

AMOUNT OF VISUAL FEEDBACK AND MOVEMENT CONTROL AND LEARNING IN
OLDER ADULTS

By

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To honor the memory of my mother and father, who taught me to pursue knowledge for its own sake.

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LIST OF ABBREVIATIONS

1-RM	One Repetition Maximum
Ag	Silver
AgCl	Silver Chloride
ANOVA	Analysis of Variance
AXWPS	Absolute Cross-Wavelet Power Spectrum
CV	Coefficient of Variation
DLPFC	Dorsolateral Prefrontal Cortex
EMG	Electromyography
FDI	First Dorsal Interosseous Muscle
Hz	Hertz
M1	Primary Motor Cortex
MVC	Maximal Voluntary Contraction
NXWPS	Normalized Cross-Wavelet Power Spectrum
PMC	Premotor Cortex
RMS	Root Mean Square
RMSE	Root Mean Squared Error
SD	Standard Deviation
SEM	Standard Error of the Mean
SMA	Supplementary Motor Area
SPI	Second Palmar Interosseous Muscle
TA	Tibialis Anterior Muscle
WPS	Wavelet Power Spectrum

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The purpose of this dissertation was to investigate the factors that influence practice induced adaptations in young and older adults and the use of visual feedback to facilitate acquisition and transfer of novel motor tasks in older adults. Two main issues in the aging literature were explored experimentally during a sinusoidal movement task. The first issue was based on the hypothesis that impaired motor planning would inhibit motor learning in older adults. The second and major issue is based on the hypothesis that age-associated amplification of motor output variability is caused by an impairment in visual feedback processing in older adults. Theoretically, an amplification in motor output variability compromises motor learning. Three experiments were designed to test these hypotheses. The findings from the first two studies showed that impaired visual feedback processing not motor planning accounted for the age-associated differences in motor performance. Specifically, the impairments in visual feedback processing were evident with greater amount of visual feedback. Moreover, there were no differences in the rate of acquisition between young and older adults. The third experiment extended these findings and showed that training with reduced amount of visual feedback enhanced motor learning in older adults. This was evident from better

motor performance of the reduced visual feedback training group during transfer compared with the groups that practiced with greater amount of visual feedback. Furthermore, older adults who exhibit lower motor output variability during practice exhibited lower movement errors during transfer. These findings suggest that: 1) Visual feedback processing is compromised in older adults and impairs motor performance and motor learning; and 2) Reduced visual feedback during task acquisition minimizes motor output variability in older adults to the level of young adults and enhances task acquisition and transfer.

CHAPTER 1 INTRODUCTION

Aging is accompanied with sensorimotor structural and functional declines in the neuromuscular system. Structural changes include adaptations in numerous structures of the brain (Dinse 2006), degeneration of cortical motor neurons and cerebral white matter (Eisen et al. 1996; Nordahl et al. 2006) and death of spinal alpha motor neurons (Masakado et al. 1994; Roos et al. 1997). Functional changes include slowing of corticospinal and reflex-pathway signals to the motor neurons (Henderson et al. 1980) and impairment in sensory information transmission as evident from changes in the aging visual system (Owsley 2010). These age-associated changes in the nervous system may alter the planning and execution of the motor command and amplify the variability of the motor output (Christou 2009; Harris and Wolpert 1998).

Motor output variability is defined as the involuntary inconsistency in the output of voluntary muscle contractions (Christou 2010b). Aging amplifies motor output variability and impairs the ability of older adults to perform motor tasks with accuracy (Christou 2010a). Recent evidence suggests that the amount of visual feedback (e.g. gain) during performance interacts with the ability of older adults to perform motor tasks. Specifically, increasing the gain of the visual feedback amplifies motor output variability only in older adults but not young adults (Kennedy and Christou 2010; Sosnoff and Newell 2006; Vaillancourt et al. 2003; Welsh et al. 2007). This suggests that impaired visual information processing amplifies motor output variability and deteriorates motor performance in older adults.

Theoretically, it has been suggested that amplified motor output variability during practice negatively influences updating of the motor command for subsequent

movements towards the same goal. Inversely, the central nervous system learns to perform new tasks with accuracy by minimizing motor output variability (Wolpert and Ghahramani 2000). Recent experimental evidence suggest that the ability to predict movement endpoint is impaired in older adults due to the age-associated amplification in motor output variability (Chen et al. 2011). The ability to predict the outcome of one's performance is necessary for the successful updating of the motor command during task acquisition (Wolpert et al 2011). Taken together amplified motor output variability in older adults would impair movement execution across practice and potentially impair their ability to learn novel tasks. Although older adults demonstrate the ability to improve motor performance with practice, their inability to match the performance of young adults also suggests that motor learning may be impaired (Christou et al. 2007a; Seidler 2007b). Nonetheless, it is unclear if they can share components of the practiced task to newer and different tasks (transfer) (Seidler 2007a).

In sum, these findings suggest that amplified motor output variability due to impaired visual information processing and motor planning potentially mediates the motor learning deficits in older adults. Therefore, the gain of visual feedback may be an important training variable to enhance the acquisition and transfer of novel motor tasks in older adults. The purpose of this dissertation is to investigate whether different amounts of visual feedback can be used in training interventions to facilitate the acquisition and transfer of novel motor tasks in older adults. The goal of this chapter is to provide background and rationale for the above highlighted issues as follows: a) Aging and motor output variability; b) Aging and motor learning; c) Training protocols to improve motor performance in older adults.

Motor Output Variability Increases with Age

Human movement is inherently variable and fluctuates around its mean performance. This variability in motor output is defined as the involuntary inconsistency in the output of voluntary muscle contractions (Christou 2010b). Motor output variability is observed during a movement (e.g. trajectory variability) (Baweja et al. 2009; Christou et al. 2010) and between successive movements towards the same goal (e.g. endpoint variability) (Christou et al. 2007a). An amplification of motor output variability is undesirable as it would impair accuracy of the motor output (Harris and Wolpert 1998) and interfere with the performance of functional activities (Kornatz et al. 2005; Kouzaki and Shinohara 2010; Lipsitz 2002). Motor output variability amplifies with advancing age and various factors such as: 1) level of force (Laidlaw et al. 2000); 2) stress (Christou 2005); 3) contraction type (Christou and Carlton 2002b); and, 4) visual feedback (Kennedy and Christou 2010), contribute to these differences.

Older adults exhibit an amplification in motor output variability during both single and multi-joint movements. These age-associated impairments in motor output variability have been demonstrated during: a) constant isometric contractions (Galganski et al. 1993; Tracy 2007a); b) rhythmic isometric contractions (Patten and Kamen 2000; Voelcker-Rehage and Alberts 2005); c) goal-directed ballistic contractions (Christou and Carlton 2001); and, d) anisometric contractions (Kornatz et al. 2005). Age-associated impairments in motor output variability have also been demonstrated during functional tasks such as reaching movements (Seidler-Dobrin et al. 1998), postural adjustments (Era and Heikkinen 1985) and gait (Grabiner et al. 2001).

Experimental Tasks

Constant tasks. One of the most common experimental tasks used to study motor output variability is the constant task. The objective of this task is to extract differences in motor behavior while sustaining various levels of force or maintaining loads at constant positions. There is amassing evidence that older adults exhibit significantly greater force variability compared with younger adults. For example, isometric force control was tested on young and older adults from 2.5-50% MVC (Galganski et al. 1993). Older adults exhibit greater force variability and errors compared with young adults across all force levels. The differences in force variability were exacerbated at low forces (< 15% MVC), which is supported by numerous subsequent findings (Enoka et al. 2003; Keen et al. 1994; Kennedy and Christou 2010; Laidlaw et al. 2000; Tracy and Enoka 2002).

Similar findings have been reported when subjects are asked to maintain loads at a constant position. Young and older adults were asked to accurately match and maintain a constant position with index finger abduction and ankle dorsiflexion at loads ranging from 2 to 50% 1-RM. Positional variability was greater in older adults for both limbs, nonetheless age-associated differences were exacerbated during ankle dorsiflexion compared with index finger abduction (Kwon et al. 2011). These findings suggest that older adults exhibit amplified motor output variability while steadily maintaining a constant force or position.

Sinusoidal tasks. Many activities of daily living require the precise modulation of motor output (e.g. controlling the gas pedal during driving). Experimentally it can be studied using sinusoidal motor tasks, which requires the production and relaxation of forces (reciprocal activity). Findings from these studies also suggest that older adults

exhibit significantly greater force variability compared with younger adults (Kamen and Knight 2004; Keogh et al. 2006; Patten and Kamen 2000; Sosnoff and Voudrie 2009; Voelcker-Rehage and Alberts 2005). For example, subjects were asked to match a sinusoidal target ranging from 5-25% MVC during a pinch grip task. Older adults exhibited larger errors and amplified force variability compared with young adults (Voelcker-Rehage and Alberts 2005). It has been reported that these differences are greater especially at the lower end of the target force range (Keogh et al. 2006). In another study, the target was a sum of multiple sine waves, therefore subjects had to modulated forces across a variable range of forces. Consistent with findings from previous studies, older adults exhibited greater motor output variability compared with young adults (Patten and Kamen 2000). The findings from these studies suggest that the ability to modulate forces rhythmically is impaired with aging.

