AGE-RELATED DIFFERENCES IN MOTOR ADAPTATION: INVESTIGATING HABITUAL MOVEMENT PATTERNS AND PERFORMANCE IN OLDER AND YOUNGER ADULTS

by

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With aging comes physiological changes in the brain, affecting key regions involved in motor adaptation, including the cerebellum, basal ganglia, and hippocampus. These changes diminish the brain's capacity for flexible motor learning, leading to difficulties in adapting motor behavior to changing environments. We hypothesized that older adults rely more on habitual movement patterns, thereby exhibiting slower motor adaptation rates and increased motor errors. To test this hypothesis, we conducted an experiment where both older and younger participants were tasked with lifting a symmetrical object with a hidden asymmetric mass (i.e., one side is heavier than the other), that switches from side to side, aiming to keep it level. To achieve task success requires generating a compensatory torque at lift onset that is equal and opposite to the object's torque. During the experimental block, the object's mass distribution alternated between sides to assess participants' task performance across successive trials, requiring generalizing and matching the object's torque in multiple directions. In contrast to our hypotheses, our results indicate suboptimal generalization by both older and younger adults. Neither group adapted optimally to the desired level of task proficiency, failing to generate sufficient compensatory torque by the end of experimental block. Given this mutual inability to reach optimal performance, we cannot definitively assert that older adults exhibit slower motor adaptation compared to their younger counterparts. Nonetheless, we observed habitual tendencies for the older adults in how they controlled and adjusted their movements, which supports the idea of older adults relying on established motor patterns.

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INTRODUCTION

Motor behavior, which encompasses the planning, execution, and regulation of voluntary movements, impacts various aspects of daily life and development and is an essential component of human functionality overall (Adolph & Franchak, 2017). Adjusting motor behavior in response to a changing environment is necessary to successfully interact with the world. Motor adaptation can be defined as the capacity of individuals to fine-tune their motor behavior in response to changing situations, allowing them to learn new tasks, modify existing skills, and reconfigure movements to suit specific environments (Rossi et al., 2019). As we age, the ability to adjust our movement deteriorates, impeding activities of daily life. This can manifest as tripping, spilling, or bumping into objects unintentionally, increasing the risk of falls and overall health issues (Wolpe et al., 2016).

The motor system deterioration in older adults' results from factors like muscle loss (sarcopenia) (Volpi et al., 2004), sensory decline (Völter* et al., 2021; Swenor et al., 2020), and compromised proprioception - our sense of body position (Ferlinc et al., 2019). Despite numerous therapies targeting these motor system deteriorations (Walter, 2022; Brach & VanSwearingen, 2013; Carmeli, 2017), older adults are still making motor errors. While some studies have shown improvement in helping older adults with motor function, others have recommended non-physical approaches like cognitive training and motor imagery for older adults when physical therapies are limited or ineffective in addressing motor errors (Marusic et al., 2018). This suggests there are likely multiple factors contributing to the slower adaptation rates observed in older adults which need to be considered for treatments to be maximally effective.

Age-related difficulties in adjusting motor behavior may stem from their inclination toward more rigid and stereotypical behavior patterns in motor tasks (Wolpe et al., 2020; King et al., 2013; Lee & Ranganathan, 2019; Anguera et al., 2012; Sombric et al., 2017). Older adults tend to rely heavily on familiar movement patterns rather than embracing new strategies or modifying their movements in response to situational changes, reflecting ingrained habitual motor responses. Such ingrained habitual responses have been shown to directly impact motor behavior adaptation, independent of sensory input (Sager et al., 2024). Examples of these habitual tendencies include consistently higher grip forces (Voelcker-Rehage & Alberts, 2005), simultaneous activation of agonist and antagonist muscles (Kubota et al., 2023), and reduced

differentiation in brain activity during task execution (Carp et al., 2011; Zapparoli et al., 2022).

However, the understanding of age-related motor adaptation is not without its complexities. Research yields conflicting findings, with some studies suggesting that older adults adapt motor behavior more slowly than younger adults, while others propose they may adapt similarly. Additionally, factors such as task complexity, novelty, cognitive intactness, and motivation to succeed can significantly influence adaptation rates, indicating that the specific context of each study can lead to varied results.

In this study, we aim to determine whether heightened habitual tendencies contribute to age-related motor errors by examining how participants perseverate on their initial motor strategies. Our experiment compares adaptation rates between older and younger participants using an object manipulation task where participants must lift an object with a hidden asymmetric mass without allowing it to tilt. This task relies on internal predictive models since sensory feedback of the key object property only becomes available after lift onset. In a critical manipulation, we switched the asymmetric weight from side to side, with participants being aware of when the switch occurs, in blocks of trials and measured the rate at which both age groups learn to generalize the ideal torque in both directions (e.g., clockwise, and counterclockwise when the mass is on the left and right, respectively). We hypothesize that older adults rely heavily on habitual behaviors, resulting in slower adjustments to motor behavior compared to younger adults, which ultimately leads to increased motor errors. If participants are perseverating (due to habitual tendencies) on the previous lift (which was on the opposite side of the object), they would fail the task.

Typically, healthy adults exhibit greater flexibility and adaptability in modifying their movements, showing a willingness to experiment with new strategies like adjusting their digit positioning. However, research suggests that even younger adults, like older adults, exhibit habitual tendencies during initial learning stages (Zhang et al., 2010). Although both age groups should initially replicate their initial motor behavior, older adults may require more time to revise their predictive models and adjust their behavior accordingly compared to younger adults. A slower achievement of success in the task would suggest a diminished rate of adaptation, possibly indicative of habitual motor behavior in older adults.

METHODS

Participants

Thirty healthy younger adults (10 males and 20 females) and thirty healthy older adults (14 males and 16 females) participated in this study. The mean age of the younger adult group was 22.7 ± 4.9 , and the mean age of the older adults was 71.4 ± 5.23 . The younger adults were recruited from the university undergraduate and graduate student population. The older adults were recruited from the community, and all were screened for eligibility to participate. All participants were able to understand and follow instructions, were independent in their mobility, had normal or corrected to normal vision, and the older participants all passed The Montreal Cognitive Assessment (MoCA) as a cognitive screening tool. Subjects scoring a 25 or lower on the MoCA exam were excluded from the study (n = 2), showing that they might have a mild cognitive impairment. They all signed a written informed consent approved by the University of Oregon's Institutional Review Board.

Materials, Design, and Procedure

We designed an object manipulation task requiring learning to generalize movements to minimize the roll of an asymmetrically weighted object, its mass of which moved from side to side. This setup was chosen to investigate if heightened habitual tendencies could explain the motor errors related to age. This task serves as an ideal platform for exploring how ingrained habits impact motor behavior, leading to a slower adaptation rate on this task. By switching the weight of the object, with participants aware of when the switch occurs, we create a scenario where participants could adhere to their initial motor strategies, offering valuable insights into the influence of habits and stereotyped behavior on motor performance across different age groups. If participants were unable to adjust their motor behavior to successfully lift our disproportionately weighted object, they would persist in using the same motor behaviors, thereby hindering performance improvement. Our aim was to assess how rapidly participants could adapt their movements to lift the object without tilting it when the weight shifted.

