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Learning new gait patterns: Age-related differences in skill acquisition and interlimb transfer

Chandramouli Krishnan, PT, PhD^{#1,2,∞}, Edward P. Washabaugh, MSE^{#1,2}, Courtney E. Reid^{#1}, Matteo M. Althoen¹, and Rajiv Ranganathan, PhD³

¹Department of Physical Medicine and Rehabilitation, Michigan Medicine, Ann Arbor, MI, USA

²Department of Biomedical Engineering, University of Michigan, Ann Arbor, MI, USA

³Department of Kinesiology, Michigan State University, East Lansing, MI, USA

These authors contributed equally to this work.

Abstract

Evidence from upper-extremity literature suggests that the normal ageing process affects an individual's ability to learn and retain a motor skill, but spares their ability to transfer the skill to the untrained, opposite limb. While this phenomenon has been well-studied in the upper-extremity, evidence in the lower-extremity is limited. Further, it is unclear to what extent age-related differences in motor learning and transfer are dependent on visual feedback of the motor task. Therefore, the purpose of this study was to examine the effects of ageing on motor learning, retention, and interlimb transfer during walking with and without visual feedback. Forty-four subjects (24 young; 20 older adults) were tested on a treadmill over two consecutive days. On day 1, subjects learned a new gait pattern by performing a foot-trajectory tracking task that necessitated greater hip and knee flexion during the swing phase of the gait. On day 2, subjects repeated the task with their training leg to test retention, then with their untrained leg to test interlimb transfer. Trials without visual feedback were also collected on both days. Results indicated that older adults had reduced ability to learn the task, and also exhibited lower retention and inter-limb transfer. However, these differences were dependent on visual feedback as the groups performed similarly when feedback was removed. The findings provide novel evidence indicating that ageing impairs learning, retention, and transfer of motor skills in the lower-extremity during walking, which may have implications for gait therapy after stroke and other geriatric conditions.

[∞] **Address for Correspondence:** Chandramouli Krishnan, Director, Neuromuscular & Rehabilitation Robotics Laboratory (NeuRRo Lab), Department of Physical Medicine and Rehabilitation, University of Michigan, 325 E Eisenhower Parkway (Suite 3013), Ann Arbor, MI - 48108, Phone: (319) 321-0117, Fax: (734-615-1770); mouli@umich.edu.

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Keywords

Aging; Consolidation; Elderly; Adaptation; Functional task

Introduction

Walking is a highly skilled motor behavior that is acquired during infancy, but can be diminished or lost with ageing. Further, ageing increases the risk of chronic diseases like diabetes and arthritis, falls, fractures, and other neurological injuries (e.g., stroke), which can lead to severe gait impairments. Hence, skill learning during walking is an important component of gait rehabilitation in the elderly (VanSwearingen and Studenski 2014); where, throughout the course of training, they will have to learn, unlearn, and relearn a number of skills related to walking. However, evidence indicates that as we age, our ability to acquire and utilize motor skills is diminished (Mahncke and others 2006; Ren and others 2013; Seidler and others 2010; VanSwearingen and Studenski 2014), and many older adults do not regain full mobility following injury. Apart from the learning process itself (i.e., skill acquisition), other components of learning, such as retention, consolidation (i.e., offline changes in motor performance after initial acquisition), and transfer (either to new task variants or to the opposite, untrained limb) are also essential processes to facilitate gait recovery during rehabilitation. However, the role of these processes in ageing and skill acquisition during gait is not well understood.

Studies that examine skill learning and other associated components of learning (i.e., retention, transfer, etc.) in older adults are often performed in the upper-extremity. Many of these studies have shown that older adults retain the ability to learn new motor skills, but both the rate at which they learn and their final performance level are reduced in comparison with young adults (Onushko and others 2014; Rogasch and others 2009; Seidler-Dobrin and Stelmach 1998; Smith and others 2005). Evidence from motor retention research, however, is conflicting, with some studies showing similar levels of retention between age groups (Rogasch and others 2009; Smith and others 2005). Interestingly, a majority of the studies that have evaluated the interlimb transfer effects suggest that older adults have greater transfer (Graziadio and others 2015; Wang and others 2011), and attribute this finding to increased recruitment of both brain hemispheres while performing basic motor skills (Graziadio and others 2015; Wang and others 2011). However, a central issue in studying the effects of ageing on motor learning is the widespread inconsistency in the findings. This inconsistency is most likely multifactorial and could be due to the learning mechanism studied (e.g., skill, adaptation, etc.), type of tasks used (continuous, discrete), characteristics of the sample population (e.g., age, cognitive and physical capacities), and data measurement and data analysis techniques (training duration, rest/breaks, measured variables, processing methods). This issue is further complicated by the fact that our broader understanding of motor learning with ageing is primarily based on a synthesis of literature from studies examining different components of learning, which is due to a lack of studies that have comprehensively evaluated multiple components of learning, such as skill acquisition, retention, interlimb transfer, etc.