Ballistic goal-directed tasks. Consistency of the motor output across successive movements towards the same goal is essential for successful task completion (e.g. reaching movements). This is tested experimentally using rapid discrete goal-directed contractions. The objective of this task is to understand the influence of motor planning and execution on motor output variability across successive movements (trial-to-trial variability). An advantage of testing a rapid ballistic contraction is that there is not enough time to correct the errors during execution of the movement. Therefore, subjects pre-plan the subsequent movement based on endpoint feedback from the preceding trials. Trial-to-trial variability also amplifies with aging and impairs endpoint accuracy (Chen et al. 2012; Christou and Carlton 2001; Christou and Enoka 2011; Poston et al. 2008). For example, young and older adults were asked to perform rapid discrete

isometric knee extension to test the control of submaximal levels of force (5-90% MVC). Older adults exhibited greater CVs of peak force and temporal errors when compared with younger adults (Christou and Carlton 2001). Additionally, these age-associated differences were greater at low intensity contractions. Similar age-associated amplification in end-point variability has been demonstrated with goal-directed contractions using the fingers (Chen et al. 2012; Poston et al. 2008). The findings from these studies suggest that trial-to-trial variability amplified with aging and is associated with impaired endpoint accuracy.

Lifting and lowering tasks. Many movements require the control of lifting and lowering objects (e.g. lifting and lowering a shopping bag). This is important because the activation of muscles is different for lifting and lowering contractions (Enoka et al. 2003). Therefore, the objective of this task is to examine the control of shortening and lengthening contractions during movements. Age-associated amplification in motor output variability has also been reported during these tasks. For example, when lifting and lowering an inertial load with the index finger or knee, older adults exhibited greater trajectory variability and lesser accuracy compared with young adults (Christou and Carlton 2002a; Christou et al. 2003a; Kornatz et al. 2005; Laidlaw et al. 2000). The age-associated differences in trajectory variability are greater during lengthening (lowering) contractions when compared with shortening (lifting) contractions. Furthermore, it has been demonstrated that this amplification in variability with aging is greater with light loads (< 10 % 1-repetition maximum) (Christou et al. 2003a; Laidlaw et al. 2000; Tracy and Enoka 2002). These findings demonstrate that the age-associated differences in trajectory variability are exacerbated during low intensity lengthening contractions.

Functional tasks. Functional movements such as balance, walking, and reaching with the arm are also influenced by the age-associated amplification in motor output variability. For example, during walking older adults exhibited greater stride width variability (Grabiner et al. 2001). During quiet standing also older adults exhibited greater postural sway compared with young adults (Era and Heikkinen 1985; Lord and Menz 2000). This amplification in postural sway and gait parameters are associated with a higher incidence of falls in older adults (Melzer et al. 2004; Rubenstein et al. 2001).

Similar age-associated amplification in movement variability is seen during goal-directed reaching movements. Older adults exhibited greater trajectory variability and slower error corrections during reaching movements with the arm (Seidler-Dobrin et al. 1998). A follow-up investigation tested the age-associated difference in control of single and multi-joint reaching movements. Subjects were asked to reach various targets with just the elbow and with both shoulder and elbow. Older adults exhibited greater movement variability during both movements. Furthermore, the movement variability in older adults was greater during multi-joint compared with single-joint reaching (Seidler et al. 2002). The findings from these studies on functional tasks suggest that amplified motor output variability negatively impacts the mobility and functional independence of older adults.

In sum, motor output variability is amplified with age. This amplification in motor output variability interacts with the ability of older adults to perform various motor tasks with accuracy. Older adults exhibit greater motor output variability during light-load and lowering tasks. These age-associated differences in motor output variability are also seen during functional movements.

Visual Feedback

Visual feedback is a major source of sensory input. Visual information provides spatial cues, trajectory feedback, and information about the appearance of the environment. The amount of visual feedback received during task performance is an important factor that interacts with motor output variability in older adults. The two most common ways of manipulating the amount of visual feedback are the complete removal of visual feedback for part(s) of the trial and by manipulating the gain of the target and performance feedback. Experimentally, amplifying the gain of visual signals enhances performance on tasks such as drawing (Prager and Contreras-Vidal 2003) and force control (Baweja et al. 2010) in young adults. In contrast, in older adults it amplifies force variability (Kennedy and Christou 2010; Sosnoff and Newell 2006; Tracy 2007b; Vaillancourt et al. 2003; Welsh et al. 2007). Moreover, reducing the amount of visual feedback by completely removing it or reducing the gain ameliorates the age-associated differences in force variability (Kennedy and Christou 2010; Tracy 2007b; Welsh et al. 2007).

Removal of visual feedback. The absence of visual feedback eliminates the need for visuomotor corrections. Older adults have impairments in visuomotor corrections due to the structural changes to the visual system and slowing down of visual information processing (Owsley 2010). Removal of visual feedback, therefore, minimizes the age-associated differences in motor output variability. For example, when young and older adults controlled knee-extension forces from 5-90% MVC and visual feedback was alternated with no-vision segments. No differences in force variability were reported between young and older adults during the no-vision segments (Christou and Carlton 2001). This means that in the absence of visuomotor corrections the

system's output is similar irrespective of age. In another study, the steadiness of ankle dorsiflexion with and without visual feedback was tested across submaximal forces. The removal of visual feedback reduced force variability by 19% in older adults compared with when visual feedback was present (Tracy 2007b). In a follow-up study, older adults exhibited significantly lower force variability compared with young adults when visual feedback was removed (Welsh et al. 2007). Recent findings from our lab support these findings during isometric contractions with the first dorsal interosseous at 2 and 30% MVC. Older adults exhibited no differences in force variability compared with young adults in the absence of visual feedback (Kennedy and Christou 2010). This age-associated amplification in motor output variability during vision suggests that the ability to make visuomotor corrections is compromised in older adults.

Manipulation of visual feedback gain. Manipulation of the visual feedback gain provides an insight to the influence of visual information processing on motor output variability. Visual feedback gain is manipulated by increasing or decreasing the spatial amplitude of the displayed feedback without changing the magnitude of the target. It has been recently suggested that different pathways are involved in the transmission of low and high gain visual feedback (Coombes et al. 2010). Furthermore, selective degeneration of certain regions of the cortex involved in these pathways accompanies aging (Raz et al. 1997).

Manipulating the visual feedback gain interacts with motor output variability in older adults. For example, young and older adults were asked to match a target line at eight different visual gains from low to high (2 - 512 pixels/Newton). It was reported that force variability exhibited a U-shaped function with visual feedback gain. Specifically,

older adults were less variable at lower amounts of visual feedback compared with young adults (Sosnoff and Newell 2006). In a follow-up study, young and older participants performed submaximal (2 and 30% MVC) constant isometric contractions with the index finger at three different visual angles (0.05°, 0.5° and 1.5°; (Kennedy and Christou 2010)). Young and older adults demonstrated similar force variability at the lowest gain and the ageing differences were exacerbated with the increase in visual feedback gain.

These age-associated differences in motor output variability with greater amount of visual feedback have recently been extended to position holding tasks with the index finger and foot (Baweja et al. 2011). Young and older adults maintained a 10% 1-RM load at 10° of index finger abduction and ankle dorsi-flexion. The gain of the visual feedback was manipulated by changing the visual angle from 0.1 - 4°. Older adults exhibited greater positional variability compared with young adults. This amplification in positional variability was exacerbated with increase in the visual feedback gain from 0.1 to 4° (Baweja et al. 2011). Our findings further demonstrate that visual feedback processing maybe impaired with aging. Specifically, this impairment is exacerbated with greater visual feedback. Therefore, the manipulation of visual feedback gain is a beneficial tool to regulate motor output variability in older adults.

Overall, impairments in visual information processing mediate the age-associated amplification of motor output variability. It has been suggested that this impairments in visual feedback processing can influence the descending drive to the spinal motor neuron pool (Scott 2004). Consequently, leading to alteration of the motor command and neural activation of muscles, and compromise motor performance.

Mechanisms that Influence Motor Output Variability in Aging

The following mechanisms have been proposed to influence motor output variability with aging (Enoka et al. 2003): 1) the changes in motor unit properties such as motor unit twitch force and discharge rate variability; 2) synergistic activation of agonist muscles; and, 3) co-activation of antagonistic muscles. These mechanisms have been investigated across the range of experimental tasks described previously. The findings from these studies will be discussed in this section.

Motor unit twitch force. Even healthy aging induces the death of spinal alpha motor neurons and the reorganization of the remaining motor neurons (Masakado et al. 1994; Roos et al. 1997). There is a reorganization of the motor neuron pool due to selective apoptosis of large alpha motoneurons (Masakado et al. 1994). The smaller alpha motoneurons re-innervate the muscle fibers from the dying large alpha motor neurons and thus increasing their innervation ratio and twitch strength (Roos et al. 1997). Initially, it was proposed that motor unit twitch strength potentially accounted for the amplified motor output variability exhibited by older adults during low forces (Galganski et al. 1993). In contrast, a 12-week strength-training program demonstrated that older adults reduced force variability with practice without changing the motor unit twitch strength (Keen et al. 1994). Thus twitch strength of the remodeled motor units appears not to be a potential contributor to the age-associated decline in motor output variability.

Motor unit discharge rate variability. A second property of motor units that could potentially influence motor output variability is their discharge rate variability. The steadiness of motor unit discharge rate can be tested using constant isometric contractions at various levels of forces. Experimentally, it has been demonstrated that

motor unit discharge rate variability potentially accounts for the amplified motor output variability in older adults. Specifically, motor unit discharge rate is more variable for older adults compared with young adults. This difference is even greater at lower force levels (<15 % MVC) (Enoka et al. 2003; Laidlaw et al. 2000; Laidlaw et al. 2002). Additional support for this notion comes from simulation studies (Moritz et al. 2005; Taylor et al. 2003). Specifically, simulations using the Fuglevand model (Fuglevand et al. 1993) of motor unit recruitment and rate coding have demonstrated that increasing the motor unit discharge variability amplifies simulated force variability across a range of force levels (4 – 85% MVC; (Moritz et al. 2005)).