An upside-down T-shaped object was used for participants to handle, crafted through 3D printing with chopped carbon fiber containing nylon material (onyx, Markforged). The object featured gray grasp surfaces on its vertical leg (width: 5 cm; height: 9 cm; depth: 3.2 cm) for the participants to hold on both sides (height: 7.4 cm; width: 4.5 cm; depth: 0.8 cm; between grasp

distance: 8.2 cm). The depth dimensions of the gray grasp surfaces were slightly greater than the diameter of the transducer surfaces (limiting the opportunity to cause torque in a horizontal direction). A lead cylinder (height: 4.5 cm; diameter: 3.8 cm; mass: 490 g) hidden within the horizontal base of the T-shaped object (height: 5.6 cm; width: 4.9 cm; depth: 18.3 cm) facilitated weight changes. The total mass of the object was 936 g with an external torque of 260 Nmm.

Participants were instructed to sit upright in a chair, facing a table with their legs uncrossed and arms resting on their lap. They were briefed on the objective of the experiment: to perform natural reaching, grasping, and lifting movements with a T-shaped object. They were informed that the object would have an uneven weight distribution, and their task was to lift it without causing it to tilt to one side. To achieve this, they needed to apply a compensatory torque force equal to the 260 Nmm torque exerted by the object. Participants were instructed to ensure that their index finger could comfortably rest on a button placed in front of them, with their forearm and upper arm forming a right angle. If needed, a seat cushion was provided to adjust the seating position.

In our experiment, participants were seated facing a table with the T-shaped object positioned in the center. They were instructed to maintain pressure on a button with their index finger and await a recorded cue indicating the heavier side of the object. Then, an audio 'go' cue would sound 1.25 seconds after the weight distribution cue, instructing participants to lift their index finger from the button and reach for the object grasp surfaces (20 cm from the button) using only their index finger and thumb. They were directed to lift the object to a specified height marker (11 cm), hold it in the air until a subsequent cue (2.5 seconds after the go cue), return it to the table surface, and then place their index finger back on the button.

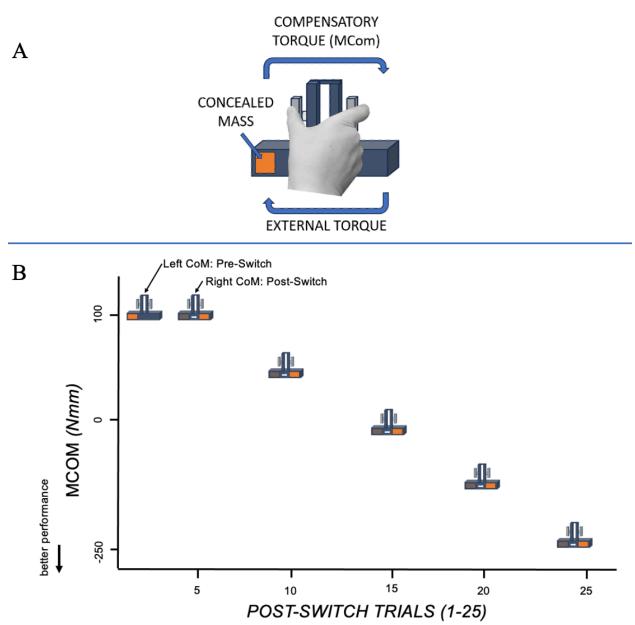


Figure 1: **Task and Design.** (A) The illustration depicts the T-shaped object with a concealed center of mass (CoM), where the task objective is to minimize tilt by generating a compensatory torque (MCom) in the opposite direction of the object's external torque. (B) We shifted the center of mass from the pre-switch trial (left in the example) to the post switch trial (right in the example) across 100 total trials. Our primary focus was on the 25 post-switch trials, during which we examined how both groups adapted their motor behavior to enhance performance, aiming to generate a compensatory torque of -250 Nmm. The example shows learning to generalize the torque over several switches, with Mcom reaching an optimal magnitude, matching the object's torque, by the 25th post-switch trial.

Participants completed a sequence of pre-switch trials, followed by a single post-switch trial (Figure 1B). Our primary focus was on evaluating participants' motor behavior adjustment following the transition of weight distribution (post-switch trial). Specifically, we aimed to investigate how their performance evolved with each subsequent post-switch. We varied the

number of times the trial was repeated (1, 2, 3, 4, 5) when lifting the object before changing the mass distribution to the opposite side. Each participant completed 25 post-switch trials (100 total trials with all the pre-switches included), with 2 initial practice trials provided, and breaks given after every 20 trials. We chose to focus on the post-switch trials with the mass in the less familiar condition (right side in Figure 1) rather than the practiced condition (left side in Figure 1). Participants had significantly more pre-switch trials (75) compared to post-switch trials (25), giving them more experience with the pre-switch lifts. This would allow both groups to perform much better when the center of mass was on the pre-switch side. We specifically wanted to examine their adaptation rate when the center of mass switched to the other side, as this was the new condition that both groups had not practiced. We aimed to observe how participants adapted their motor behavior over the 25 post-switch trials to achieve a –250 Nmm compensatory torque to counteract the object's external torque.

Force/torque transducers (Mini27 Titanium, ATI Industrial Automation, NC) measured grip forces and torque on the grip surfaces. A three-camera motion tracking system (Precision Point Tracking System; Worldviz) with a frame rate of 150 Hz, camera resolution of 1,280 \times 1,024 VGA, and two near-infrared LED markers measured object lift and tilt. These cameras provided precise spatial accuracy within a 3 \times 3 \times 3 m volume, accurate to within 1 mm. A python script was used for task execution and data recording, including behavioral timestamps, motion tracking, and force data (when the object moved and how much force was applied). LED markers were attached to the covers of the object's horizontal base. The collected data underwent filtration via a fourth-order low-pass Butterworth filter with a cutoff frequency set at 5 Hz.

Data Processing

We defined the onset of the lifting action as the moment when the object's vertical position rose above 1 mm and remained at or above this threshold for a duration of 20 samples. The force/torque transducers were employed to gather outcome measures for both the thumb and index finger sides:

1) The compensatory moment, denoted as Mcom, occurs at the initiation of lifting, and represents the anticipatory torque produced by the digits (Nmm), as a response to the external torque exerted by the object. We calculated Mcom using the following formula:

$$M_{\rm com} = (LF_{\rm diff} \times (d/2)) + (GF_{\rm mean} \times COP_{\rm diff})$$

Here, *d* represents the width between the two grip surfaces, which is 8.2 cm. A positive value of Mcom indicates a clockwise moment, whereas a negative value of Mcom signifies a counterclockwise moment.