Despite the large body of work in ageing and motor learning, there is a paucity of research examining the effects of ageing on motor learning of a functionally relevant task, such as walking. This is particularly important considering that many of the findings in the upper-extremity may not be applicable to learning with the lower extremity. Much of what we know about age-related differences in motor learning in the lower-extremity is from investigations that have studied the effects of ageing during motor adaptation on a split belt treadmill (Bruijn and others 2012; Malone and Bastian 2016; Roemmich and others 2014; Sombric and others 2017). While motor adaptation is an important aspect of learning, there are fundamental differences between skill learning and motor adaptation, which limit the generalizability of the results between these paradigms (Bastian 2008; Krakauer and Mazzoni 2011; Sternad 2018). For example, motor adaptation tasks typically involve perturbation, where the participant adapts and learns to improve performance to pre-perturbation levels through sensory-prediction errors (followed by an aftereffect when the perturbation is removed); whereas, skill acquisition tasks generally do not involve perturbation and the participant improves performance based on success-based exploration (Krakauer and Mazzoni 2011).

To our knowledge, only one study has examined the age-related differences in skill learning in the lower extremity: van Hedel and Dietz (2004) found that older subjects had learning deficits while performing a discrete obstacle avoidance task while walking. While this study makes an important contribution to the existing literature, there is ample evidence to suggest that the learning and retention characteristics of continuous and discrete tasks are quite different (Lee and Genovese 1989; Schmidt and others 2018), such that continuous tasks have better retention than discrete tasks (Schmidt and others 2018). Further, virtually no studies in either the upper- or lower-extremities have performed comprehensive evaluation of learning, retention, consolidation, and interlimb transfer to provide a complete picture of the effects of ageing. Therefore, this study was performed to investigate the differences in motor learning, retention, and interlimb transfer between older and young adults when performing a continuous skill learning task during walking. To investigate these effects, subjects performed a foot trajectory-tracking paradigm that has been previously used for gait rehabilitation (Krishnan and others 2013; Krishnan and others 2012; Srivastava and others 2015). The paradigm requires participants to alter their foot trajectory during the swing phase of gait by increasing their hip and knee excursions in the sagittal plane. We hypothesized that older adults would exhibit reduced learning, retention, and interlimb transfer when compared to the young adults.

Methods

Participants

Participants consisted of 44 adults: 20 older (13 women and 7 men) and 24 young (13 women and 11 men) adults. The age criterion for the older adults was 60-75 years, while young adults were eligible if aged between 18 and 35 years. All participants were right leg dominant as determined by their preferred leg for kicking a ball (Krishnan and others 2017). Participants with a major lower extremity injury or surgery (e.g., joint replacement), history of neurological disorder, or significant cardiac conditions were excluded from the study.

Given that skill learning involves a significant cognitive demand, individuals with significant cognitive deficits (Mini-Mental State Examination [MMSE] score < 24) were also excluded. Written informed consent was obtained prior to participation and all procedures were approved by the University of Michigan Human Subjects Institutional Review Board. Full demographics of the participants can be found in Table 1.

Experimental Protocol

A schematic of the experimental protocol is shown in Figure 1A. Participants in both groups performed a motor learning task on two consecutive days (older adults: 25.0 ± 5.5 hours and young adults: 22.3 ± 2.0 hours) wearing the same foot- and legwear (i.e., shorts or spandex). The motor learning task was performed while the participant was walking on a motorized treadmill (Woodway, USA) at 0.89 m/s (2mph) with their hands placed over a custom-built treadmill rail system (Figure 2A). On Day 1, the participant practiced the task with their training (Tr) leg. On Day 2, the participant first practiced the same task with their training leg and then with their untrained (i.e., transfer [Tf]) leg. Before beginning the study, it was randomly determined if the participant's right or left leg would be the training leg (older adults: 10 right leg and 10 left leg; young adults: 13 right leg and 11 left leg).

On each day (and for each leg), the experiment consisted of three phases: (1) pre-test phase (Pre), (2) training phase, and (3) post-test phase (Post). During the pre-test phase, the initial performance was established using a foot-trajectory tracking paradigm, where the participant changed their gait to match a target projected on the monitor (Krishnan and others 2013; Krishnan and others 2012; Krishnan and others 2017; Krishnan and others 2015). The target was created by scaling ($1.3\times$) the swing phase ensemble average of the hip and knee angles obtained from the normal walking (NW) trajectory, and projecting it in the end-point space (further details are given below). Target-matching performance was evaluated both with (TM) and without visual feedback (NV) of their actual trajectory. The training phase consisted of repeated practice of the foot-trajectory tracking task – 8 blocks of practice were performed with each block lasting for one minute and separated by a one-minute rest period. In the post-test phase, the changes in target-tracking performance were evaluated.

Target-matching Task

We used a custom-designed real-time motion tracking system developed using LabVIEW 2011 and NI Vision Assistant (National Instruments Corp., Austin, TX, USA) for the motor learning task (Figure 2A) (Krishnan and others 2015; Saner and others 2017). The system computed the sagittal plane hip and knee kinematics during walking in real-time by tracking the 19mm retroreflective markers placed on the participant's greater trochanter, lateral epicondyle of the femur, and the lateral malleolus of the ankle. The target template trajectory for the motor learning task was created for each leg (training and transfer legs) from the participant's sagittal plane hip and knee kinematics data obtained from the respective legs during normal walking. For each day of testing, a new template was created based on the kinematic patterns of that particular day and leg during normal walking. This recalibration procedure ensured that slight differences in marker placements and-or variations in gait patterns (between days and legs) did not affect the subject's inherent target-matching ability. Extensive care was also taken to replicate marker placements between legs and days (e.g.,

same researcher placed the markers on both days, distances between markers were measured and matched between days, joint angles during quiet standing were measured and matched between days, etc.).

