimulus value

Healthy aging coincides with a decreased ability to learn the value of a stimulus from its history of reward (Eppinger et al., 2011). This raises the possibility that in the older group, their reluctance to increase speed of reaching may have been due to a reduced ability to learn the value of the stimulus. However, we found that in response to the rewarding stimulus, older participants decreased their reaction time by amounts comparable to the young. This suggests that lack of reward-dependent modulation in reach speed was not because of a deficit in learning value of the stimuli.

Older and young adults executed movements similarly toward nonrewarded quadrants

In Experiment 2, while older adults on average made slower reaches, we found no significant differences between the two groups when selecting peak speed in the absence of reward.

These findings go against previously reported observations showing an age-dependent decrease in execution across a range of representative movements (Waters et al., 1988; Ketcham et al., 2002; Kozak et al., 2003; Laufer, 2005; Irving et al., 2006; Welsh et al., 2007; Huang and Ahmed, 2013; Dowiasch et al., 2015; Van Halewyck et al., 2015; Kitchen and Miall, 2018; Healy et al., 2023). When making pointing movements, individuals adjust the speed of their movements according to the size and amplitude of the endpoint (Fitts, 1954). Ketcham et al. (2002) reported that when reaching toward targets of decreasing size, older adults were slower and less accurate than young and were less willing to adjust the speed of their movements in response to changing task difficulty. Van Halewyck et al., (2015) had young and older adults make wrist flexion movements according to different instructions and with changing feedback. In one condition, they were given visual feedback via a cursor and asked to move that cursor as quickly as possible to the center of a target. Under these constraints, older adults made slower and less continuous movements when compared to the young adult group. In a second condition, the researchers removed visual feedback of the cursor and instructed the participants to move the invisible cursor as fast as possible through the target. In this second condition, they found that older adults were able to make movements that were equally as fast and with similar variability as the young adults, suggesting that the decreased speed in reaching exhibited by older adults when given full visual feedback was not due to an inability to reach faster but was rather a result of a change in movement strategies aimed at minimizing accuracy costs.

To best capture the relationship between effort and reward, it was vital that we minimized the cost of accuracy. The quadrants used in our experiments were of a very large size that allowed for a minimal influence of accuracy constraints. We also attempted to minimize error by removing visual feedback of the cursor during the outward portion of the movement. As long as the movement was directed toward the correct quadrant, no amount of naturally occurring signal dependent or independent noise would cause a trial to fail. These two combined factors allowed us to mitigate the cost of accuracy and instead isolate how effort and reward interact to establish vigor in older adults. They may have also mitigated the magnitude of age-dependent effects on movement speed.

Limitations

The reward used in this study was binary. Either a reach resulted in delivery of the reward or no reward at all. Because of this design, we are unable to comment on whether an effect of reward was present, but just too small to detect, on reach speed of older adults.

A few studies suggest that animals change behavior not just because of a change in reward quality, but also a change in reward rate (Haith et al., 2012). This means that the reward landscape can be additionally manipulated by changing the frequency of reward, either by changing the relative number of rewards, or the amount of time elapsed between trials. A similar constraint implemented with older adults could further explain how they consider changing reward when establishing movement vigor.

We did not determine the exact energetic costs of moving faster with more effort. Changes in movement vigor were quantified in terms of absolute differences in movement duration and reaction time, in which we saw reductions in both when responding to reward (Figs. 2–4). Focusing specifically on movement duration, we did not consider the exact energetic cost (in Joules) of moving x cm/s more quickly, nor did we scale the

added mass to the participant's mass or strength. That is, it remains possible that individuals were willing to allocate the same additional n Joules to gain reward in both the low and high effort environments; however, movement speeds simply increased less in the high effort condition because those additional n Joules had less of an absolute effect, or because the fixed mass was more effortful for individuals with less upper limb mass or strength.

Conclusion

We found that the metabolic cost of reaching as a function of duration and distance was elevated in older adults. As a result, the optimum reach speed, defined as the movement that maximized reward acquired minus energy expended divided by time, was slower for older adults than the young. When exposed to added reward, both young and older adults responded by decreasing reaction time. However, when executing the movement toward these rewards, only young adults increased their speed. When explicitly forced to reach with higher effort, a new cohort of young adults responded to reward like older adults: in a high effort environment, the proportion of time savings due to changing movement speed decreased while reaction time's proportion increased. Thus, the increased metabolic cost of reaching in older adults appears to be a significant contributor to age-related movement slowing.

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