These findings extend to sinusoidal tasks. Specifically, older adults exhibit greater motor unit discharge rate variability compared with younger adults during variable force contractions (5-60 % MVC; (Patten and Kamen 2000)). Furthermore, older adults demonstrate greater variability in force per change in motor unit firing rate (Knight and Kamen 2007) compared with young adults. This means that an amplification in motor output variability is positively associated with an increase in the motor unit discharge rate variability. Therefore, a reduction in motor output variability should be associated with a decrease in the discharge rate variability. Interestingly, it has been shown that practice leads to a reduction in motor output variability in older adults (Patten and Kamen 2000; Sosnoff and Voudrie 2009; Voelcker-Rehage and Alberts 2005). This improvement was accompanied with an increase in the maximal motor unit discharge rates in older adults (Patten and Kamen 2000). Further support for this comes from studies on anisometric contractions using shortening and lengthening contractions (Kornatz et al. 2005; Laidlaw et al. 2002).

These studies also report that motor unit discharge rate is more variable in older adults when compared with young adults. The impairment is exacerbated during lengthening (eccentric) contractions where lesser motor units are recruited (Laidlaw et al. 2002) and the discharge rate is more variable (Kornatz et al. 2005; Laidlaw et al. 2002). Furthermore, age-associated differences in trajectory variability can be reduced with practice and are accompanied with lowering of the motor unit discharge rate variability in older adults (Kornatz et al. 2005). These findings suggest that motor unit discharge rate variability significantly contributes to the amplification of motor output variability in older adults.

Activation of agonist muscles. The surface EMG signal recorded from the agonist muscle is a proxy of multiple simultaneously activated motor units. It is evident from the single motor unit studies that altered neural activation of the agonist muscle influences motor output variability in aging. Agonist muscle activity can be quantified in terms of oscillations in the surface EMG signal of the primary agonist or simultaneous activation of synergistic muscles involved in the task. During goal directed contractions older adults exhibit slower time-to-peak force generation in agonist EMG bursts (Poston et al. 2008). The amplification in variability during a sinusoidal pinch-grip task is associated with an altered activation of synergistic muscles in older adults. Older adults also exhibited a greater time lag in synergistic muscle activation (Keogh et al. 2006). This indicates that aging is accompanied with a decline in the timing of activation of agonist muscles. Recent findings from our lab demonstrate that age-associated amplification in trial-to-trial variability was associated with an altered activation of synergistic hand muscles from 13-30 and 30-60 Hz in the EMG (Chen et al. 2012).

Oscillations from 13-30 Hz in EMG are associated with the synchronization of motor unit discharges (Moritz et al. 2005). The 30-60 Hz EMG band is believed to reflect modulation of the descending drive with an increase in voluntary effort (Neto et al. 2010; Neto and Christou 2010). These findings suggest that there is an age-associated alteration in the modulation of the agonist muscle activation which contributes to the amplification of motor output variability.

Activation of antagonistic muscles. Changes in the agonist-antagonist activation pattern also contribute to the motor output variability during different tasks. For example, during anisometric contractions older adults exhibited greater coactivation of knee flexors and extensors during lifting and lowering inertial loads compared with young adults (Tracy and Enoka 2002). Furthermore, older adults coactivate more during the lowering phase of the contraction (Christou and Enoka 2011). With practice older adults have been shown to reduce their endpoint errors to the level of young adults, although the antagonistic muscle activation patterns were different for young and older adults. Specifically, while young adults shortened the timing of agonist-antagonist muscle activation, older adults exhibited a prolongation in this timing primarily due to modulation of the agonist muscle (Christou et al. 2007a). In another study, Patten and Kamen (2000) reported that older adults reduced motor output variability with practice, which was accompanied with a decrease in antagonistic coactivation (Patten and Kamen 2000). During reaching movements older adults exhibit greater trajectory variability and these are associated with an increased coactivation of shoulder and arm muscles (Seidler-Dobrin et al. 1998; Seidler et al. 2002). It has also been demonstrated that older adults exhibit greater coactivation of lower limb muscles when descending

stairs as preemptive means to increase stability (Hortobagyi and DeVita 1999).

Together, these findings suggest that altered agonist-antagonist activation patterns contribute to the aging differences in motor output variability during various tasks.

Overall, the global finding of all these investigations is that motor output variability amplifies with age and impairs performance in older adults. This amplification in motor output variability is: 1) predominant at low-intensity contractions; 2) coupled with impaired visual information processing in older adults; and 3) associated with altered modulation of the spinal motor neuron pool.

Functional Significance of Motor Output Variability

The age-associated amplification of motor output variability impacts the functional independence of older adults. Amplified motor output variability in older adults has been demonstrated during functional tasks such as postural control, gait and reaching movements. Recently, a study independently tested ankle plantar flexion force variability and postural sway during quiet standing in young and older adults. There was a positive correlation between plantar-flexion force variability and center of pressure variability during quiet standing. Specifically, amplified plantar-flexion force variability during low-intensity contractions predicted the poorer postural stability in older adults (Kouzaki and Shinohara 2010). Studies on balance during quiet standing further support these findings and indicate that older adults exhibit larger amplitude and frequency of postural sway during quiet stance compared with young adults (Era and Heikkinen 1985; Lord and Menz 2000). During walking older adults have greater stride-width variability when compared with younger adults (Grabiner et al. 2001). These impairments in balance and gait are associated with a higher incidence of falls in older adults (Rubenstein et al. 2001). It has also been reported that older drivers exhibit

greater ankle movement variability compared with young drivers. Moreover, this amplification in foot movement variability has been implicated to errors in pedal control during driving (Cantin et al. 2004; Gamache et al. 2010). Together, these findings underscore the importance and impact of single-joint control on functional outcomes substantiating the need to reduce motor output variability in older adults.

Motor Output Variability Interacts with Motor Learning

An important functional consequence of motor output variability is its role in motor learning. Theoretically, amplified motor output variability leads to errors in execution and negatively influences updating of the motor command for subsequent movements (Harris and Wolpert 1998). Therefore, the central nervous system learns to perform new tasks with accuracy by minimizing motor output variability (Wolpert and Ghahramani 2000). Reduction in the motor output variability and continuous updating of the motor command enhances reinforcement of the task constraints and is associated with further reduction of motor output variability with sustained practice (Wolpert et al. 2011).

Motor output variability amplifies with age. The amplification in motor output variability negatively impacts the functional independence of older adults as discussed previously. Therefore, it is necessary to reduce motor output variability in older adults and improve motor learning. Amplification in motor output variability with aging would impair the planning and updating of the motor command, therefore, weakening motor learning in older adults. Recent evidence from our lab provides empirical support to the theoretical concepts that link motor output variability and learning. Young and older adults practiced unloaded goal-directed contractions that involved accurately matching a position-time target. After each trial, subjects were asked to predict their performance by reporting the endpoint coordinates in terms of position and time. Following the

prediction, performance trajectory and target was provided to the subjects for feedback and error correction. Older adults exhibited poorer prediction ability and motor performance compared with young adults. The impaired ability to predict movement endpoint was associated with the amplified motor output variability in older adults (Chen et al. 2011). Our findings suggest that amplified motor output variability in older adults compromises motor planning and the ability to learn novel tasks.

Motor Learning is Impaired with Age

Motor learning is defined as *a set of processes that are associated with practice or experience leading to relatively permanent changes in the capability for producing skilled action* (Schmidt and Lee 2011). The improvements in performance during practice (acquisition phase) are often associated with changes to the sensory and motor systems. Such changes include the extraction of task-relevant information from sensory resources and the selection and implementation of strategies that revise the motor command to improve task performance (Wolpert et al. 2011). The initial rapid improvements that are often observed during the acquisition phase occur primarily due to adjustments that aim to reduce the error relative to the target (Floyer-Lea and Matthews 2005). Once the learner matches the average performance to the target, subsequent adjustments are associated with the reduction in the variability of performance (reinforcement; (Wolpert et al. 2011)), which are slower than the initial adjustments (Floyer-Lea and Matthews 2005; Wolpert et al. 2011). The relatively permanent changes are evaluated with transfer tasks (Seidler 2007a; b). Transfer tasks are those that share identical features with the practiced task, yet are newer and distinct from the practiced task. Such tasks reflect the ability of the learner to generalize parameters of the practiced task to newer tasks and evaluate the permanence of

practice-induced adaptations (Schmidt and Lee 2011; Seidler 2007a; Wolpert et al. 2011).

There is evidence suggesting that motor learning is impaired in older adults when compared with young adults (Harrington and Haaland 1992; Howard and Howard 1997; Shea et al. 2006). Age-associated declines in motor learning have been demonstrated in studies testing sequence-learning, visuo-motor rotations and goal-directed tasks. The investigations that have applied these paradigms to study acquisition and transfer in aging are discussed further.

Acquisition

Sequence-learning. Studies investigating the effects of planning on motor learning suggest that the ability to organize subsequent movements reduces with aging. The findings from these studies also note that older adults learn at slower rates and are unable to improve performance beyond a certain limit while young adults continue to improve. For example, Harrington and Haaland (1992) tested a group of subjects on a serial reaction-time task. For this task sequences of hand postures were repeated in a cyclical pattern and then shifted to random sequences. Practice involved learning a 10-element sequence for the first four blocks followed by two blocks of random element sequence and last two blocks of the initial practice sequence. A second group of subjects comprising of both young and older adults practiced only random sequences of the task. Improvements in performance were quantified as lowering in movement times to the stimuli. The authors reported that older adults did not benefit from practicing either the repeated or random training protocols compared with young adults. Furthermore, random presentations of the task during practice amplified the learning impairments in older adults (Harrington and Haaland 1992). In another study, subjects

practiced a serial reaction-time key-pressing task. They were presented with either a fixed or random sequence of 4 stimuli, each corresponding to one of 4 keys on the keyboard. Subjects practiced 21 blocks of 90 trials for 6 days. Older adults demonstrated a slower rate of learning the pattern compared with young adults. The authors concluded that older adults could not explicitly memorize the sequence in which the stimuli were presented. Furthermore, even by the end of practice older adults could not match the performance of young adults (Howard and Howard 1997).