The target template was created by scaling (1.3×) the hip and knee angles from the normal walking trial and projecting this template in the end-point space (i.e., trajectory of the ankle relative to the hip on the sagittal plane) using the following forward kinematic equation.

$$\begin{bmatrix} X_a \\ Y_a \end{bmatrix} = \begin{bmatrix} \sin(\theta_h) & -\sin(\theta_k - \theta_h) \\ -\cos(\theta_h) & -\cos(\theta_k - \theta_h) \end{bmatrix} \begin{bmatrix} l_1 \\ l_2 \end{bmatrix}$$

where X_a and Y_a are the x and y positions of the ankle lateral malleolus (referred to as the foot trajectory) relative to the hip, l_1 is the distance between hip and knee markers, l_2 is the distance between knee and ankle markers, θ_h and θ_k are the hip and knee angles. The target template trajectory was smoothed using a Hanning window to prevent any abrupt scaling both in the beginning and at the end of swing phase. The template was then displayed concurrently with the participant's actual foot trajectory on a computer monitor placed in front of the participant (Figure 2B). The duration of the concurrent visual feedback on the screen was adjusted such that the participant could see the entire trajectory produced over the previous gait cycle. During target-matching trials, the participant was instructed to match the target as precisely as possible by altering their gait during the swing phase of the gait. They were also instructed not to alter the normal gait patterns of their opposite leg that was not involved in the target-matching task.

Data Analyses

Tracking error was computed for each trial (i.e., block) to determine task performance (i.e., how closely the participant's actual trajectory matched the target trajectory). Tracking error was calculated as the difference in area (i.e., non-overlapping area) in pixels between the subject's actual foot trajectory and the target foot trajectory for each stride (Figure 2C). This stride-by-stride tracking error was then normalized as a percentage of the area within the participant's target template and average across strides for each trial.

Trials used in the data analyses were abbreviated based on the testing leg (training or transfer), day, trial type (normal walking, target-matching, target-matching without visual feedback), and testing phase (pre or post).

$$\text{Abbreviation: [Testing Leg]}_{[\text{Day}]} - [\text{Trial Type}][\text{Testing Phase}]$$

Based on these conventions, Tr₁-TM Pre and Tr₁-TM Post refers to the initial and final tracking error of the training leg on Day 1, respectively. Tr₂-TM Pre and Tr₂-TM Post refers to the initial and final tracking error of the training leg on Day 2, respectively. Tf-TM Pre and Post refers to initial and final tracking error of the transfer leg (performed only on Day 2;

hence the subscript for day was not used). Similar conventions were used for the no visual feedback trials, except the acronym TM was replaced with NV.

Statistical Analyses

Sample size was estimated in G*Power 3.1 (Faul and others 2009; Faul and others 2007) based on a conservative effect size ‘f’ of 0.50 (partial $\eta^2 = 0.2$) to detect a significant main effect using analysis of covariance (ANCOVA). The chosen sample size ($n = 44$) provides 90% power to detect significant differences between groups with a type I error (α) of 5 %.

All statistical analyses were performed using SPSS for windows version 24 (SPSS Inc., Chicago, IL, USA). To evaluate whether ageing affected motor learning, retention, and interlimb transfer, we tested the differences in the amount of *learning* (improvement in tracking error over entire 2 days: Tr_2 -TM Post relative to Tr_1 -TM Pre), *retention* (initial tracking error on Day 2 relative to initial tracking error on Day 1: Tr_2 -TM Pre relative to Tr_1 -TM Pre), and *transfer* (initial tracking error of the untrained leg [i.e., transfer leg] relative to initial tracking error of the trained leg: Tf-TM Pre relative to Tr_1 -TM Pre) between the older and young adults. We also did additional exploratory analyses on the amount of motor *performance* (improvement in tracking error at the end of Day 1: Tr_1 -TM Post relative to Tr_1 -TM Pre), *consolidation* (initial tracking error on Day 2 relative to tracking error at the end of Day 1: Tr_2 -TM Pre relative to Tr_1 -TM Post), and *final transfer* (i.e., acquisition after transfer; final tracking error of the untrained leg relative to initial tracking error of the trained leg: Tf-TM Post relative to Tr_1 -TM Pre) to get a complete picture of the effects of ageing on motor learning and transfer. These analyses are depicted graphically in Figure 1B.

For all dependent variables, comparisons were made between older and young adults using ANCOVA. The initial performance on Day 1 (Tr_1 -TM Pre) was used as covariate for all analyses except for consolidation for which performance at the end of Day 1 (Tr_1 -TM Post) was used as a covariate. A similar analysis was also performed on the no visual feedback trials to examine if differences between older and young adults were dependent on visual feedback. We note that using ANCOVA of the error is statistically equivalent to using ANCOVA of the change in error to compare groups (Laird 1983; Rausch and others 2003; van Breukelen 2013). To evaluate the amount of interlimb transfer with respect to the training leg, we compared the relationship between (Tr_1 -TM Pre – Tr_2 -TM Post) and (Tr_1 -TM Pre – Tf-TM Pre) for initial transfer, and (Tr_1 -TM Pre – Tr_2 -TM Post) and (Tr_1 -TM Pre – Tf-TM Post) for final transfer using linear regression through origin. A significance level of $\alpha = 0.05$ was used for all statistical analyses.