2) The center of pressure (COP) is a metric characterizing the positional arrangement of the digits on the grip surface, pinpointing the point where each digit contacts the surface relative to the center of the transducer (mm). We computed this using the following formula:

$$\text{COP}_{\text{digit}} = (T \boldsymbol{x}_{\text{digit}} - (\text{LF}_{\text{digit}} \times \text{grip surface thickness})) / \text{GF}_{\text{digit}}$$

In this equation, "Tx" represents the torque generated by each digit on the grip surface in the frontal plane (Nmm). The thickness of the grip surface was 0.8 cm, and "GF" stands for the digit grip force at the initiation of lifting, which is the normal force component generated by each digit and measured in newtons (N).

The difference in COP between the thumb and index finger, denoted as COP_{diff} , describes the vertical distance between digits and is calculated as follows:

$$COP_{diff} = COP_{thumb} - COP_{index}$$

Positive values of COP_{diff} indicate a higher position of the thumb's COP compared to the index finger's COP (typically observed when manipulating an object with a left CoM. Conversely, negative values indicate a higher position of the index finger's COP compared to the thumb's COP (typically observed when manipulating an object with a right CoM). The magnitude of COP_{diff} indicates the degree of asymmetry in the grip configuration, with larger absolute values indicating a more asymmetric grip, while a value of zero signifies a symmetric grip configuration.

3) The average grip force (denoted as GF_{mean}) represents the immediate mean value of grip force for each digit at lift onset. This was determined through a numerical averaging approach as follows:

$$GF_{mean} = (GF_{thumb}) + (GF_{index})/2)$$

4) Lift force difference (LF_{diff}) at lift onset represents the sideways force exerted by each individual finger, measured in newtons (N).

Lift force difference
$$(LF_{diff}) = LFthumb-LFindex$$

A positive LF_{diff} value indicates greater force exerted by the thumb compared to the index finger, while a negative value suggests the opposite. Higher absolute values signify a more imbalanced distribution of lifting force, while a value of zero signifies an equal distribution of lifting force.

5) The load phase is the duration starting from when the net lift force surpasses 0.2 N and continues to rise for 20 samples until the onset of lifting.

6) The reach phase refers to the duration between releasing the keyboard button and the subject's grasp of the object.

To accommodate the center of mass (CoM) shifting from left to right or vice versa, adjustments were made in the dataset. Participants who initially encountered the task with the CoM on the right had their Mcom, COP, and LF values multiplied by -1. This correction ensured consistency across all subjects and groups, avoiding statistical complications arising from varying signs of Mcom when handling an object with a left versus a right CoM. A negative Mcom, approaching or matching the object's external torque on post-switch trials, indicated successful torque generation, minimizing roll. Similar adjustments were made to COP and LF values to maintain accuracy and consistency in data analysis. A positive COP value indicated aligned thumb and index finger positioning, while a negative COP value suggested non-aligned finger placement. A successful post-switch lift typically resulted in a negative COP value. Additionally, a more positive LFdiff indicated a successful post-switch lift.

Data Analysis

We compared how older and younger adults adapted their motor behavior to successfully lift an object with an asymmetric weight that switches from side to side. This involved analyzing compensatory torque (Mcom) following center of mass switches throughout a task block using a two-way ANOVA, with age (younger, older) and post-switch number (switch 1, 2, 4, 6, 8, 16, and 25) as factors. We selected these trial numbers to emphasize the significance of the beginning post-switch trials (where most of the adaptation should be made) and then doubled each subsequent number for comprehensive analysis. Significant effects of switch number on Mcom were followed up with post hoc tests to identify which specific post-switch trials are significantly different from post-switch 25, and adjusted alpha-level to account for multiple comparisons. Additionally, we assessed the effect of motor adaptation and age on various factors that contribute to Mcom performance (GFmean, LFdiff, COPdiff), as well as key phases of movement (reach phase and load phase). We examined the effects of age (younger, older) and post-switch number (switch 1 and 25) on each of these outcome variables. Finally, we conducted post hoc tests on the factors influencing Mcom performance, revealing a significant effect of switch number.

RESULTS

We conducted an experiment where older and younger participants had to lift a symmetrical object with a hidden asymmetric mass that shifted sides, with the goal of keeping it level. If slower adaptation rates were observed in older adults, this could be attributed to their stereotypical motor behavior. In the experiment, participants lifted an inverted T-shaped object with a concealed asymmetric weight to minimize tilt. To accomplish the lifting task, participants needed to produce a compensatory torque of -250 Nmm to offset the object's external torque. We compared age-related motor adaptation by analyzing performance enhancements over subsequent post-switch trials for both age groups. However, our findings reveal that neither age group managed to achieve a -250 Nmm compensatory torque, suggesting insufficient adaptation in motor behavior.

Figure 2 illustrates performance in generating a compensatory torque (Mcom) of sufficient magnitude and direction from the first to the last post-switch trial (trials 1, 2, 4, 8, 16, and 25), in both the older and younger groups. Both groups increased performance in the lifting task with increasing post-switch trial number, progressively approaching a -250 Nmm torque by the end of the block. However, neither group achieved the target performance of -250 Nmm. This improvement aligns with a significant effect of switch number (F(5, 145) = 0.56, p < 0.56) 0.0001, $\eta p = 0.26$), indicating improvement in generalizing Mcom in multiple directions over successive post-switch trials. We followed up with post hoc tests to identify which specific postswitch trials are significantly different from post-switch 25, with significant effects between post-switch 1 and 25 (p < 0.0001), 2 and 25 (p < 0.0001), 3 and 25 (p = 0.0048), and between 4 and 25 (p = 0.0043). Figure 2 additionally indicates a marginally slower motor adaptation in older than younger adults when trying to successfully lift T-shaped object in our experiment. While the younger adults have a significant increase in performance early in the experiment, it takes the older adults more post-switches to reach their best performance. However, there was no interaction or age effect, suggesting a small or negligible trend to slower adaptation in older than young participants (all p's > 0.05).

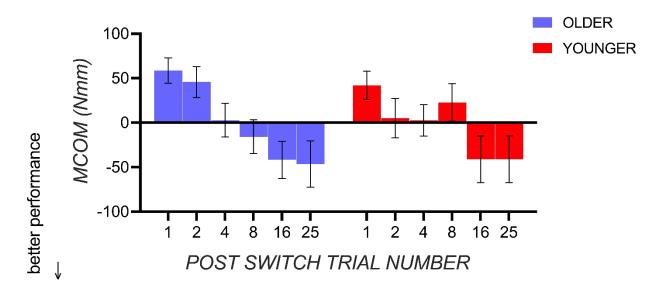


Figure 2: Post-CoM Switch Trials. Performance is quantified as the group mean compensatory torque (Mcom, with error bars +/- 1 std. error) in older (blue bars) and in younger (red bars). Both groups improved their performance over 25 post-switches, with a marginally slower adaptation rate in the older than younger group. Nonetheless, neither attained the target -250 Nmm compensatory torque, indicating inadequate adaptation in motor behavior.