Shea and colleagues (2006) tested whether older adults could organize lengthy movement sequences as well as young adults. Subjects practiced a 16-element sequence with a manipulandum trying to match a series of dots projected onto a table with flexion and extension at the elbow. Training involved 16 blocks of 10 trials each. Improvements in performance were quantified in terms of how quickly the sequence was executed by the subjects. The authors reported that older adults performed the sequences significantly slower than young adults. Furthermore, the age-associated differences in the rate of improvements increased with practice because only younger adults improved significantly. The authors concluded that older adults exhibited impairments in sequence learning because they could not explicitly breakdown their movements into sub-sequences (chunks) as effectively as young adults (Shea et al. 2006). Findings from these studies suggest that deficits in organizing information during acquisition influences the updating of motor commands and compromises motor learning in older adults.

Goal-directed tasks. Studies evaluating the effects of motor planning on acquisition have also been performed using goal-directed tasks. The findings from these

studies suggest that the ability to estimate and correct performance may be impaired with aging, hence, compromising motor learning in older adults. For example, young and older adults practiced unloaded goal-directed contractions that involved accurately matching a position target in 180 milliseconds. Subjects performed these movements with ankle dorsiflexion and elbow flexion movements over two days in a counter balanced fashion. After each trial, subjects were asked to predict their performance by reporting the endpoint coordinates in terms of position and time. Following the prediction, performance trajectory and target was provided to the subjects for feedback and error correction. Older adults exhibited impairment in their ability to predict their end-point accurately compared with young adults. The impaired ability of older adults to predict their performance accuracy was associated with their amplified motor output variability (Chen et al. 2011). These findings suggest that amplified motor output variability during practice negatively influences updating of the motor command for subsequent movements (Faisal et al. 2008; Harris and Wolpert 1998; Wolpert and Ghahramani 2000). Together, compromised motor planning and execution contribute to the impaired task acquisition in older adults.

Visuo-motor adaptation. Studies evaluating the effects of visuo-motor transformations on motor learning suggest that the ability to adapt to sensory transformations reduces with aging. For example, young and older adults practiced a reaction-time line-tracing task. During practice, visual feedback of the target and performance trace was rotated in 8 directions at intervals of 45°, presented in random order. Subjects practiced 6 blocks of 30 trials each with the rotation. The authors reported that older adults showed deficits in acquisition with the visual rotations when

compared with young adults (McNay and Willingham 1998). Seidler (2006) verified that older adults exhibited impaired adaption to visuo-motor transformations during a joystick-aiming task compared with young adults. Subjects were divided into three groups to learn a sequence of actions under conditions involving either visual rotations of the feedback (30° and 45°) or a 1.5 times magnification of the visual feedback. Subjects performed 7 blocks of 24 trials: with the first two being the same for all feedback groups, the next three blocks involved practicing with the respective feedback manipulations and the last two blocks were baseline again. Older adults exhibited poorer and slower performance adaptation during the visual rotation trials as compared with young adults (Seidler 2006). This suggests that visuo-motor transformations and processing of visual information interacts with the ability of older adults to acquire a task. In a follow-up study, Seidler demonstrated that older adults exhibit poorer adaptation to visuo-motor rotation at 15°, 30° and 40° presented in a sequential fashion (Seidler 2007b). These findings confirm the results from motor output variability studies that visual-information processing declines with aging. This impairment compromises the ability of older adults to effectively adapt to the demands of the task as well as young adults.

The global finding from all these studies is that practice-induced adaptations are compromised in older adults. In part, these are due to impairments in visual information processing and motor planning. Specifically, these age-associated discrepancies are related to impaired visuo-motor adaptations during practice and the degree of impairment is task dependent. Moreover, an inability to effectively organize movements into sub-sequences impairs motor learning in older adults.

Transfer

Transfer of learning is the hallmark of motor learning because it reflects the learner's ability to share components of a learned skill to newer and different tasks (Schmidt and Lee 2011; Wolpert et al. 2011). The ability to transfer (generalizability) the acquired behavior renders a functional usefulness to practice. There is limited evidence whether transfer of learning is impaired in older adults.

Protocols using visuo-motor adaptations for testing acquisition have also been used to test transfer in young and older adults. For example, McNay and Willingham (1998) trained young and older adults on a line-tracing serial reaction-time task. During practice, visual feedback of the target and performance trace was rotated in 8 directions at intervals of 45°, presented in random order. Subjects practiced 6 blocks of 30 trials with the rotations. Transfer tests between each block and at the end of practice were performed without visual rotations (0°). The authors reported that older adults did not exhibit any differences in performance during the transfer tests when compared with young adults (McNay and Willingham 1998). In a follow-up study, Seidler (2007) demonstrated that older adults exhibit deficits in adaptation to visuo-motor rotation at 15°, 30° and 40° presented in a sequential fashion. Transfer was tested on trials without any visuo-motor rotation (0°) and older adults demonstrated similar performance as young adults during transfer (Seidler 2007a).

In contrast, findings from our lab suggest that transfer of learning is impaired in older adults and it is influenced by practice difficulty. Young and older adults practiced a visual feedback tracking task that required coordinated force production using the index and little fingers. Subjects were divided into three groups: Easy (0° relative phase), Hard (90° relative phase) and Control (no training) groups. To test motor learning all subjects

performed three transfer tracking tasks (45°, 135° and 180° relative phases) 24 hours after practice. Older adults exhibited poorer performance at transfer compared with young adults (Onuskhko et al. 2012). These findings suggest that transfer of learning maybe compromised on older adults.

In sum, motor learning is impaired with aging. There are deficits in extraction of sensory information with aging (McNay and Willingham 1998; Seidler 2006; 2007b) and motor planning is compromised in older adults (Shea et al. 2006). It is also unclear whether the ability to transfer information from the acquired task is compromised with aging. This necessitates the requirement to develop simple training paradigms that promote the effective use of visual information, lower motor output variability, and enhance acquisition and transfer in older adults.

Training Protocols to Reduce Motor Output Variability in Older Adults

The aging nervous system remains remarkably plastic, which is apparent from studies on motor learning in older adults. The inability of older adults to match the performance of young adults suggests that motor learning may be impaired with aging. Nonetheless, plasticity is evident in aging from benefits with practice seen as reductions in errors and motor output variability. Various long-term and short-term interventions have been explored to improve these age-associated declines in motor performance. The most prominent interventions include strength training (Tracy et al. 2001), light-load training (Kornatz et al. 2005), the martial art of Taiji (Christou et al. 2003b; Yan 1999), and protocols that emphasize co-ordination (Patten and Kamen 2000) and skill (Ranganathan et al. 2001).

Most of the studies on aging and practice suggest that older adults can reduce motor output variability with practice. Moreover, the reductions in motor output variability

are independent of increments in strength. For instance, Hortobagyi et al. (2001) reported an increase in the knee extensor strength after 10 weeks of high- and low-intensity training in older adults. Regardless of the type of training older adults exhibited similar declines in the SD of force during submaximal (12% MVC) contractions. The authors further reported that the declines in force variability were not correlated with the changes in strength following training (Hortobagyi et al. 2001). Supporting evidence comes from training studies of the FDI. Older adults participated in a low-intensity training (10% 1-repetition maximum) for 2 weeks followed by 4 weeks of strength training with 70% 1-repetition maximum. At the end of 2 weeks, older adults showed increases in maximal strength at weeks 2 and decreases in motor output variability. Nonetheless, at the end of the 4 weeks of strength training, they exhibited further increases in strength without additional reductions in motor output variability (Kornatz et al. 2005). Similar findings have been reported across various other studies. For example, Tracy et al. (2001) reported that following 16 weeks of strength training, young and older adults increased knee extensor strength without reducing motor output variability (Tracy et al. 2001). Similarly, Bellew (2002) reported that following 12 weeks of strength training older adults increased the MVC of knee extensors but did not reduce the CV of force during submaximal isometric contractions (Bellew 2002). Findings from training studies using Taiji have shown that both strength and force control improved in older adults following training. Nonetheless, these improvements in muscular strength and motor control were not associated (Christou et al. 2003b). These findings suggest that mechanisms other than the strength increases mediate the practice-induced improvements in motor performance. On the contrary, interventions emphasizing low-

intensity contractions and coordination seem to enhance the reduction of motor output variability in older adults.

Long-term low-intensity training emphasizing skill over strength is beneficial in reducing motor output variability in older adults. For instance, older adults practiced skillful control of 2 marble sized balls with the fingers. Following 8 weeks of training, older adults reduced their motor output variability and exhibited improved manual dexterity compared with age-matched controls (Ranganathan et al. 2001). Similar findings have been reported from studies that used Taiji as an intervention to train muscle coordination in older adults (Christou et al. 2003b; Yan 1999). Participants underwent 20 weeks of Taiji training 3 times a week. The movements were chosen to emphasize balance, weight shifting, range of motion, and whole body coordination. The authors reported that motor output variability in older adults decreased significantly following the Taiji training (Christou et al. 2003b). These studies, therefore, suggest that reductions in motor output variability in older adults can be achieved via training protocols focusing on skill and coordination.