Results

Learning and Transfer

During target-matching with visual feedback, there was a significant effect of group on the amount of learning and transfer (Figure 3; Table 2). The older adults had higher tracking error in the *training* leg both at the end of Day 1 (performance: $F_{1,41} = 4.962$, $p = 0.031$) and Day 2 (learning: $F_{1,41} = 7.348$, $p = 0.010$) in comparison with the young adults (Figure 4A).

They also showed reduced transfer of the motor skill in their untrained leg (transfer: $F_{1,41} = 5.445$, $p = 0.025$) in comparison with the young adults (Figure 4C). This reduced transfer of motor skill in the untrained leg persisted even at the end of practice with their transfer leg (final transfer: $F_{1,41} = 13.434$, $p = 0.001$) (Figure 4C). During target-matching with no visual feedback, there was no significant effect of group on the amount of learning or transfer ($F_{1,41} = 0.027$ to 2.033 , $p = 0.162$ to 0.869) (Figure 5; Table 3).

Retention and Consolidation

When evaluating the differences in the amount of retention (i.e., initial tracking error on Day 2 relative to tracking error at the beginning of Day 1) and consolidation of the motor task (i.e., initial tracking error on Day 2 relative to tracking error at the end of Day 1) during target-matching with visual feedback, we found that the older adults had reduced retention ($F_{1,41} = 18.883$, $p < 0.001$) and consolidation ($F_{1,41} = 12.215$, $p = 0.001$) in comparison with the young adults (Figure 4B). However, there was no significant effect of group on the amount of retention ($F_{1,41} = 0.686$, $p = 0.412$) or consolidation ($F_{1,41} = 3.542$, $p = 0.067$) during target-matching with no visual feedback (Figure 5; Table 3).

Relationship between Learning and Transfer

Regression analyses indicated that there was a significant linear relationship between the amount of learning on the training leg and the amount of transfer to the untrained leg in both the older (transfer: $r = 0.753$, $p < 0.001$; final transfer: $r = 0.890$, $p < 0.001$) and young (transfer: $r = 0.910$, $p < 0.001$; final transfer: $r = 0.987$, $p < 0.001$) adults. Evaluation of regression slopes in older adults indicated that for every 1% change in tracking error of the training leg there was a change of 0.56% on the transfer leg (i.e., ~56% of transfer of learning between legs) at the beginning and this slope value increased to 0.78% at the end (final transfer). Evaluation of regression slopes in young adults indicated that for every 1% change in tracking error of the training leg there was a change of 0.79% on the transfer leg (i.e., ~79% of transfer of learning between legs) at the beginning and this slope value increased to 1.04% at the end (final transfer).

Discussion

The goal of the current study was to evaluate the differences in learning, retention, and interlimb transfer between older and young adults using a continuous skill learning task during walking. We found that the older adults, in comparison with young adults, had a reduced ability to learn the task and had lower retention of the learned task after a consolidation period. Older adults also showed reduced transfer of the learned walking task to the opposite limb in comparison with the young adults. These findings provide novel evidence indicating both motor skill acquisition and transfer of learned skills to the untrained, opposite limb are affected in the lower-extremity with ageing.

Reduced motor performance and learning in older adults

In this study, the older adults showed a decreased ability to learn the continuous skill learning task during walking. They performed this task with a larger tracking error than the young adults while using the training leg (i.e., lower performance and learning), despite both

the groups starting at the same level of tracking error. This finding is similar to what was seen in another study that tested differences in skill learning during walking in young and older adults (van Hedel and Dietz 2004). In this study, they reported that older adults were more likely to hit the obstacle than young adults (they studied learning using an obstacle avoidance task), which was particularly pronounced when feedback was removed (van Hedel and Dietz 2004). While we also found reduced learning in the older adults, we did not see any differences between the two groups when visual feedback was removed. This contradiction may be due to the difference in task type, as the foot-trajectory tracking used in this study is a continuous task, whereas obstacle avoidance is a more discrete task. Meanwhile, the adaptation literature is split as to the effect of ageing on motor learning. Some studies that investigated the effect of ageing on motor adaptation over a split-belt treadmill found that older adults were slower in adapting to a new walking pattern and had difficulties switching walking patterns according to the context (Bruijn and others 2012; Sombric and others 2017). However, others did not find any difference between the older and young adult groups (Malone and Bastian 2016; Roemmich and others 2014). Although the paradigm was largely the same between these studies, these different findings could have arose due to differences in age of the older cohorts tested—decreased adaptation was detected when the average age of the group was relatively higher. This discrepancy could indicate that motor learning decreases on the spectrum of age, but also reinforces the idea that ageing and motor learning literature is often confounded by inconsistencies in methodologies (e.g., study design, subject populations, type of learning being studied, etc.).