We conducted comparisons across grip force, lift force difference, load phase, digit positioning, and reach phase between post-switch 1 and 25 for both age groups. Both Figure 3A and 3D show an effect of age between the older and younger adults, with higher grip force (*F* (1, 58) = 0.29, *p* = 0.018, η_p^2 = 0.09) and more default collinear digit positioning (*F* (1, 58) = 0.23, *p* = 0.049, η_p^2 = 0.07) in older and younger participants. We also found a significant effect of switch number on digit position (*F* (1, 58) = 0.40, *p* = 0.002, ηp^2 = 0.15), and after running a post hoc test we found significance (*p* = 0.0074 between post-switch 1 and 25 for the younger adults indicating that they started to adapt their digit positioning. We found no effect of switch number on grip force and no interactions on grip force or digit position (*p* '*s* > 0.05). Figure 3B, 3C, and 3E show no significant differences in lift force difference, load phase, and reach phase between the two groups or when comparing post-switch 1 to 25, and no interactions (all *p*'s > 0.05). This lack of significant effects supports our claim that neither group is effectively adapting. Although there is some improvement with changes in digit position, both groups struggle with lift force difference, load phase, and reach phase, indicating they are copying what they did before and not adapting properly, which leads to their failure in achieving the desired performance.

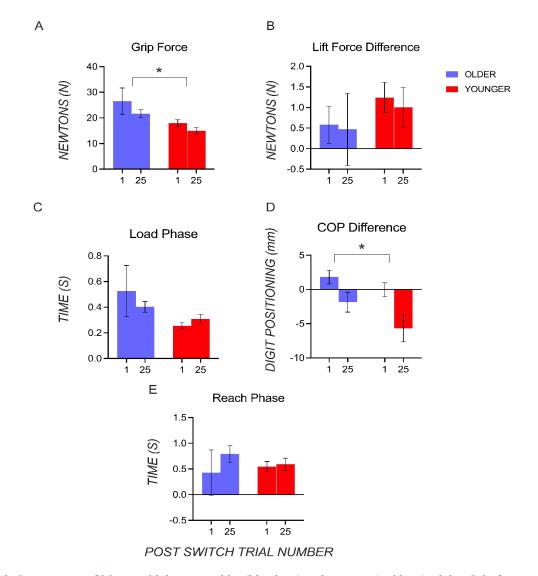


Figure 3: Components of Mcom with between older (blue bars) and younger (red bars) adults. Grip force mean (A) measured in Newtons (N, with error bars +/- 1 std. error). Older adults show a larger grip force than younger adults throughout all post-switches. Lift force difference (B) measured in Newtons (N, with error bars +/- 1 std. error). Load Phase (C) measured in seconds (S, with error bars +/- 1 std. error). Center of pressure (COP) difference (D) measured in digit positioning (mm, with error bars +/- 1 std. error). Older adults show a more colinear digit position than younger adults, and younger adults adapt their digit positioning from post-switch 1 to 25. Reach phase (E) measured in seconds (S, with error bars +/- 1 std. error).

DISCUSSION

Our study aimed to compare motor adaptation rates between older and younger adults, with a specific focus on older adults' reliance on fixed motor patterns. We conducted an experiment where both older and younger participants were tasked with lifting a symmetrical object with a hidden asymmetric mass, which alternated sides. Participants aimed to keep the object level by generating a compensatory torque at lift onset that matched and opposed the object's torque. This setup allowed us to assess their ability to generalize force and torque application across different weight distributions. The comparison of age-related motor adaptation was centered around examining the timing of ceiling performance attainment in both groups. Here, we discuss the implications of our findings and their contribution to understanding age-related differences in motor adaptation.

Contrary to our hypothesis, our results indicated minimal differences in motor adaptation rates between older and younger adults. Both groups showed progressive improvement in performance over the 25 post-switch trials, as evidenced by their increasing approach towards generating a -250 Nmm torque. This improvement was consistent across both age groups. Although older adults were slightly slower at motor adaptation than younger counterparts, the differences were minimal, and only trending.

Our findings support previous research showing comparable motor adaptation between older and younger adults with both groups adapting similarly in leading limb movements (Ryota et al., 2022), locomotor adaptation rates regardless of sensory manipulations (Kuhman et al., 2022), and similarity in adaptation to perturbations across different age groups (Bansal et al., 2023). Studies suggest that individuals can adapt their movements to subtle environmental changes regardless of age when safety is at stake (Ryota et al., 2022). However, age may negatively influence adaptive limb movements in low-risk scenarios, such as when encountering slightly lowered obstacles. Given that older adults are more prone to encountering these low-risk scenarios, like small divots in the sidewalk, older adults might not be able to adapt their motor behavior quickly enough to catch themselves from tripping and falling.

Our findings do not corroborate with other studies that indicate age-related differences in motor adaptation rates, where older adults typically adapt slower (Voelcker-Rehage, 2008), manifesting in challenges with movement coordination (Krehbiel et al., 2017), heightened variability in action execution, and slowed movements (Sallard et al., 2014). These difficulties

impact not only upper limb movements, but also gait and balance (Konrad, et al., 1999; Cruz-Jimenez, 2017), suggesting that older adults may experience reduced motor adaptation due to declines in grey matter in motor regions (Wolpe, 2020). Nevertheless, previous research presents conflicting findings, with some studies suggesting that older adults adapt motor behavior more slowly than younger adults, while others propose they may adapt similarly. This highlights the importance of further investigating the multiple factors influencing motor adaptation to better understand why older adults experience more motor errors.

In our study, even though both older and younger individuals adapted similarly, neither group achieved optimal performance, suggesting a lack of effective adaptation for both groups. Unlike previous studies, our task involved a novel object with an asymmetric mass that switched sides, requiring participants to adapt without prior practice. We might see discrepancy in our results compared to previous research due to this complexity of our reaching task, as well as the lack of variability in cognition of the older adults, and the participants overall motivation for completing the task.

The complexity of our lifting task may have hindered our ability to accurately assess agerelated differences in motor behavior adaptation. Specifically, the younger adults' inability to effectively generalize torque direction to match the external torque of the object might have contributed to the absence of an age effect in our findings. Previous studies have found task performance to be lower in both older and younger groups after being presented with a complex sequence (Krüger et al., 2024). While we did observe a marginally slower adaptation rate among older adults, this alone does not sufficiently prove slower adaptation. To succeed in this lifting task, participants were required to generate a compensatory torque of -250 Nmm to counteract the object's external torque, which neither age group achieved, indicating inadequate motor behavior adaptation. Although younger adults began adjusting their digit positioning by the 25th post-switch trial, they failed to sufficiently alter their lift force difference, reach phase, or load phase to enhance task performance. This suggests that task complexity may have obscured both age groups in their adaptation rates. Given our knowledge that older adults typically exhibit motor adaptation challenges (Voelcker-Rehage, 2008; Wolpe et al., 2020), future studies should aim to mitigate potential confounding factors to show clearer age effects. Simplifying task complexities and familiarizing participants with the task could help elucidate age-related differences in motor behavior adaptation. Additionally, extending the number of post-switch

trials beyond 25 could provide both groups with more time to acclimate to the task, potentially reducing its complexity and enabling clearer distinctions in motor adaptation between the two groups.