Short-term low-intensity training has also proven to be beneficial in reducing motor output variability in older adults. Kornatz et al. (2005) demonstrated that after 2 weeks of light-load (10% MVC) movement training older adults significantly reduced their movement variability. Furthermore, they exhibited significantly higher manual dexterity scores at the end of training (Kornatz et al. 2005). In another study, young and older adults underwent 2 weeks of isometric force modulation training with ankle dorsiflexors. With practice older adults progressively reduced their motor output variability (Patten and Kamen 2000). These findings provide evidence that short-term low-intensity

coordination training reduces motor output variability and improve function (e.g. manual dexterity) in older adults.

In summary, practice reduces motor output variability and improves motor performance in older adults. This improvement in motor output variability is independent of strength gains. Interventions emphasizing coordination seem to be more beneficial for reducing motor output variability in older adults.

Visual Feedback Gain to Enhance Motor Learning in Older Adults

When learning to perform a novel motor task, the integration of visual information is necessary to make appropriate adjustments for successful completion of the task. Visual feedback is used to control and correct the ongoing movements and for updating the motor command for subsequent movements. Processing of visual information influences the formation and modification the descending drive to the spinal motor neuron pool (Scott 2004). Alterations in activation of the motor neuron pool consequently influence the magnitude of motor output variability (Faisal et al. 2008; Harris and Wolpert 1998). Furthermore, visual information processing is important to correct errors and reinforce the initial adaptations during learning (Hikosaka et al. 2002; Wolpert et al. 2011).

The interaction of aging and visual feedback is critical for the magnitude of motor output variability. Specifically, magnification of visual feedback (gain) impairs motor performance in older adults (Kennedy and Christou 2010; Sosnoff and Newell 2006) whereas it has a beneficial effect in young adults (Baweja et al. 2010). Because the age-associated amplification in motor output variability exacerbates with more visual feedback, it is unclear which amount of visual feedback should be provided to older adults during a training protocol.

Collectively, findings from studies suggest that impairments in visual information processing mediate the age-associated amplification of motor output variability. Additionally, the amount of visual feedback needed for minimizing motor output variability in young and older adults is different. Nonetheless, our understanding of the interaction of aging and visual feedback on motor output variability and learning novel fine motor tasks is limited from the following: 1) most of the investigations on the interaction of visual feedback gain and motor output variability in older adults were performed on constant isometric contractions; and, 2) there is no evidence on the magnification of visual feedback as an intervention to train novel fine motor tasks. Therefore, it is necessary to identify the influence of visual feedback manipulations on motor learning in older adults.

Summary

In summary, amplified motor output variability with advancing age is a realistic deterrent to the activities of daily life and functional independence in older individuals. This age-associated amplification of motor output variability is related to the altered neural activation of the spinal motor neuron pool. Furthermore, greater amount of visual feedback compounds these age-associated amplification in motor output variability. Therefore, suggesting that impaired visual information processing amplifies motor output variability in older adults when compared with young adults.

Practice seems to reduce motor output variability in older adults and improve motor performance. Regardless of the beneficial effects of practice age-associated differences in motor output variability and performance persist. Furthermore, higher visual feedback gain exacerbates the age-associated amplification in motor output variability. Recent evidence from our lab suggests that amplified motor output variability

negatively interacts with motor learning in older adults. Taken together, amplified motor output variability due to impaired visual information processing and motor planning potentially mediates the motor learning deficits in older adults. Therefore, the amount of visual feedback may be an important training variable to enhance motor learning in older adults.

The purpose of this dissertation was to investigate whether different amounts of visual feedback could be used as interventions to facilitate acquisition and transfer of novel motor tasks in older adults. This was examined across three studies described in Chapters 2 and 3. The first set of two studies (Chapter 2) investigated whether the short-term adaptations accompanying practice differ for young and older adults due to impaired visual information processing or altered motor planning. The third study (Chapter 3) investigated the effects of low- and high-gain visual feedback training in enhancing acquisition and transfer in older adults. The overall conclusions and future directions are discussed in Chapter 4.

CHAPTER 2

PROCESSING OF VISUAL INFORMATION COMPROMISES THE ABILITY OF OLDER ADULTS TO CONTROL FINE NOVEL MOTOR TASKS

Neural changes that accompany aging include adaptations in numerous structures of the brain (Dinse 2006), degeneration of cortical motor neurons (Eisen et al. 1996; Nordahl et al. 2006) and death of spinal alpha motor neurons (Masakado et al. 1994; Roos et al. 1997), as well as, the slowing of the signal transmitted from the corticospinal and reflex pathways to the motor neurons (Henderson et al. 1980). In addition, sensory information transmission appears to be impaired as it is evident from changes in the visual system (Owsley 2010). These age-associated changes in the nervous system may alter the planning and execution of the motor command, amplify the variability of the motor output (Christou 2009; Harris and Wolpert 1998), and consequently impair the ability of older adults to perform and learn novel motor tasks (Christou 2010a).

Learning of a motor task includes both short- (acquisition) and long-term adaptations (e.g. retention and transfer) to the nervous system (Hikosaka et al. 2002). In this paper we were primarily interested in the age-associated differences in short-term adaptations because, although controversial (Seidler 2007b), there have been reports that older adults exhibit impaired adaptations during practice compared with young adults (Christou 2009; Seidler 2007a). The two primary mechanisms proposed as explanation for the impaired short-term adaptations in older adults are altered motor planning (Shea et al. 2006) and processing of visual feedback (Kennedy and Christou 2010). The evidence for motor planning comes from Shea et al. (2006) who demonstrated that with practice of a sequential elbow task older adults do not learn to adapt their sequential movements (chunking) as well as young adults. In terms of processing of visual feedback, numerous recent studies provide evidence that older

adults exhibit an impaired ability to process greater amount visual information (Sosnoff and Newell 2006; Tracy 2007b; Welsh et al. 2007). Interestingly, increased gain of visual feedback amplifies motor output variability in older adults (Kennedy and Christou 2010), which theoretically could result in impaired learning (Faisal et al. 2008; Wolpert and Ghahramani 2000). Furthermore, young adults alter the neural activation of the agonist muscle with changes in the gain of visual feedback, whereas older adults do not (Kennedy and Christou 2010).

Visual information is unquestionably an important source of feedback for movement planning, execution, and control (Scott 2004). Nonetheless, the interaction of aging and visual feedback on short-term adaptations is not well understood. The purpose of this study, therefore, was to determine whether short-term adaptations that occur during the practice of a novel motor task differ for young and older adults due to altered motor planning or impaired processing of visual information. To address this purpose we performed two experiments, which primarily manipulated visual feedback to determine the contributions of motor planning and processing of visual information on short-term adaptations. Part of the findings have been reported in abstract form (Baweja et al. 2010; Christou et al. 2010).

Methods

Experiment 1

Participants. Twelve young adults (aged 20-32 years, 7 men and 5 women) and twelve older adults (aged 65-85 years, 6 men and 6 women) volunteered to participate in this study. All subjects were naïve to the aims of the study. All subjects reported being healthy without any known neurological problems, were right-handed according to a standardized survey (Oldfield 1971), and had normal or corrected vision. The

Institutional Review Board at Texas A&M University approved the procedures, and subjects provided written informed consent before participation in the study.

Experimental arrangement. Each subject was seated comfortably in an upright position facing a 27 inch computer screen (Samsung Syncmaster™ 275T+, Samsung Electronics America, NJ, USA) that was located 1.25 m away at eye level. The monitor was used to display the movement produced by the abduction of the index finger. All subjects affirmed that they could see the display clearly. The left arm was abducted by 45° and flexed to ~90° at the elbow. The left forearm was pronated and secured in a specialized air pillow (Versa Form™, AB Germa, Sweden). The thumb, middle, ring, and fifth fingers of the left hand were restrained with metal plates and there was approximately a right angle between the index finger and thumb. Only the left index finger was free to move. The left index finger was placed in an adjustable finger orthosis to maintain extension of the middle and distal interphalangeal joints and was abducted 5° from the neutral position. This arrangement allowed abduction-adduction of the index finger about the metacarpophalangeal joint in the horizontal plane, a movement produced almost exclusively by the contraction of the first dorsal interosseous (FDI) muscle (Chao et al. 1989). The primary antagonist muscle is the second palmar interosseous (SPI) muscle (Christou and Enoka 2011).

Measurement of index finger movement. Movement was produced by the abduction-adduction of the left index finger over a 10° range of motion about the second metacarpophalangeal joint. The abduction–adduction movement of the index finger was measured with a low-friction potentiometer (SP22GS-5K, Mouser electronics, Mansfield, TX, USA) that was located directly under the metacarpophalangeal joint. The index

finger movement was sampled at 1 kHz with a Power 1401 data acquisition system (Cambridge Electronic Design, Cambridge, UK) and stored on a computer.

EMG measurement. Activation of the FDI and SPI muscles was measured with intramuscular bipolar electrodes. Each electrode comprised of a Formvar-insulated stainless steel wire (50 μm diameter; California Fine Wire Company, Grover Beach, CA, USA). The recording area of the wire (electrode) was ~ 0.5 cm to ensure that global muscle activity from multiple active motor units was recorded. The wire was threaded through a single use, 30-gauge hypodermic needle and inserted percutaneously into the belly of each muscle; the needle was removed after the wires were inserted. Reference electrodes were placed on the ulnar styloid process for FDI and on the radial styloid process for SPI. The EMG signals were amplified ($\times 5,000$) and band-pass filtered (5–6,000 Hz; Grass Model 15LT system, Grass Technologies, West Warwick, RI, USA). The EMG signals were sampled at 10 kHz with a Power 1401 data acquisition system (Cambridge Electronic Design, Cambridge, UK) and stored on a personal computer.