We note that, in our study, the differences in tracking performance were primarily observed in the target-matching trials with visual feedback and not during the trials with no visual feedback. This observation is consistent with a previous study that reported that age-related differences in movement error and variability during a sinusoidal position tracking task were only observed when visual feedback was provided during target tracking (Baweja and others 2015). Thus, our results are in line with others who have suggested that older adults may have difficulties processing visual information when learning fine motor tasks and that visual information during learning could increase motor variability and deteriorate motor performance and skill acquisition (Baweja and others 2015; Kennedy and Christou 2011). Another interesting observation was that the older adults appeared to rely more on visual feedback than young adults (higher initial tracking performance in the no visual feedback trials – i.e., Tr₁-NV Pre), but were able to overcome their reliance on visual feedback with training. This decreased reliance on visual feedback also appeared to carry over to the transfer leg after training.

Lower retention and consolidation of motor skills in older adults

Apart from the learning process itself, consolidation and retention of motor skills are also important when characterizing age-related differences in motor skill acquisition. When evaluating the tracking performance between days, young adults did not show any reduction in performance after a period of consolidation (i.e., between the final block of Day 1 and the first block of Day 2), whereas older adults showed greater tracking error after a period of consolidation. Similarly, the amount of retention also differed significantly between the young and older adults. Our results are similar to the findings from split-belt motor

adaptation studies, which have shown time-related forgetting in older adults (Malone and Bastian 2016; Sombric and others 2017). The precise mechanisms for the observed differences in retention and consolidation between the older and younger adults are currently not clear. Physical or mental fatigue could have contributed to these differences; however, this is unlikely considering the timing of our retention testing (i.e. at the beginning of Day 2). Another possible explanation is related to altered cognitive processes associated with learning (Malone and Bastian 2016; Ren and others 2013; Sombric and others 2017); however, retention deficits are likely multifaceted and need to be examined in greater depth in future studies.

Interlimb transfer reduced in older adults

The concept of interlimb transfer is highly relevant to rehabilitation after neural injury (e.g., stroke), as therapists often train the less-impaired limb to improve impaired limb function (De Luca and others 2017; Sainburg and others 2016). However, the effects of ageing on interlimb transfer have been primarily studied in the upper-extremity and have not been studied in the lower-extremity, which may have implications for gait rehabilitation. Here, we studied the differences in the amount of interlimb transfer between older and young adults using a functionally relevant motor learning task (Krishnan and others 2012; Krishnan and others 2017; Srivastava and others 2015). We found that the amount of interlimb transfer was lower in older adults when compared with young adults. This finding is contradictory to some of the interlimb transfer studies in the upper extremity, which have shown increased interlimb transfer in older adults (Graziadio and others 2015; Wang and others 2011). This increased interlimb transfer in older adults has been attributed to increased engagement of the ipsilateral hemisphere during training (Graziadio and others 2015; Wang and others 2011). It is possible that we did not see increased transfer to the untrained limb because walking is believed to have greater subcortical inputs (Dimitrijevic and others 1998; Nielsen 2003), although recent research has shown that there is cortical involvement during walking (Gwin and others 2011). More likely, we believe that age-related reductions in structural integrity of transcallosal pathways may have resulted in reduced interlimb transfer in older adults (Fling and others 2011), as both animal and human studies indicate that callosal pathways are critical for intermanual transfer (Bentin and others 1984; Hunter and others 1975). The reduced integrity of transcallosal pathways seen with ageing may not have affected the outcomes of past studies that showed increased transfer (Graziadio and others 2015; Wang and others 2011), as these studies used motor adaptation paradigms, which are known to be mediated primarily by the cerebellar-cerebral pathways (Spampinato and others 2017). This premise is indeed supported by the findings from a recent upper-extremity study, which examined the effects of ageing on interlimb transfer using a ballistic finger abduction skill learning task and found that older adults have reduced interlimb transfer in comparison with young adults (Hinder and others 2011). We also found a strong relationship between the amount of learning in the training leg and the amount of transfer, which suggests that the amount of transfer is proportional to the amount of learning and thus, any reductions in learning ability will be reflected in the amount of transfer observed in the untrained limb.

Conclusion

This study compared the differences in motor learning, retention and interlimb transfer between older and young adults when performing a continuous skill learning task during walking. We found that the older adults learned less and exhibited lower retention and interlimb transfer of motor skills during walking; however, these differences were dependent on visual feedback such that performance differences diminished when feedback was removed during target-matching. While our findings of reduced learning and retention are consistent with other upper-extremity and motor adaptation studies, the observation of reduced interlimb transfer is contradictory to studies that report equal or greater interlimb transfer in older adults. These findings may have implications when designing therapies that focus on motor relearning for individuals with stroke or other geriatric conditions.

