

Effort cost of reaching increases with aging

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Movement vigor is influenced by both the opportunity for reward and the effort needed to obtain that reward (Shadmehr et al. 2016). As people age, they move slower: vigor declines across a broad spectrum of movements, including walking (Waters et al. 1988), reaching (Ketcham et al. 2002), and saccades (Irving et al. 2006). Is this decline due to a reduced sensitivity to reward, increased effort cost, or both? Lower dopamine levels in older adults (Dreher et al. 2008) suggest a reduced sensitivity to reward. However, the effort requirements of movement also increase with age (Martin et al. 1992). Here, we quantified metabolic expenditure during reaching as an objective measure of effort in young and aged people, and also quantified reward sensitivity in the same population. We found that while the metabolic cost of reaching increased with aging, reward sensitivity remained stable. Our results suggest that the decline in vigor with aging may be due to objective increases in energetic requirements of movement, and not decreased sensitivity to reward.

Experiment 1: Thirteen young adults (YA: 25 ± 2 years, 7F, 6M, 65 ± 12 kg) and twelve older adults (OA: 75 ± 8 years, 6F, 6M, 73 ± 18 kg) performed reaching movements across a range of speeds (Fig 1A). Speed was varied across 10 blocks, with each block consisting of a single distance (10 or 20cm) matched with one of five durations (125-2100ms). In each block, effort was quantified by measuring the metabolic rate of reaching via indirect calorimetry. For each age group, we parameterized metabolic rate j as a function of distance d and duration T : $j = a + bd^i/T^j$ (YA: $R^2 = 0.93$, OA: $R^2 = 0.93$). Using a linear mixed effects model, we probed the effect of age, distance and duration on metabolic rate. Metabolic rate increased with distance ($\beta=0.300$, $p<0.001$), and decreased with duration ($\beta=-0.599$, $p<0.001$). Importantly, metabolic rate was elevated in the older adults ($\beta=0.186$, $p=0.016$, Fig 2, upper row). We calculated the metabolic expenditure during a given movement (Fig 2, bottom row) and found the duration at which the cost was minimized. We found that the optimum duration was greater in older adults (10cm: YA 430ms, OA 530ms; 20cm: YA 585ms, OA 710ms). Therefore, the elderly expend a greater amount of energy to make a reaching movement than the young. To minimize energetic cost of reaching, older people should reach slower than young people.

Experiment 2: One of the most robust effects of reward is that it reduces reaction time of movements. To measure sensitivity to reward, we asked twenty young adults (26 ± 4 years, 10F, 10M) and twenty older adults (72 ± 6 years, 10F, 10M) to move a cursor from the center of a large circle ($r = 14$ cm) through the arc of the circle in one of four alternating 100° quadrants (Fig 1B). The protocol consisted of 4 blocks. In each block, a single quadrant was paired with an audiovisual reward. As a result, the protocol removed accuracy requirements of the movement. We compared reaction time when a quadrant was paired with reward and when that same quadrant was not rewarded. In response to reward, both young and older adults reduced their reaction times ($p's<0.001$, Fig 3). Indeed, in both groups reaction time increased in trials immediately following reward (Fig 5A,B, paired t-tests, $p's<0.001$). This suggested that the two groups showed similar sensitivity to reward. However, when *executing* movements towards reward, only the young adults increased peak velocity and maximum excursion (Fig 4, $p_{\text{peakv}}=0.044$, $p_{\text{maxex}}<0.001$; Fig 5C,D, paired t-tests, $p's<0.001$). Therefore, reaction time response of the elderly to reward was indistinguishable from the young. However, in elderly, reward had little or no effect on reach vigor.

Conclusions: We found that in older adults, the metabolic cost of reaching was greater and the metabolically optimal reach duration was slower. These results indicate that previous reports of age-related movement slowing may in part be explained by increased effort costs. We also found that while reward led older adults to *initiate* movements faster, they did not *execute* these movements faster. Together, these findings suggest that young and older adults are equally sensitive to reward, but the elevated effort to execute the reaching movement may partially explain older adults' slower movements, and their reluctance to adjust vigor in response to opportunity for reward.