Another reason why we might not see slower motor adaptation in the older group could be because our study exclusively recruited older adults who scored 26 or higher on the MoCA exam, indicating intact cognitive function. Scoring a 26 or higher on the MoCA does not represent the cognitive diversity within the broader older adult population, as cognitive impairment varies widely. The well-established correlation between age and cognition (Murman, 2015) suggests that including cognitively impaired individuals could yield different outcomes. Cognitive intactness may imply preserved brain regions responsible for motor adaptation, enabling older adults to adapt as rapidly as younger counterparts. Previous research has contradicted the notion that healthy aging entails a widespread decline in motor function (Ruitenberg & Koppelmans, 2021). Despite observed decreases in reaction time and accuracy, healthy aging does not seem to affect action planning or adaptability, and certain cognitive aspects of motor control may remain relatively unaffected by aging. There also may be agerelated compensatory mechanisms that change brain recruitment during a task that allow older adults to maintain intact performance (Ruitenberg & Koppelmans, 2021). Future studies should incorporate older participants with varying degrees of cognitive impairments, ranging from mild to severe, to investigate potential differences in how they adapt their motor behavior compared to cognitively intact older adults, as well as combining behavioral paradigms with neuroimaging methods to see how different brain regions are recruited for compensation in older compared to younger adults.

A third reason why we see similar motor adaptation between both groups may be because both age groups in our study may have lacked motivation to excel due to the absence of consequences for suboptimal performance (Ryota et al., 2022). Unlike real-world scenarios where failure to adapt carries immediate risks, our task lacked tangible consequences, potentially impacting performance. Previous research suggests that rewards and negative feedback can enhance motor learning, highlighting the importance of incentivizing improved performance (Sadnicka & Edwards, 2015).

Despite seeing no age-related difference in performance, analyses of various performance components showed age-related differences in motor behavior. Older adults exhibited

significantly higher overall grip force compared to younger adults, possibly suggesting a compensatory strategy due to difficulties in adapting other performance components. This observation aligns with previous studies where older adults consistently applied higher grip force during object manipulation, irrespective of the required force for the task (Gilles & Wing, 2003; Voelcker-Rehage & Alberts, 2005). Moreover, older adults exhibited greater collinearity in digit positioning throughout the study, contrasting with younger adults who behave more variably in their digit positioning and subsequent force modulation. This finding aligns with prior research wherein participants learned to minimize object roll of a T-shaped object within three trials (Fu et al., 2010), utilizing smaller grip forces but exhibiting larger variability in digit positions. Additionally, previous studies have highlighted challenges faced by older adults in adjusting finger positions during lifting tasks (Holt et al., 2013). Higher grip force and collinear digit position are metrics of stereotypy; using greater grip forces may obviate the need for modulation in lift force and digit position to minimize tilting, resulting in more similar lift force and digit positioning of our object with different center of mass distributions. Our findings contribute to the growing body of literature demonstrating stereotypy in motor behavior among older adults (Wolpe et al., 2020; King et al., 2013; Lee & Ranganathan, 2019; Anguera et al., 2012; Sombric et al., 2017).

Lastly, our analysis revealed no significant differences in lift force difference, load phase, center of pressure difference, and reach phase between post-switch 1 and 25 for the older adults. This observation suggests that the consistently elevated grip forces employed during the lifting task may serve as a compensatory mechanism for older adults, allowing them to rely on increased force application as a consistent approach to lifting tasks (McDonnell et al., 2005; Parikh et al., 2020), thereby minimizing the need for additional motor behavior adjustments.

Our results support the notion that older adults exhibit habitual tendencies in various performance components, particularly evident in their grip force and digit positioning during object lifting. Three competing hypotheses attempt to explain stereotyped behavior observed with age, including heightened reliance on the hippocampus, increased dependence on the basal ganglia, and the degradation of the cerebellum. Various research studies have provided evidence supporting these hypotheses. However, since all three of them present contradictory findings, this highlights the necessity for further exploration into these brain regions. It is essential to determine which hypothesis best explains the habitual tendencies observed in older adults.

One hypothesis posits that increased hippocampal activity during motor sequence learning compensates for age-related degradation in the striatum, a component of the basal ganglia (Wolpe et al., 2020; Rieckmann et al., 2010). Previous studies have shown that the basal ganglia employ reinforcement learning mechanisms to adjust motor behavior, reinforcing actions with positive outcomes while suppressing those with negative consequences (Kim et al., 2017). Through Hebbian learning, the basal ganglia forms habits, storing them in the prefrontal cortex (PFC). When a familiar action becomes ineffective, the basal ganglia engage in reversal learning to replace it with a new one. However, if older adults rely more on their hippocampus than their basal ganglia, it suggests that the reversal learning pathway is impaired due to age-related degradation, resulting in the persistence of well-learned behaviors. This implies that older adults may resort to stored habits in the PFC when the hippocampus compensates for declining basal ganglia function (Kim et al., 2017). This compensatory mechanism might explain why older adults often exhibit habitual tendencies.

A second hypothesis suggests that the decline in motor adaptation with age is linked to a decrease in explicit learning (Vandevoorde & Orban de Xivry, 2019), and as individuals age, motor control increasingly relies on central mechanisms, such as the prefrontal and basal ganglia systems (Seidler et al., 2010). While the basal ganglia may be relied upon more, it might not efficiently adjust stored motor memories in the prefrontal cortex through reverse learning. For individuals to adapt their motor behavior, the basal ganglia must adjust stored behaviors in the PFC to fit specific motor situations. However, if the basal ganglia are unable to do this due to age-related degradation, older adults will rely more on stereotyped behaviors, leading to increased motor errors.

A third hypothesis proposes that age-related changes in the cerebellum could result in slower motor adaptation over time. Long-term studies monitoring brain size, particularly focusing on the cerebellum, have revealed a notable decline in cerebellar volume at a rate of 1.2% per year (Yong Tang et al., 2001). Studies have observed a positive correlation between cerebellar volume and early learning across all ages (Raz et al., 2000), suggesting that significant changes in cerebellar volume among older adults could explain their delayed motor adaptation when performing tasks such as lifting a T-shaped object. Other research shows significant age-related differences in both gray and white matter volume within the cerebellum, accompanied by shifts in connectivity patterns, which have been associated with older adults' performance on

various tasks (Bernard & Seidler, 2014). Functional brain imaging studies have further implicated the cerebellum in age-related declines in performance. It is hypothesized that the decline in cerebellar function with age may generalize internal models, affecting the ability to learn new tasks and adjust to novel situations which could contribute to the motor challenges seen in older adults (Bernard & Seidler, 2014). If these internal models become overly generalized, it might explain the stereotyped behaviors and resistance to change observed in older adults, posing difficulties in approaching novel situations and successfully adapting motor behavior to interact with new environments.