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References:

- Bastian AJ Understanding sensorimotor adaptation and learning for rehabilitation. *Curr Opin Neurol.* 21:628–633; 2008 [PubMed: 18989103]
- Baweja HS; Kwon M; Onushko T; Wright DL; Corcos DM; Christou EA Processing of visual information compromises the ability of older adults to control novel fine motor tasks. *Exp Brain Res.* 233:3475–3488; 2015 [PubMed: 26298044]
- Bentin S; Sahar A; Moscovitch M Intermanual information transfer in patients with lesions in the trunk of the corpus callosum. *Neuropsychologia.* 22:601–611; 1984 [PubMed: 6504300]
- Bruijn SM; Van Impe A; Duysens J; Swinnen SP Split-belt walking: adaptation differences between young and older adults, *J Neurophysiol.* 108:1149–1157; 2012 [PubMed: 22623488]
- De Luca A; Giannoni P; Verneti H; Capra C; Lentino C; Checchia GA; Casadio M Training the Unimpaired Arm Improves the Motion of the Impaired Arm and the Sitting Balance in Chronic Stroke Survivors. *IEEE Trans Neural Syst Rehabil Eng.* 25:873–882; 2017 [PubMed: 28114023]
- Dimitrijevic MR; Gerasimenko Y; Pinter MM Evidence for a spinal central pattern generator in humans. *Ann N Y Acad Sci.* 860:360–376; 1998 [PubMed: 9928325]
- Faul F; Erdfelder E; Buchner A; Lang AG Statistical power analyses using G*Power 3.1: tests for correlation and regression analyses. *Behav Res Methods.* 41:1149–1160; 2009 [PubMed: 19897823]
- Faul F; Erdfelder E; Lang AG; Buchner A G*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behav Res Methods.* 39:175–191; 2007 [PubMed: 17695343]
- Fling BW; Peltier SJ; Bo J; Welsh RC; Seidler RD Age differences in interhemispheric interactions: callosal structure, physiological function, and behavior. *Front Neurosci.* 5:38; 2011 [PubMed: 21519384]
- Graziadio S; Nazarpour K; Gretenkord S; Jackson A; Eyre JA Greater intermanual transfer in the elderly suggests age-related bilateral motor cortex activation is compensatory. *J Mot Behav.* 47:47–55; 2015 [PubMed: 25575222]
- Gwin JT; Gramann K; Makeig S; Ferris DP Electroocutaneous activity is coupled to gait cycle phase during treadmill walking. *Neuroimage.* 54:1289–1296; 2011 [PubMed: 20832484]
- Hinder MR; Schmidt MW; Garry MI; Carroll TJ; Summers JJ Absence of cross-limb transfer of performance gains following ballistic motor practice in older adults. *J Appl Physiol* (1985). 110:166–175; 2011 [PubMed: 21088207]

- Hunter M; Ettlinger G; Maccabe JJ Intermanual transfer in the monkey as a function of amount of callosal sparing. *Brain Res.* 93:223–240; 1975 [PubMed: 809101]
- Kennedy DM; Christou EA Greater amount of visual information exacerbates force control in older adults during constant isometric contractions. *Exp Brain Res.* 213:351–361; 2011 [PubMed: 21800256]
- Krakauer JW; Mazzoni P Human sensorimotor learning: adaptation, skill, and beyond. *Curr Opin Neurobiol.* 21:636–644; 2011 [PubMed: 21764294]
- Krishnan C; Ranganathan R; Dhaher YY; Rymer WZ A pilot study on the feasibility of robot-aided leg motor training to facilitate active participation. *PLoS One.* 8:e77370; 2013 [PubMed: 24146986]
- Krishnan C; Ranganathan R; Kantak SS; Dhaher YY; Rymer WZ Active robotic training improves locomotor function in a stroke survivor. *J Neuroeng Rehabil.* 9:57; 2012 [PubMed: 22906099]
- Krishnan C; Ranganathan R; Tetarbe M Interlimb transfer of motor skill learning during walking: No evidence for asymmetric transfer. *Gait Posture.* 56:24–30; 2017 [PubMed: 28482202]
- Krishnan C; Washabaugh EP; Seetharaman Y A low cost real-time motion tracking approach using webcam technology. *J Biomech.* 48:544–548; 2015 [PubMed: 25555306]
- Laird N Further comparative analyses of pretest-posttest research designs. *The American Statistician.* 37:329–330; 1983
- Lee TD; Genovese ED Distribution of practice in motor skill acquisition: different effects for discrete and continuous tasks. *Res Q Exerc Sport.* 60:59–65; 1989 [PubMed: 2489826]
- Mahncke HW; Bronstone A; Merzenich MM Brain plasticity and functional losses in the aged: scientific bases for a novel intervention. *Prog Brain Res.* 157:81–109; 2006 [PubMed: 17046669]
- Malone LA; Bastian AJ Age-related forgetting in locomotor adaptation. *Neurobiol Learn Mem.* 128:1–6; 2016 [PubMed: 26589520]
- Nielsen JB How we walk: central control of muscle activity during human walking. *Neuroscientist.* 9:195–204; 2003 [PubMed: 15065815]
- Onushko T; Kim C; Christou EA Reducing task difficulty during practice improves motor learning in older adults. *Exp Gerontol.* 57:168–174; 2014 [PubMed: 24909352]
- Rausch JR; Maxwell SE; Kelley K Analytic methods for questions pertaining to a randomized pretest, posttest, follow-up design. *J Clin Child Adolesc Psychol.* 32:467–486; 2003 [PubMed: 12881035]
- Ren J; Wu YD; Chan JS; Yan JH Cognitive aging affects motor performance and learning. *Geriatr Gerontol Int.* 13:19–27; 2013 [PubMed: 22817645]
- Roemmich RT; Nocera JR; Stegemoller EL; Hassan A; Okun MS; Hass CJ Locomotor adaptation and locomotor adaptive learning in Parkinson's disease and normal aging. *Clin Neurophysiol.* 125:313–319; 2014 [PubMed: 23916406]
- Rogasch NC; Dartnall TJ; Cirillo J; Nordstrom MA; Semmler JG Corticomotor plasticity and learning of a ballistic thumb training task are diminished in older adults. *J Appl Physiol* (1985). 107:1874–1883; 2009 [PubMed: 19833810]
- Sainburg RL; Maenza C; Winstein C; Good D Motor Lateralization Provides a Foundation for Predicting and Treating Non-paretic Arm Motor Deficits in Stroke. *Adv Exp Med Biol.* 957:257–272; 2016 [PubMed: 28035570]
- Saner RJ; Washabaugh EP; Krishnan C Reliable sagittal plane kinematic gait assessments are feasible using low-cost webcam technology. *Gait Posture.* 56:19–23; 2017 [PubMed: 28482201]
- Schmidt RA; Lee T; Winstein C; Wulf G; Zelaznik H Motor Control and Learning, 6E: Human kinetics; 2018
- Seidler-Dobrin RD; Stelmach GE Persistence in visual feedback control by the elderly. *Exp Brain Res.* 119:467–474; 1998 [PubMed: 9588781]
- Seidler RD; Bernard JA; Burutolu TB; Fling BW; Gordon MT; Gwin JT; Kwak Y; Lipps DB Motor control and aging: links to age-related brain structural, functional, and biochemical effects. *Neurosci Biobehav Rev.* 34:721–733; 2010 [PubMed: 19850077]
- Smith CD; Walton A; Loveland AD; Umberger GH; Kryscio RJ; Gash DM Memories that last in old age: motor skill learning and memory preservation. *Neurobiol Aging.* 26:883–890; 2005 [PubMed: 15718047]