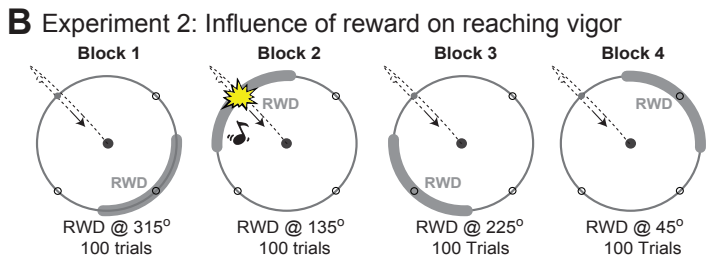
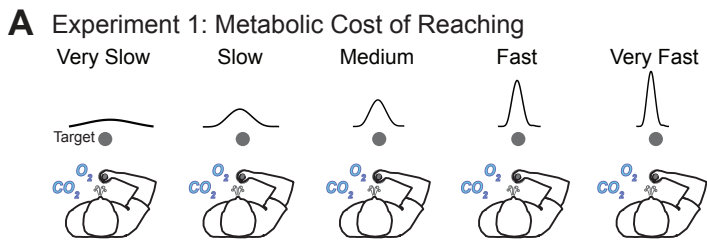


Figure 1. Protocols. A. Experiment 1: Metabolic rate was measured while individuals completed ten blocks of reaching, each across five constrained durations. B. Experiment 2: Individuals reached to alternating quadrants over four blocks. Within each block, one quadrant was consistently paired with reward. Reward location switched location at the start of each new block.

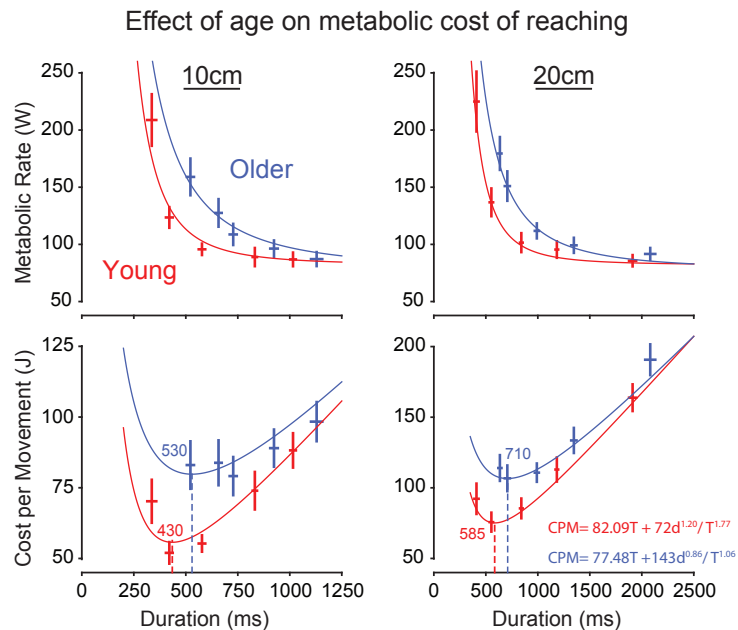


Figure 2. Metabolic rate (top) and cost per movement (CPM, bottom) of reaching for young (red) and older adults (blue) at 10 and 20cm. Dashed lines in CPM plots indicate durations at which CPM is minimized.

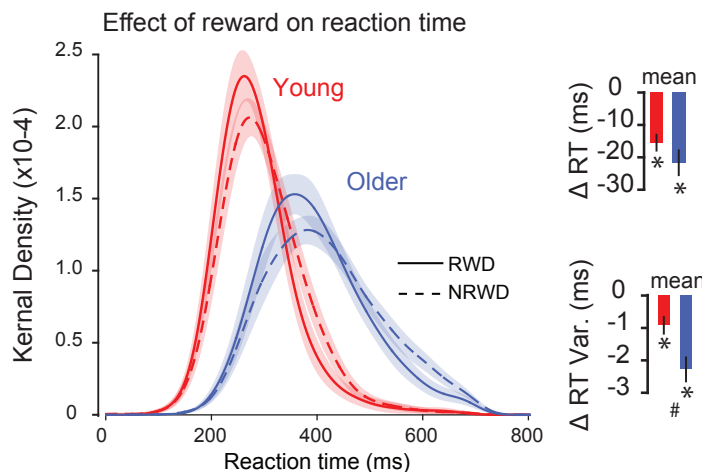


Figure 3. Effect of reward on movement initiation. Curves represent non-parametric kernel density estimations of reaction time for rewarded (solid) and non-rewarded (dashed) trials in young (red) and older (blue) adults. Bin size = 5ms. Insets: change in reaction time (RT) mean and variance (rewarded minus non-rewarded). * $p < 0.05$ between mean and zero, # $p < 0.05$ between groups.