All three of these conflicting hypotheses emphasize different aspects of brain function and decline that may contribute to the motor adjustment problems observed in older adults, suggesting a complex interplay rather than a single causal factor. The first hypothesis highlights the compensatory role of the hippocampus in response to basal ganglia degradation, suggesting the habitual behaviors in older adults may stem from a reliance on hippocampal activity, which compensates for the degraded basal ganglia. The second hypothesis focuses on a decline in explicit learning and increased reliance on central mechanisms, such as the prefrontal cortex and basal ganglia. It posits that the basal ganglia's diminished ability to update stored motor memories through reversal learning contributes to stereotyped behaviors and motor errors. The third hypothesis considers age-related changes in the cerebellum, proposing that decreased cerebellar volume and altered connectivity patterns result in generalized internal models that hinder the ability to adapt to new tasks and environments. It is plausible that these mechanisms are not mutually exclusive but rather interact in a way that collectively contributes to the increased motor errors observed in older adults.

Our study adds to the expanding literature on the stereotypy of motor behavior, aiming to identify possible factors contributing to problems in motor adjustments with advanced age, particularly concerning grip force and digit positioning components of performance. While our findings did not reveal age-related differences in motor adaptation, they do not detract from the existing literature indicating that older adults tend to exhibit more motor errors, possibly due to slower adaptation abilities linked to habitual behaviors. Further investigation using simpler tasks, introducing consequences for non-adaptation, and considering a wider cognitive range could offer a more comprehensive understanding of the factors shaping motor behavior across different life stages.

Limitations

In our experiment, we defined post-switch instances as occurring when the orientation of the T-shaped object positioned the center of mass on the less familiar side; we looked at the left CoM when the participants started with the CoM on the right and vice versa. This approach allowed us to examine how both older and younger adults adapted their motor behavior to counteract the directional change of the compensatory torque with the same magnitude as the pre-switch side. However, focusing exclusively on the post-switch trials with the mass in the less familiar condition might not provide a comprehensive understanding of the participants' overall adaptation capabilities. The disparity in the number of trials (75 pre-switch vs. 25 post-switch) means that the participants had significantly more experience and opportunity to improve in the pre-switch condition. As a result, their performance in the pre-switch condition could be artificially high, making it difficult to compare directly with the post-switch performance. Additionally, the limited number of post-switch trials might not be sufficient to fully capture the adaptation process, potentially underestimating the participants' true ability to adjust to the new condition. This focus also ignores how participants might gradually adapt if given more post-switch trials, which could provide a more accurate measure of their adaptive capabilities.

CONCLUSION

Our study examined how habitual tendencies observed in older adults might contribute to a higher incidence of motor errors compared to younger individuals, stemming from challenges in adjusting motor behavior to new situations. Contrary to our initial hypothesis, we found minimal differences in motor adaptation rates between the two age groups; neither group adapted their motor behavior sufficiently to fully counteract the object's external torque and maintain balance. While older adults exhibited marginally slower adaptation rates compared to younger adults, these differences were not clinically significant. However, our findings do suggest that older adults may rely on rigid motor strategies such as increased grip force and decreased variability in digit positioning. This finding suggests the potential for intervention strategies aimed at enhancing motor adaptability in aging populations by addressing habitual tendencies and reducing reliance on them.

REFERENCES

- Adolph, K. E., & Franchak, J. M. (2017). The development of motor behavior. *Wiley Interdisciplinary Reviews. Cognitive Science*, 8(1–2), 10.1002/wcs.1430. <u>https://doi.org/10.1002/wcs.1430</u>
- Albouy, G., King, B. R., Maquet, P., & Doyon, J. (2013). Hippocampus and striatum: Dynamics and interaction during acquisition and sleep-related motor sequence memory consolidation. *Hippocampus*, 23(11), 985–1004. <u>https://doi.org/10.1002/hipo.22183</u>
- Anguera, J.A., Bo, J., Seidler, R.D. (2012). Aging Effects on Motor Learning. In: Seel, N.M. (eds) Encyclopedia of the Sciences of Learning. Springer, Boston, MA. https://doi.org/10.1007/978-1-4419-1428-6_453
- Anguera, J. A., Reuter-Lorenz, P. A., Willingham, D. T., & Seidler, R. D. (2010). Contributions of spatial working memory to visuomotor learning. Journal of cognitive neuroscience, 22(9), 1917–1930. https://doi.org/10.1162/jocn.2009.21351
- Bansal, A., 't Hart, B. M., Cauchan, U., Eggert, T., Straube, A., & Henriques, D. Y. P. (2023). Motor adaptation does not differ when a perturbation is introduced abruptly or gradually. Experimental brain research, 241(11-12), 2577–2590. https://doi.org/10.1007/s00221-023-06699-2
- Bernard, J. A., & Seidler, R. D. (2014). Moving forward: Age effects on the cerebellum underlie cognitive and motor declines. *Neuroscience & Biobehavioral Reviews*, 42, 193–207. <u>https://doi.org/10.1016/j.neubiorev.2014.02.011</u>
- Brach, J. S., & Vanswearingen, J. M. (2013). Interventions to Improve Walking in Older Adults. Current translational geriatrics and experimental gerontology reports, 2(4), 10.1007/s13670-013-0059-0. https://doi.org/10.1007/s13670-013-0059-0
- Buch, E. R., Young, S., & Contreras-Vidal, J. L. (2003). Visuomotor adaptation in normal aging. Learning & memory (Cold Spring Harbor, N.Y.), 10(1), 55–63. https://doi.org/10.1101/lm.50303
- Carmeli E. (2017). Physical Therapy for Neurological Conditions in Geriatric Populations. Frontiers in public health, 5, 333. https://doi.org/10.3389/fpubh.2017.00333
- Carp, J., Park, J., Hebrank, A., Park, D. C., & Polk, T. A. (2011). Age-Related Neural Dedifferentiation in the Motor System. *PLoS ONE*, 6(12), e29411. https://doi.org/10.1371/journal.pone.0029411
- Christou, A. I., Miall, R. C., McNab, F., & Galea, J. M. (2016). Individual differences in explicit and implicit visuomotor learning and working memory capacity. Scientific reports, 6, 36633. https://doi.org/10.1038/srep36633