- Sombric CJ; Harker HM; Sparto PJ; Torres-Oviedo G Explicit Action Switching Interferes with the Context-Specificity of Motor Memories in Older Adults. *Front Aging Neurosci.* 9:40; 2017 [PubMed: 28321188]
- Spampinato DA; Block HJ; Celnik PA Cerebellar-M1 Connectivity Changes Associated with Motor Learning Are Somatotopic Specific. *J Neurosci.* 37:2377–2386; 2017 [PubMed: 28137969]
- Srivastava S; Kao PC; Kim SH; Stegall P; Zanutto D; Higginson JS; Agrawal SK; Scholz JP Assist-as-Needed Robot-Aided Gait Training Improves Walking Function in Individuals Following Stroke. *IEEE Trans Neural Syst Rehabil Eng.* 23:956–963; 2015 [PubMed: 25314703]
- Sternad D It's not (only) the mean that matters: variability, noise and exploration in skill learning. *Current opinion in behavioral sciences.* 20:183–195; 2018 [PubMed: 30035207]
- van Breukelen GJ ANCOVA Versus CHANGE From Baseline in Nonrandomized Studies: The Difference. *Multivariate Behav Res.* 48:895–922; 2013 [PubMed: 26745598]
- van Hedel HJ; Dietz V The influence of age on learning a locomotor task. *Clin Neurophysiol.* 115:2134–2143; 2004 [PubMed: 15294216]
- VanSwearingen JM; Studenski SA Aging, motor skill, and the energy cost of walking: implications for the prevention and treatment of mobility decline in older persons. *J Gerontol A Biol Sci Med Sci.* 69:1429–1436; 2014 [PubMed: 25182600]
- Wang J; Przybyla A; Wuebbenhorst K; Haaland KY; Sainburg RL Aging reduces asymmetries in interlimb transfer of visuomotor adaptation. *Exp Brain Res.* 210:283–290; 2011 [PubMed: 21424842]

Highlights

- Leg motor skill learning during walking diminishes with ageing
- Ageing also affects retention and interlimb transfer of motor skills during walking
- Age-related differences were dependent on visual feedback
- Interlimb transfer is proportional to the amount of learning irrespective of age

Figure 1:

(A) Schematic of the experimental protocol. Target-match trials indicate training blocks where participants performed a foot-trajectory tracking task while receiving visual feedback, and no vision trials indicate blocks in which participants performed the tracking task without any visual feedback. Pre and Post refers to the initial and final training blocks. Following each block, subjects were given approximately one minute of rest. (B) Schematic of the experimental variables and statistical comparisons used to test age-related differences in motor learning, retention, and interlimb transfer. The left column indicates the blocks that were used as covariates in the analyses and the right column indicates the blocks that were compared between the groups.

Figure 2:
(A) Schematic showing the setup used for the continuous skill learning task during walking.
(B) Schematic depicting construction of the target template. **(C)** Schematic showing the computation of tracking error (shaded region).

Figure 3:

Mean tracking error in older and young adults for each target-matching (TM) block on (A) Day 1 with the training leg (Tr_1), (B) Day 2 with the training leg (Tr_2), and (C) Day 2 with the transfer leg (Tf). Error bars represent the standard error of the mean.

Figure 4:

Improvements in tracking error during the various components of learning and interlimb transfer in older and young adults. Bars represent the marginal means of the change in tracking error and error bars represent standard error of the mean. Positive values indicate a reduction in tracking error. Asterisks indicate a significant difference between older and young adults ($p < 0.05$).