Experimental procedures. Subjects participated in one experimental session that lasted approximately 2.5 hours. Each subject began the session with a familiarization of the experimental procedures. The familiarization included a demonstration of the abduction-adduction movement and an explanation of the feedback provided on the monitor. After the familiarization, each subject performed the following procedures: 1) maximal voluntary contractions (MVC) with the FDI (abduction of the index finger) and SPI (adduction of the index finger) muscles; 2) 40 trials with visual feedback (vision) of movement trajectory (eight blocks of five contractions) and 8 trials without visual feedback (no-vision) of the movement trajectory at the end of every block of practice

trials; 3) watch a 1 hour movie (interference task); 4) 5 no-vision trials and 5 vision trials to test retention of the task (see Figure 2-1A for schematic of the protocol); and, 5) MVCs with the FDI and SPI muscles.

MVC task. Subjects were instructed to exert maximal abduction (FDI) and adduction (SPI) forces with the index finger. MVC force was measured with a one-dimensional transducer (FORT 250 rigid-lever force transducer, World Precision Instruments Inc., FL, USA). Subjects were instructed to increase the force from baseline to maximum over a 2 s period and maintain the maximal force for about 4 s. Five such recordings were made or until two of the maximal trials were within 5% of each other. Each subject was given a 60 s rest between consecutive trials. The maximal voluntary contraction (MVC) force was quantified as the average force over 3 s (constant part) of the highest trial. MVC's were performed for two reasons: 1) To normalize the submaximal EMGs of the FDI and SPI muscles; and 2) To test whether the experimental task induced muscle fatigue (difference in MVC before and after the session).

Sinusoidal task. A custom-written program in Matlab® (Math Works™ Inc., Natick, Massachusetts, USA) was used to provide the targeted movement and visual feedback condition (presence or absence of the movement trajectory). The gain of visual feedback remained constant at 5.4° throughout the experiment. The subjects had to match a position-time sinusoidal target with amplitude of 10° and a frequency of 0.1 Hz. The target was provided as a red line in the middle of the screen and the movement of the subjects as a blue line progressing with time from left to right (Figure 2-1A). Abduction of the index finger corresponded to the blue line going up on the screen and

adduction corresponded to the blue line going down on the screen. The movements were completely unloaded and subjects were asked to match the sinusoidal target as accurately and as smoothly as possible. Each trial lasted 40 s and subjects performed a total of 48 trials (40 vision and 8 no-vision trials) with 30 s between trials and 1 minute between blocks. Following these 48 trials subjects watched a movie for 1 hour and then performed 5 no-vision and 5 vision trials.

Data analysis

Movement error and variability. Movement error was quantified in three ways: 1) total movement error as the root mean square error (RMSE) between the target and the position-time sinusoid created by the subject; 2) time error (milliseconds; ms) as the horizontal absolute error between the peaks of the subject position-time sinusoid and the target (Figure 2-3); and, 3) spatial error (degrees) as the vertical absolute error between the peaks of the subject position-time sinusoid and the target (Figure 2-3). Prior to data analysis, the movement signal was filtered with a 4th-order (bi-directional) Butterworth filter using a 0.15 - 50 Hz band-pass. Movement variability was quantified as the standard deviation (SD) of the detrended movement trajectory. This was done because any drift from the targeted template (especially during the absence of visual feedback condition) could influence the trajectory variability (Figure 2-3).

Short-term motor learning To investigate short-term motor learning in this experiment we examined the change in movement error and variability across the protocol for both age groups with the following: 1) acute adjustments – % change in movement error and variability from Block 1 to Block 8; 2) savings – % change in movement error and variability between Block 1 and retention trials; and, 3)

consolidation – % change in movement error and variability between Block 8 and retention trials. The % change for each variable was quantified as:

$$\% \Delta = \left(\frac{\text{Values Later Block} - \text{Values Initial Block}}{\text{Values Initial Block}} \right) \times 100$$

Antagonistic EMG activity. Neural activation was quantified as the normalized amplitude of the EMG signals (RMS amplitude of interference signal). In addition, coactivation of FDI and SPI during each movement was quantified with the index developed by Falconer and Winter (1985):

$$\text{Abduction Coactivation} = \left(\frac{2 \text{ FDI EMG}}{\text{FDI EMG} + \text{SPI EMG}} \right) \times 100$$

Furthermore, to determine the common oscillations between pairs of antagonistic EMG signals, cross-wavelet spectra of the interference FDI and SPI EMG signals were obtained:

$$W(s, \tau)^{XY} = W(s, \tau)^X W(s, \tau)^{Y*}$$

where $W(s, \tau)^{XY}$ is the cross-wavelet transform of signals $X(t)$ and $Y(t)$, $W(s, \tau)^X$ is the wavelet transform of signal $X(t)$, and $W(s, \tau)^{Y*}$ is the complex conjugate of the wavelet transform of signal $Y(t)$. We defined the absolute scale-averaged cross-wavelet power spectrum (AXWPS) as the scale averaged modulus of the cross-wavelet transform.

$$\text{AXWPS}(s, \tau)^{XY} = |W^{XY}(s, \tau)| / s$$

Similarly, we defined the normalized scale-averaged cross-wavelet power spectrum (NXWPS) as AXWPS normalized by the sum of AXWPS over all scales for each instant to time.

$$N X W(s, \tau) S \stackrel{y}{=} \frac{|W^x(s, \tau)|/s}{\sum_s \left(\frac{|W^x(s, \tau)|}{s} \right)} \times 100\%$$

The normalized scale averaged cross-wavelet power spectrum shows the relative importance of each frequency of the wavelet power spectrum. It considers the relative importance of the commonalities in the variance of the two signals in different frequencies as a function of time.

We used the normalized cross-wavelet spectra of EMG signals from 5-100 Hz for the following reasons: 1) Power in the EMG signal from 5-100 Hz reflects the modulation of the motor neuron pool with voluntary effort (Brown 2000; Neto et al. 2010) and it is not associated with the shape of the motor unit action potential (Myers et al. 2004; Neto et al. 2010; Neto and Christou 2010); 2) the cross-wavelet spectrum but not the coherence from two EMG signals can potentially demonstrate the amplitude of common oscillations to the spinal motor neuron pool (Neto et al. 2010). Thus, the cross-wavelet spectrum can be used to compare changes in the strength of modulation of the spinal motor neuron pool as a function of time. The reasons for using interference EMG and not rectified EMG are outlined in recent publications from our lab (Christou and Neto 2010a; Christou and Neto 2010b; Neto et al. 2010; Neto and Christou 2010). For statistical comparisons, the frequency data of the EMG signal were divided into bands from 5-12, 12-30, 30-60 and 60-100 Hz as we have done previously (Neto et al. 2010). The dependent variable for the spectral analysis of the EMG signals was the normalized cross-wavelet power in the above bands averaged across trials.

Statistical Analysis

A mixed three-way ANOVA (2 age groups x 2 feedback conditions x 8 blocks) with repeated measures on feedback conditions and blocks compared movement accuracy, trajectory variability, time error, spatial error and EMG amplitudes of the two age groups. A mixed two-way ANOVA (2 age groups x 2 feedback conditions) with repeated measures on feedback conditions compared % changes in movement error and variability between the two groups. A mixed four-way ANOVA (2 age groups x 2 feedback conditions x 4 frequency bands x 8 blocks) with repeated measures on feedback conditions and blocks compared the absolute and normalized power in the EMG cross spectrum for the different visual feedback conditions and blocks of the two groups.

Analyses were performed with the PASW® 18.0 statistical package (SPSS Inc., Chicago, IL, USA). Significant interactions from the ANOVA models were followed by appropriate post-hoc analyses. For example, age-associated differences were followed by independent t-tests and differences among conditions and frequencies were followed with one-way ANOVAs and paired t-tests. Multiple t-test comparisons were corrected using Bonferroni corrections. The alpha level for all statistical tests was 0.05, unless corrected. Data are reported as means \pm SD within the text and as means \pm SEM in the figures. Only significant age-associated main effects and interactions are presented, unless otherwise noted.

Experiment 2

Experiment 1 clearly demonstrated that movement variability was greater for older adults compared with young adults only during contractions that received visual feedback. The second experiment, therefore, was performed to determine whether the

amplified movement variability exhibited by older adults was associated with their impaired ability to process visual information about their movements. In addition, for Experiment 2, we tried to determine whether these effects are robust across other effectors. Specifically, in addition to abduction of the index finger we chose dorsiflexion of the foot, which extends the findings from the upper limb (used in Experiment 1) to the lower limb.

Participants. Twelve young adults (aged 18-35 years, 5 men and 7 women) and ten older adults (aged 65-85 years, 4 men and 6 women) volunteered to participate in this study. All participants were naïve to the aims of the study. Inclusion criteria for the study were the same as those for Experiment 1. The Institutional Review Board at Texas A&M University approved the procedures, and subjects provided written informed consent before participation in the study.

Experimental arrangement. In this experiment subjects were tested with movements of their left index finger and left ankle. The experimental setup and the monitor used to display the movement produced by the abduction of the index finger and dorsiflexion of ankle was identical to those described for Experiment 1. For movements with the index finger, the setup was the same as described for Experiment 1, except that a light load (10% 1RM) was attached medially at the level of the proximal interphalangeal joint on the finger orthosis and was suspended using a pulley away from the subject (Figure 2-2A). For movements with the left ankle, subjects were seated comfortably in an upright position with the left hip flexed at 90° and abducted by ~10°. The knee joint was also flexed at ~90°. The left ankle was secured in a customized

ankle device that isolated the movement of the ankle to the dorsiflexion and plantar flexion plane (Figure 2-2B). A light load (10% 1RM) was attached to the front of the foot.