- Claudino, R., Mazo, G. Z., & Santos, M. J. (2013). Age-related changes of grip force control in physically active adults. Perceptual and motor skills, 116(3), 859–871. https://doi.org/10.2466/10.06.PMS.116.3.859-871
- Cruz-Jimenez, M. (2017). Normal Changes in Gait and Mobility Problems in the Elderly. Physical Medicine and Rehabilitation Clinics of North America, 28(4), 713–725. https://doi.org/10.1016/j.pmr.2017.06.005
- Doyon, J., Bellec, P., Amsel, R., Penhune, V., Monchi, O., Carrier, J., Lehéricy, S., & Benali, H. (2009). Contributions of the basal ganglia and functionally related brain structures to motor learning. Behavioural Brain Research, 199(1), 61–75. https://doi.org/10.1016/j.bbr.2008.11.012
- Ehsani, F., Abdollahi, I., Mohseni Bandpei, M. A., Zahiri, N., & Jaberzadeh, S. (2015). Motor Learning and Movement Performance: Older versus Younger Adults. *Basic and Clinical Neuroscience*, 6(4), 231–238.
- Ferlinc, A., Fabiani, E., Velnar, T., & Gradisnik, L. (2019). The Importance and Role of Proprioception in the Elderly: A Short Review. *Materia Socio-Medica*, 31(3), 219–221. <u>https://doi.org/10.5455/msm.2019.31.219-221</u>
- Fernández-Ruiz, J., Hall, C., Vergara, P., & Díiaz, R. (2000). Prism adaptation in normal aging: slower adaptation rate and larger aftereffect. Brain research. Cognitive brain research, 9(3), 223–226. https://doi.org/10.1016/s0926-6410(99)00057-9
- Gilles, M. A., & Wing, A. M. (2003). Age-related changes in grip force and dynamics of hand movement. Journal of motor behavior, 35(1), 79–85. https://doi.org/10.1080/00222890309602123
- Godde, B., & Voelcker-Rehage, C. (2017). Cognitive Resources Necessary for Motor Control in Older Adults Are Reduced by Walking and Coordination Training. *Frontiers in Human Neuroscience*, 11, 156. <u>https://doi.org/10.3389/fnhum.2017.00156</u>
- Hibino, H., & Gorniak, S. L. (2020). Effects of aging on rapid grip force responses during bimanual manipulation of an active object. Experimental brain research, 238(10), 2161– 2178. https://doi.org/10.1007/s00221-020-05865-0
- Holt, R. J., Lefevre, A. S., Flatters, I. J., Culmer, P., Wilkie, R. M., Henson, B. W., Bingham, G. P., & Mon-Williams, M. (2013). Grasping the changes seen in older adults when reaching for objects of varied texture. PloS one, 8(7), e69040. https://doi.org/10.1371/journal.pone.0069040

- Kuhman, D., Moll, A., Reed, W., Rosenblatt, N., Visscher, K., Walker, H., & Hurt, C. P. (2022). Effects of sensory manipulations on locomotor adaptation to split-belt treadmill walking in healthy younger and older adults. IBRO neuroscience reports, 12, 149–156. https://doi.org/10.1016/j.ibneur.2022.01.007
- Kim, T., Hamade, K. C., Todorov, D., Barnett, W. H., Capps, R. A., Latash, E. M., Markin, S. N., Rybak, I. A., & Molkov, Y. I. (2017). Reward Based Motor Adaptation Mediated by Basal Ganglia. *Frontiers in Computational Neuroscience*, 11. <u>https://doi.org/10.3389/fncom.2017.00019</u>
- King, B., Fogel, S., Albouy, G., & Doyon, J. (2013). Neural correlates of the age-related changes in motor sequence learning and motor adaptation in older adults. Frontiers in Human Neuroscience, 7. https://www.frontiersin.org/articles/10.3389/fnhum.2013.00142
- Knol, H., Huys, R., Temprado, J. J., & Sleimen-Malkoun, R. (2019). Performance, complexity and dynamics of force maintenance and modulation in young and older adults. PloS one, 14(12), e0225925. https://doi.org/10.1371/journal.pone.0225925
- Konrad, H. R., Girardi, M., & Helfert, R. (1999). Balance and Aging. The Laryngoscope, 109(9), 1454–1460. https://doi.org/10.1097/00005537-199909000-00019
- Kostadinov, D., & Häusser, M. (2022). Reward signals in the cerebellum: Origins, targets, and functional implications. *Neuron*, 110(8), 1290–1303. <u>https://doi.org/10.1016/j.neuron.2022.02.015</u>
- Krüger, M., Puri, R., Summers, J. J., & Hinder, M. R. (2024). Influence of age and cognitive demand on motor decision making under uncertainty: a study on goal directed reaching movements. Scientific reports, 14(1), 9119. <u>https://doi.org/10.1038/s41598-024-59415-7</u>
- Krehbiel, L. M., Kang, N., & Cauraugh, J. H. (2017). Age-related differences in bimanual movements: A systematic review and meta-analysis. Experimental Gerontology, 98, 199– 206. https://doi.org/10.1016/j.exger.2017.09.001
- Kubota, K., Yokoyama, M., Hanawa, H., Miyazawa, T., Hirata, K., Onitsuka, K., Fujino, T., & Kanemura, N. (2023). Muscle co-activation in the elderly contributes to control of hip and knee joint torque and endpoint force. *Scientific Reports*, 13(1), 7139. <u>https://doi.org/10.1038/s41598-023-34208-6</u>
- Laura, Zapparoli., Ma., Luisa, D., Mariano., Eraldo, Paulesu. (2022). How the motor system copes with aging: a quantitative meta-analysis of the effect of aging on motor function control. Communications biology, 5(1) doi: 10.1038/s42003-022-03027-2
- Lee, M. H., & Ranganathan, R. (2019). Age-related deficits in motor learning are associated with altered motor exploration strategies. Neuroscience, 412, 40–47. https://doi.org/10.1016/j.neuroscience.2019.05.047

- Marusic, U., & Grosprêtre, S. (2018). Non-physical approaches to counteract age-related functional deterioration: Applications for rehabilitation and neural mechanisms. European journal of sport science, 18(5), 639–649. https://doi.org/10.1080/17461391.2018.1447018
- Mattay, V. S., Fera, F., Tessitore, A., Hariri, A. R., Das, S., Callicott, J. H., & Weinberger, D. R. (2002). Neurophysiological correlates of age-related changes in human motor function. *Neurology*, 58(4), 630–635. <u>https://doi.org/10.1212/WNL.58.4.630</u>
- McDonnell, M. N., Ridding, M. C., Flavel, S. C., & Miles, T. S. (2005). Effect of human grip strategy on force control in precision tasks. Experimental brain research, 161(3), 368– 373. https://doi.org/10.1007/s00221-004-2081-0
- Murman D. L. (2015). The Impact of Age on Cognition. Seminars in hearing, 36(3), 111–121. https://doi.org/10.1055/s-0035-1555115
- Nakamura, T., Kodama, K., Sakazaki, J., & Higuchi, T. (2023). Relationship between adaptability during turning and the complexity of walking before turning in older adults. Journal of motor behavior, 55(4), 331–340. https://doi.org/10.1080/00222895.2023.2199692
- Parikh, P. J., Fine, J. M., & Santello, M. (2020). Dexterous Object Manipulation Requires Context-Dependent Sensorimotor Cortical Interactions in Humans. Cerebral cortex (New York, N.Y.: 1991), 30(5), 3087–3101. https://doi.org/10.1093/cercor/bhz296
- Popa, L. S., & Ebner, T. J. (2019). Cerebellum, Predictions and Errors. Frontiers in Cellular Neuroscience, 12, 524. <u>https://doi.org/10.3389/fncel.2018.00524</u>
- Raz, N., Williamson, A., Gunning-Dixon, F., Head, D., & Acker, J. D. (2000). Neuroanatomical and cognitive correlates of adult age differences in acquisition of a perceptual-motor skill. *Microscopy Research and Technique*, 51(1), 85–93. https://doi.org/10.1002/1097-0029(20001001)51:1<85::AID-JEMT9>3.0.CO;2-0
- Rieckmann, A., Fischer, H., & Bäckman, L. (2010). Activation in striatum and medial temporal lobe during sequence learning in younger and older adults: Relations to performance. *NeuroImage*, 50(3), 1303–1312. <u>https://doi.org/10.1016/j.neuroimage.2010.01.015</u>
- Rossi, C., Chau, C. W., Leech, K. A., Statton, M. A., Gonzalez, A. J., & Bastian, A. J. (2019). The capacity to learn new motor and perceptual calibrations develops concurrently in childhood. *Scientific Reports*, 9(1), Article 1. <u>https://doi.org/10.1038/s41598-019-45074-6</u>
- Ruitenberg, M. F. L., & Koppelmans, V. (2021). Cognition in Motion: Evidence for Intact Action Control With Healthy Aging. The journals of gerontology. Series B, Psychological sciences and social sciences, 76(2), 252–261. https://doi.org/10.1093/geronb/gbaa184