Figure 5:
Mean tracking error in the training (Tr) and transfer (Tf) legs during no visual feedback (NV) trials in older and young adults. Breaks in the x-axis indicate that there was a change in the day or the leg that was performing the task. Error bars represent the standard error of the mean.

Table 1.

Demographics of older and young adults.

Group	Age (Years)	Weight (kg)	Height (m)	MMSE ^a	Sleep Rating ^b
Old	67.2 ± 4.1	73.4 ± 12.1	1.7 ± 0.1	29.4 ± 0.8	3.4 ± 3.3
Young	24.8 ± 6.9	68.0 ± 12.7	1.7 ± 0.1	29.5 ± 0.8	2.5 ± 1.8

Note. Mini-mental state examination (MMSE)

^aThe mini-mental state examination is scored on a range from 0-30.

^bSelf-reported sleep rating was scored on a range from 0-10, with 0 being the best possible sleep and 10 being the worst possible sleep.

Table 2.

Average tracking error in older and young adults during target-matching trials with visual feedback (Mean $\pm$ SEM).

Training Leg (Day 1)											
Group	Tr ₁ -TM Pre	Tr ₁ -TM1	Tr ₁ -TM2	Tr ₁ -TM3	Tr ₁ -TM4	Tr ₁ -TM5	Tr ₁ -TM6	Tr ₁ -TM7	Tr ₁ -TM8	Tr ₁ -TM Post	
Older	21.6 $\pm$ 1.4	18.9 $\pm$ 1.3	18.2 $\pm$ 1.3	17.2 $\pm$ 1.3	16.6 $\pm$ 1.2	16.5 $\pm$ 1.2	17.5 $\pm$ 1.4	16.7 $\pm$ 1.3	16.7 $\pm$ 1.6	15.3 $\pm$ 1.0	
Young	20.1 $\pm$ 1.4	17.3 $\pm$ 1.1	15.7 $\pm$ 1.7	14.9 $\pm$ 1.6	13.8 $\pm$ 1.6	14.0 $\pm$ 1.5	13.8 $\pm$ 1.6	12.7 $\pm$ 1.6	12.5 $\pm$ 1.6	12.8 $\pm$ 1.5	
Training Leg (Day 2)											
Group	Tr ₂ -TM Pre	Tr ₂ -TM1	Tr ₂ -TM2	Tr ₂ -TM3	Tr ₂ -TM4	Tr ₂ -TM5	Tr ₂ -TM6	Tr ₂ -TM7	Tr ₂ -TM8	Tr ₂ -TM Post	
Older	17.9 $\pm$ 1.2	17.2 $\pm$ 1.3	15.3 $\pm$ 1.1	15.8 $\pm$ 1.4	16.4 $\pm$ 1.7	14.9 $\pm$ 1.2	15.7 $\pm$ 1.4	14.6 $\pm$ 1.1	14.1 $\pm$ 1.1	13.6 $\pm$ 1.9	
Young	12.4 $\pm$ 0.6	11.7 $\pm$ 0.5	11.7 $\pm$ 0.7	11.3 $\pm$ 0.5	11.6 $\pm$ 0.5	11.7 $\pm$ 0.7	10.9 $\pm$ 0.5	11.3 $\pm$ 0.4	11.2 $\pm$ 0.5	11.1 $\pm$ 0.4	
Transfer Leg (Day 2)											
Group	Tf-TM Pre	Tf-TM1	Tf-TM2	Tf-TM3	Tf-TM4	Tf-TM5	Tf-TM6	Tf-TM7	Tf-TM8	Tf-TM Post	
Older	17.5 $\pm$ 1.3	16.0 $\pm$ 1.4	14.6 $\pm$ 0.9	14.6 $\pm$ 0.9	14.4 $\pm$ 0.8	14.5 $\pm$ 1.0	15.8 $\pm$ 1.1	16.1 $\pm$ 1.4	15.0 $\pm$ 1.2	14.2 $\pm$ 0.9	
Young	13.9 $\pm$ 0.8	12.3 $\pm$ 0.7	12.1 $\pm$ 0.6	11.8 $\pm$ 0.6	11.8 $\pm$ 0.6	11.7 $\pm$ 0.5	11.1 $\pm$ 0.5	11.0 $\pm$ 0.4	11.0 $\pm$ 0.5	10.8 $\pm$ 0.4	

Table 3.

Average tracking error in older and young adults during no vision trials (Mean $\pm$ SEM).

Group	Training Leg (Day 1)		Training Leg (Day 2)		Transfer Leg (Day 2)	
	Tr ₁ -NV Pre	Tr ₁ -NV Post	Tr ₂ -NV Pre	Tr ₂ -NV Post	Tf-NV Pre	Tf-NV Post
Older	33.8 $\pm$ 3.1	21.4 $\pm$ 2.2	23.7 $\pm$ 2.7	19.6 $\pm$ 2.0	18.7 $\pm$ 1.5	18.4 $\pm$ 1.3
Young	23.8 $\pm$ 2.3	19.1 $\pm$ 1.8	17.6 $\pm$ 1.5	14.8 $\pm$ 1.0	20.1 $\pm$ 1.6	15.5 $\pm$ 1.2