Measurement of limb movement. Movement of the index finger was produced by the abduction-adduction of the left index finger over a 10° range of motion (5-15°) about the second metacarpophalangeal joint. The abduction–adduction movement of the index finger was measured with a low-friction potentiometer (SP22GS-5K, Mouser electronics, Mansfield, TX, USA) that was located directly under the metacarpophalangeal joint. Movement of the foot was produced by the plantar flexion-dorsiflexion of the left ankle over a 10° range of motion (90-110°) about the left talocrural joint. Similar to the index finger, the dorsiflexion-plantar flexion movement of the ankle was measured with a low-friction potentiometer (SP22G-5K, Mouser electronics, Mansfield, TX, USA) that was located directly lateral to the fibular malleolus. The position signals were sampled at 2 kHz with a Power 1401 data acquisition system (Cambridge Electronic Design, Cambridge, UK) and stored on a computer.

EMG measurement. The FDI muscle is involved significantly when lifting and lowering a light load with the index finger in this experimental setup (Christou & Enoka 2010). The FDI muscle activity was recorded with a pair of Ag-AgCl sintered fixed-wire electrodes (4 mm diameter, model E220N-LS, In Vivo Metric, Healdsburg, CA, USA) and taped on the skin distally to the innervation zone (Homma and Sakai 1991). The reference electrode was placed over the ulnar styloid. The Tibialis Anterior (TA) muscle is involved significantly when lifting and lowering a light load with the foot in this experimental setup (Griffith et al. 2010). The TA muscle activity was recorded with a pair of Ag-AgCl sintered fixed-wire electrodes (8mm diameter, model E220N, In Vivo

Metric, Healdsburg, CA, USA) and taped on the skin distally to the innervation zone. The reference electrode was placed over the patella. The recording electrodes were placed in line with the muscle fibers. The center-to-center distance between the two electrodes was 10 mm. The EMG signals were amplified (x2000) and band pass filtered at 3-500 Hz (Grass Model 15LT system, Grass Technologies, West Warwick, RI, USA). The EMG signals were sampled at 1 kHz with a Power 1401 A/D board (Cambridge Electronic Design, UK) and stored on a personal computer.

Experimental procedures. Subjects participated in one experimental session that lasted approximately 2 hours. Each subject began the session with familiarization of the experimental procedures. The familiarization period included a demonstration of the index finger and ankle movements and an explanation of the visual feedback provided on the monitor. The order of the abduction of the index finger and ankle dorsiflexion was counter balanced among subjects. After the familiarization, each subject performed the following procedures: 1) 1 repetition maximum (1RM) with the FDI (abduction of the index finger) and TA (dorsiflexion of the ankle) muscles; 2) 5 sinusoidal movement trials at three different visual angles (0.25°, 1°, 5.4°; randomly assigned and blocked at every visual angle); 3) repeat 1RM to assess the level of fatigue; 4) repeat 1 through 3 with the index finger or ankle depending on which joint was used for the first set (counter-balanced); and 5) repeat 1RMs to assess the level of fatigue.

Visual feedback manipulation. The visual feedback gain was manipulated by varying the visual angle. The use of visual angle to manipulate visual feedback gain ensures that the amount of feedback provided is the same across subjects (Vaillancourt et al. 2006a). Visual angle (degree) was quantified as the inverse tangent of the height

of the character (height of the sinusoidal template in meters) divided by the distance from the feedback monitor (meters):

$$\alpha = \tan^{-1} \left(\frac{h}{d} \right)$$

Where, α is the visual angle, h is the height of character (sinusoidal template) and d is the distance of the eye from the computer screen. This can be achieved by manipulating the ordinate scale of the feedback and the seating distance from the feedback monitor. Because the distance to the monitor was kept constant throughout the experiment, we varied visual angle by manipulating the ordinate scale (Figure 2-2C).

1RM task. The 1 repetition maximum (1-RM) force was quantified as the heaviest load that was lifted at a normal pace ($\sim 2^\circ/\text{s}$) through the assigned range of motion during one of three trials each, with the index finger and ankle respectively. The EMGs for FDI and TA were normalized to the peak EMG recorded during the 1-RM task. 1RMs were also performed at the end of the session to test whether the experimental task induced muscle fatigue.

Sinusoidal movement task. A custom-written program in Matlab® (Math Works™ Inc., Natick, Massachusetts, USA) was used to provide the targeted movement and visual angle (0.25° , 1° , and 5.4°). The sinusoidal target was provided as a red line in the middle of the screen and the movement of the subjects in blue progressing with time from left to right (Figures 2-2C, D). Abduction of the index finger corresponded to the blue line going up (lifting) and adduction corresponded to the blue line going down (lowering) on the screen. Similarly for the foot, dorsiflexion corresponded to the blue line going up (lifting) and plantar flexion corresponded to it coming down (lowering). Subjects were asked to match the sinusoidal target as accurately and smoothly as

possible. Each trial lasted 35 s with 30 s between trials and 1 minute between visual angles.

Data analysis

Data were acquired with the Spike2 software (Version 6.02; Cambridge Electronic Design, Cambridge, UK) and analysed off-line using custom-written programs in Matlab® (Math Works™ Inc., Natick, Massachusetts, USA). Movement data were analysed as in Experiment 1 and the dependent variables were movement error and trajectory variability. Neural activation was quantified as the root mean square (RMS) amplitude of the FDI and TA interference EMG signals. Because we only measured EMG activity of the primary agonists in this experiment, continuous wavelet transforms were performed on the interference EMG signals of the FDI and TA muscles. Wavelet transforms were calculated using a base Matlab function developed by Torrence and Compo (1998) (available at URL: <http://paos.colorado.edu/research/wavelets>).

$$W(s, \tau)^X = \int X(t) \Psi_{s, \tau}^*(t) dt$$

where s represents the dilation parameter (scale shifting), τ represents the location parameter (time shifting) and the basic function $\Psi_{s, \tau}(t)$ is obtained by dilating and translating the mother wavelet $\Psi_0(t)$ (Addison 2002). From the wavelet transform we defined the absolute wavelet spectra (WPS) as:

$$WPS(s, \tau)^X = |W^X(s, \tau)|^2$$

Similarly, we quantified the normalized scale-averaged wavelet power spectrum (NWPS) as WPS normalized by the sum of WPS over all scales for each instant to time:

$$NW_{(B,S)}^x = \frac{|W^x(s, \tau)|^2 / s}{\sum_s \left(\frac{|W^x(s, \tau)|^2}{s} \right)} \times 100\%$$

The dependent variable for the spectral analysis of the FDI and TA EMG signals was the normalized wavelet power (%) in the 5-12, 12-30, 30-60, and 60-100 Hz frequency bands averaged across trials.

Statistical analysis

A mixed three-way ANOVA (2 age groups x 3 visual angles x 2 limbs) with repeated measures on visual angles and limbs compared movement accuracy, trajectory variability, time error, spatial error and agonist EMG amplitude for the two age groups. A four-way ANOVA (2 age groups x 2 visual angles x 2 limbs x 4 frequency bands) with repeated measures on visual angles and limbs compared the normalized wavelet power in the EMG spectrum for the different visual feedback conditions and blocks of the two groups. Similar statistical procedures were used as in Experiment 1.

Results

Experiment 1

Strength and Fatigue

Young and older adults exhibited similar FDI MVCs (25.12 ± 9.11 N vs. 22.09 ± 6.41 N; $P=0.692$). Therefore differences in movement accuracy and variability between the two groups of subjects were not related to the strength of the subjects. Furthermore, to determine whether our experimental protocol induced muscle fatigue, we compared the FDI MVC before and immediately after the experimental session. The FDI MVC decreased by ~13 % by the end of the protocol (pre: 23.4 ± 7.67 N vs. post: 19.9 ± 6.37 N; $P = 0.009$) indicating that the experimental protocol may have reduced muscle force

production in all our subjects. There was no age interaction and thus this mild fatigue does not affect our aging comparisons.

Short-term adaptations in movement error

Total movement error ($F_{1, 22} = 5.762$, $P = 0.025$) and spatial error ($F_{1, 22} = 4.733$, $P = 0.041$) were significantly greater for older adults (total movement error: $3.86 \pm 1.16^\circ$; spatial error: $6.92 \pm 3.5^\circ$) compared with younger adults (total movement error: $3.21 \pm 1.04^\circ$; spatial error: $5.11 \pm 2.74^\circ$). The age x condition x blocks interaction was significant ($F_{7, 154} = 3.005$, $P = 0.006$; Figures 2-4A, B) and based on post hoc tests indicated the following: 1) older adults exhibited significantly greater movement error during vision trials and these age-associated differences were minimized with the removal of visual feedback during the no-vision trials; 2) older adults exhibited significantly greater movement error only during blocks 6 and 7 of the no-vision trials. Spatial error (Figure 2-5A) was significantly lower during the vision trials (testing condition main effect: $F_{1, 22} = 95.957$, $P < 0.001$) and significantly reduced across the 8 blocks of trials (block main effect: $F_{7, 154} = 4.125$, $P = 0.002$). Temporal error (Figure 2-5B) was significantly lower during the vision trials (testing condition main effect: $F_{1, 22} = 72.524$, $P < 0.001$) and was lower for younger adults compared with older adults although there was no significant age main-effect or interaction. All other age-associated main effects and interactions were not significant.

To further investigate short-term adaptations in movement error we quantified: 1) acute adjustments; 2) savings; and 3) consolidation. The findings for all the three measures suggested that there were no age-associated differences in the rate of improvement of the movement error with our protocol.

Short term adaptations in movement variability

Movement variability was quantified as the SD of the detrended movement trajectory. Older adults exhibited significantly greater movement variability compared with younger adults only during the vision trials and these differences were eliminated during the no-vision trials (age x testing condition interaction: $F_{1, 22} = 13.746$, $P = 0.001$; Figure 2-6A, B). All other age-associated main effects and interactions were not significant.