- Sallard, E., Spierer, L., Ludwig, C., Deiber, M.-P., & Barral, J. (2014). Age-related changes in the bimanual advantage and in brain oscillatory activity during tapping movements suggest a decline in processing sensory reafference. Experimental Brain Research, 232(2), 469–479. https://doi.org/10.1007/s00221-013-3754-3
- Sadnicka, A., & Edwards, M. J. (2015). The influence of reward and punishment on motor learning. Movement disorders : official journal of the Movement Disorder Society, 30(13), 1724. https://doi.org/10.1002/mds.26372
- Sager, C. A., Diamond, E., Hulsey-Vincent, M. R., & Marneweck, M. (2024). Repeated contextspecific actions disrupt feedforward adjustments in motor commands in younger and older adults. Journal of neurophysiology, 131(5), 891–899. https://doi.org/10.1152/jn.00455.2023
- Schendan, H. E., Searl, M. M., Melrose, R. J., & Stern, C. E. (2003). An fMRI Study of the Role of the Medial Temporal Lobe in Implicit and Explicit Sequence Learning. Neuron, 37(6), 1013–1025. https://doi.org/10.1016/S0896-6273(03)00123-5
- Seidler R. D. (2007). Aging affects motor learning but not savings at transfer of learning. Learning & memory (Cold Spring Harbor, N.Y.), 14(1-2), 17–21. https://doi.org/10.1101/lm.394707
- Seidler, R. D., Bernard, J. A., Burutolu, T. B., Fling, B. W., Gordon, M. T., Gwin, J. T., Kwak, Y., & Lipps, D. B. (2010). Motor Control and Aging: Links to Age-Related Brain Structural, Functional, and Biochemical Effects. *Neuroscience and Biobehavioral Reviews*, 34(5), 721–733. https://doi.org/10.1016/j.neubiorev.2009.10.005
- Sombric, C. J., Harker, H. M., Sparto, P. J., & Torres-Oviedo, G. (2017). Explicit Action Switching Interferes with the Context-Specificity of Motor Memories in Older Adults. Frontiers in aging neuroscience, 9, 40. https://doi.org/10.3389/fnagi.2017.00040
- Swenor, B. K., Lee, M. J., Varadaraj, V., Whitson, H. E., & Ramulu, P. Y. (2020). Aging With Vision Loss: A Framework for Assessing the Impact of Visual Impairment on Older Adults. *The Gerontologist*, 60(6), 989–995. <u>https://doi.org/10.1093/geront/gnz117</u>
- Vandevoorde, K., & Orban de Xivry, J.-J. (2019). Internal model recalibration does not deteriorate with age while motor adaptation does. *Neurobiology of Aging*, *80*, 138–153. https://doi.org/10.1016/j.neurobiolaging.2019.03.020
- Voelcker-Rehage, C., & Alberts, J. L. (2005). Age-related changes in grasping force modulation. *Experimental Brain Research*, *166*(1), 61–70. https://doi.org/10.1007/s00221-005-2342-6
- Voelcker-Rehage, C. Motor-skill learning in older adults—a review of studies on age-related differences. Eur Rev Aging Phys Act 5, 5–16 (2008). https://doi.org/10.1007/s11556-008-0030-9

- Volpi, E., Nazemi, R., & Fujita, S. (2004). Muscle tissue changes with aging. *Current Opinion in Clinical Nutrition and Metabolic Care*, 7(4), 405–410.
- Völter*, C., Peter Thomas*, J., Maetzler, W., Guthoff, R., Grunwald, M., & Hummel, T. (2021). Sensory Dysfunction in Old Age. *Deutsches Ärzteblatt International*, 118(29–30), 512– 520. <u>https://doi.org/10.3238/arztebl.m2021.0212</u>
- Frontera W. R. (2022). Rehabilitation of Older Adults with Sarcopenia: From Cell to Functioning. Progress in rehabilitation medicine, 7, 20220044. https://doi.org/10.2490/prm.20220044
- Wolpe, N., Ingram, J. N., Tsvetanov, K. A., Geerligs, L., Kievit, R. A., Henson, R. N., Wolpert, D. M., & Rowe, J. B. (2016). Ageing increases reliance on sensorimotor prediction through structural and functional differences in frontostriatal circuits. *Nature Communications*, 7, 13034. <u>https://doi.org/10.1038/ncomms13034</u>
- Wolpe, N., Ingram, J. N., Tsvetanov, K. A., Henson, R. N., Wolpert, D. M., & Rowe, J. B. (2020). Age-related reduction in motor adaptation: Brain structural correlates and the role of explicit memory. *Neurobiology of Aging*, 90, 13–23. https://doi.org/10.1016/j.neurobiolaging.2020.02.016
- Yong Tang, Gregory T. Whitman, Ivan Lopez, & Robert W. Baloh. (2001, October). Brain Volume Changes on Longitudinal Magnetic Resonance Imaging in Normal Older People—Tang—2001—Journal of Neuroimaging—Wiley Online Library. https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1552-6569.2001.tb00068.x?sid=nlm%3Apubmed
- Zapparoli, L., Mariano, M. & Paulesu, E. (2022). How the motor system copes with aging: a quantitative meta-analysis of the effect of aging on motor function control. *Commun Biol* 5, 79. https://doi.org/10.1038/s42003-022-03027-2
- Zhang, W., Gordon, A. M., Fu, Q., & Santello, M. (2010). Manipulation After Object Rotation Reveals Independent Sensorimotor Memory Representations of Digit Positions and Forces. *Journal of Neurophysiology*, 103(6), 2953–2964.