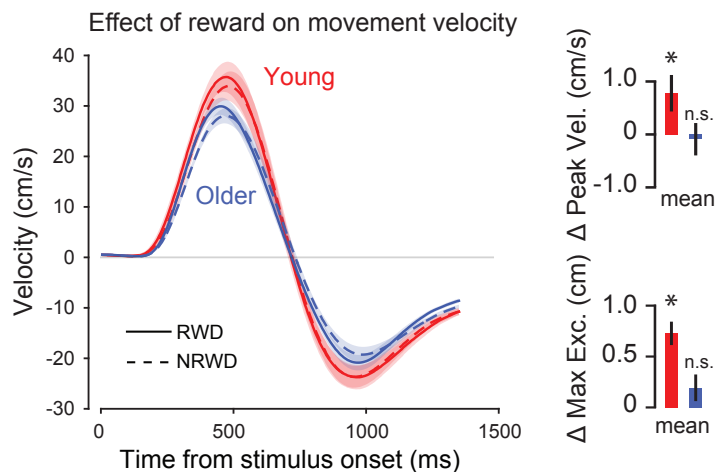


Figure 4. Effect of reward on movement execution. Curves represent average velocity profiles for rewarded (RWD) and non-rewarded (NRWD) movements in young (red) and older (blue) adults. Insets: change in mean peak velocity (vel.) and maximum excursion (max exc.) due to reward (rewarded minus non-rewarded). * $p < 0.05$ between mean and zero, n.s. not significant.

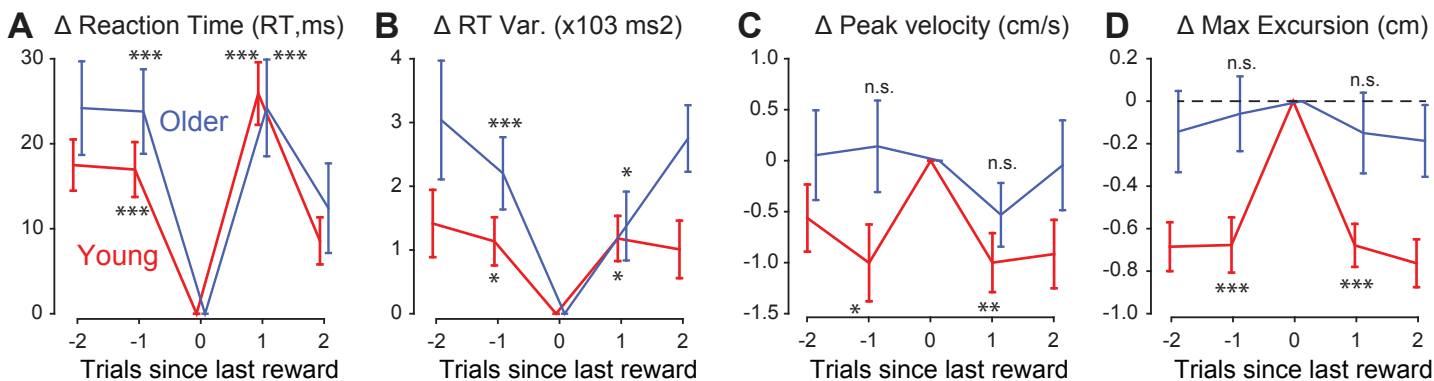


Figure 5. Reward effects relative to surrounding non-reward movements for young (red) and older adults (blue). Movement initiation for both young and older adults was earlier (A) and more consistent (B) in rewarded compared to non-rewarded trials immediately preceding reward. Following reward, movement initiation returned to non-rewarded levels. Reward influenced movement execution (C,D) in young adults when compared to surrounding non-rewarded movements. There was no effect of reward on either peak velocity or maximum excursion in older adults. RT=reaction time, Var.=variance, n.s.=not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$