To further investigate short-term adaptations in movement variability we quantified: 1) acute adjustments (Figure 2-7A); 2) savings (Figure 2-7B); and 3) consolidation (Figure 2-7C). The findings for all the three measures suggested that there were no age-associated differences in the rate of improvement of the trajectory variability with our protocol.

Antagonistic muscle activity

Two indices of antagonistic muscle activation were quantified as described previously (see methods): a) Coactivation; and b) normalized EMG cross-wavelet power spectrum.

Coactivation: The age x block ($F_{7, 70} = 3.384$, $P = 0.021$) interaction for the index of coactivation was significant. Post hoc analyses indicated that older adults exhibit greater coactivation during the last three blocks of the acquisition phase (Figure 2-8A, B).

Normalized EMG cross-wavelet power: Older adults exhibited greater normalized EMG cross-wavelet power (age main effect: $F_{1, 11} = 5.814$, $P = 0.035$) compared with young adults. The age x frequency band interaction was significant ($F_{3, 33} = 4.945$, $P = 0.025$) for the normalized cross-wavelet spectrum. Post hoc analyses indicated that

older adults exhibited greater normalized cross-wavelet power from 5-12 Hz ($7.815 \pm 2.29\%$ vs. $1.002 \pm 0.1\%$), 12-30 Hz ($14.35 \pm 3.74\%$ vs. $1.63 \pm 0.2\%$) and 30-60 Hz ($10.5 \pm 2.28\%$ vs. $2.6 \pm 0.22\%$) compared with younger adults (Figure 2-8C). All other age-associated main-effects and interactions were not significant.

Experiment 2

Strength and fatigue

Young and older adults lifted similar 1RM loads (5.33 ± 3.85 kg vs. 4.20 ± 2.92 kg; $P=0.069$). Therefore differences in movement accuracy and variability between the two groups of subjects were not related to the strength of the subjects. Furthermore, to determine whether our experimental protocol induced muscle fatigue, we compared the 1 RM before and immediately after the experimental session. The 1-RM did not significantly change ($P = 0.686$). Specifically, the 1RM for the index finger abduction before and after the experimental session were: young adults: 2.06 ± 0.61 kg vs. 1.87 ± 0.87 kg and older adults: 1.88 ± 0.58 kg vs. 1.86 ± 0.56 kg. In the case of ankle dorsiflexion the 1RM were: young adults: 8.64 ± 2.44 kg vs. 8.68 ± 2.53 kg and older adults: 6.50 ± 2.44 kg vs. 6.43 ± 2.39 kg. These findings demonstrate that the experimental protocol did not induce any fatigue to our subjects.

Movement error and variability

Total movement error was significantly ($F_{1,20} = 41.575$, $P < 0.001$) greater for older adults compared with younger adults. The total movement error decreased significantly with increase in visual gain (Visual gain main effect: $F_{2,40} = 49.433$, $P < 0.001$) indicating that subjects were more accurate with greater amount of visual feedback (Figure 2-9A). All other age-associated main effects and interactions were not significant.

Older adults exhibited significantly greater movement variability compared with younger adults ($F_{1, 20} = 34.553$, $P < 0.001$). Movement variability increased with higher visual gains ($P < 0.001$) and limb used ($P < 0.001$). The age x visual gain interaction was significant ($F_{2, 40} = 8.668$, $P = 0.001$) and post hoc analyses indicated that older adults exhibited lower movement variability at 0.25° compared with 1° of visual angle. This suggests that greater amount of visual feedback amplifies the movement variability in older adults (Figure 2-9 B). All other age-associated main effects and interactions were not significant.

Agonist muscle activity

The amplitude of FDI and TA EMG was quantified as the RMS amplitude of the interference signals. The age x visual gain interaction for the normalized EMG wavelet power was significant ($F_{2, 36} = 4.393$, $P = 0.02$) and indicated that visual gain influenced the modulation of the descending drive (5-100 Hz) to the agonist muscles differentially in young and older adults (Figures 2-10 A, B). All other age-associated main effects and interactions were not significant.

Discussion

The results of Experiment 1 show that removal of visual feedback eliminates age-associated differences in motor performance and thus age-associated differences in movement control cannot be explained by altered planning or proprioception. The findings from Experiment 2 confirmed that lowering the gain of visual feedback reduces movement variability in older adults. This finding was observed for both the finger and the foot. Collectively these results show that there is a reduced capacity of the visuomotor system to transform visual input into motor output in older adults.

Aging and Visual Feedback

Based on the findings from studies on force control (Kennedy and Christou 2010; Sosnoff and Newell 2006; Tracy et al. 2007; Vaillancourt et al. 2003), we expected that older adults would exhibit impaired control with greater amount of visual feedback. Our findings support and extend this expectation to the control of sinusoidal movements. A major finding of our study was that age-associated differences in movement variability were eliminated with the removal of vision (Figures 2-5 & 2-6) and minimized with lesser amount of visual feedback (Figure 2-9B). This finding may seem counterintuitive given the beneficial effects of visual feedback on the accuracy of motor performance. Nonetheless, this finding argues that greater amount of visual feedback amplifies movement variability in older adults independent of improvements in accuracy. Therefore, it is possible that more visual feedback may improve movement accuracy but impair movement control in older adults.

Our results demonstrate that older adults exhibited significantly greater movement variability during trials with visual feedback (Experiment 1) and when the gain of the visual feedback is high (Experiments 1 & 2). It is possible that movement control with greater visual feedback is impaired in older adults due to the following factors: 1) impaired integration of visual information with the execution of movement that may be caused by a delay in transmission of visual information to the primary motor cortex due to a selective degeneration of the dorso-lateral prefrontal cortex with aging (Raz et al. 1997); 2) selective loss of functional specialization of the neurons in the ventral visual cortex with aging (Park et al. 2004), which has been implicated to high visual gain (>1° of visual angle) information transmission (Blumberg and Kreiman 2010; Coombes et al. 2010); 3) older adults employ greater visuomotor corrections that modulate the

descending command to the spinal motoneuron pool when visual feedback of the task is provided (Sosnoff and Newell 2006; Tracy et al. 2007; Welsh et al. 2007); and, 4) high visual gain imposes greater attentional demands (Schmied et al. 2000) and hence is more stressful to older adults. There is evidence that older adults exhibit greater impairments in force variability than young adults under stressful conditions (Christou 2004). In summary, it appears that numerous mechanisms may be causing the impaired movement control with greater amount of visual information in older adults.

Aging and Short-term Adaptations

A major goal of our paper was to determine whether the practiced-induced adaptations of novel motor tasks differ for young and older adults because the findings in the literature are controversial. There is evidence that the adaptations that occur with practice may be impaired in older adults due to impaired motor planning (Shea et al. 2006). For example, work by Shea suggests that older adults exhibit impaired practice-induced adaptations of sequential elbow movements due to their inability to organize their motor output into sub-sequences as effectively as young adults (Shea et al. 2006). In contrast, there is evidence that practiced-induced adaptations are similar for young and older adults (Seidler 2007b). The primary evidence comes from an experiment performed by Seidler (2006), which demonstrated that the rate of improvement with practice was similar for young and older adults during wrist aiming movements. Nonetheless, when a visuomotor perturbation was imposed (rotation of the visual feedback by 30 and 45 degrees) during the task, the ability of older adults to adjust was significantly impaired compared with that of young adults (Seidler 2006).

Our findings suggest that practice-induced adaptations were similar for young and older adults. We demonstrate this with the following findings: a) there were no age-

associated differences in all the measures with which we quantified short-term adaptations. Specifically, young and older adults exhibited similar acute adjustments, savings, and consolidation in response to practice (see Figure 2-7). b) There were no age-associated differences in motor planning because motor performance was similar for the two age groups in trials without visual feedback (trials that stressed retrieval of a motor plan and memory). Thus, our results support and extend findings by Seidler (2006). Overall, these findings suggest that planning of movements and initial stages of motor learning are not impaired in older adults and thus older adults can learn new motor skills (Seidler 2007b).

Mechanisms that Contribute to Age-associated Differences in Motor Performance

Numerous mechanisms have been suggested to contribute towards the age-associated differences in motor performance. In addition to visual feedback and motor planning, which have been discussed above, the following mechanisms have been implicated to the impaired motor performance in older adults: 1) proprioception (Goble et al. 2009); 2) altered neural activation of the involved muscles (Christou et al. 2007b; Kennedy and Christou 2010); and, 3) noisier descending input to the spinal motoneuron pool (Christou 2010b).

In this study, we compared the contribution of proprioception (amplified the contribution of proprioception towards performance) in young and older adults by removing visual feedback. We found no age-associated differences in motor performance during the no-vision trials in our study, which suggest that older adults utilize proprioception equally well as young adults. In addition, we compared the neural activation of muscles by examining coactivation and the normalized EMG cross-wavelet of antagonist muscles. Our findings suggest that older adults exhibited greater

coactivation during the last three blocks of the acquisition phase and also exhibited greater normalized EMG cross-wavelet power from 5-60 Hz compared with young adults (Figure 2-8B). This behavior is reminiscent of movement stabilization (Hortobagyi and DeVita 1999) in older adults to improve motor performance with practice (Christou et al. 2007b; Gordon and Ghez 1987). Previously, Seidler-Dobrin et al. (1998) have also demonstrated that older adults exhibit greater agonist-antagonist muscle coactivation to reduce movement variability (Seidler-Dobrin et al. 1998). Finally, we compared the noise in the motor output in young and older adults by examining movement variability (Christou 2009; Christou 2010a; Christou 2010b). Our results are consistent with previous studies and demonstrate that older adults exhibit greater movement variability and impaired movement accuracy, supportive of a noisier descending input in older adults compared with younger adults. Therefore, these results suggest that impaired motor performance in older adults may be due to altered neural activation of muscles and greater motor output variability.

In conclusion, it is clear that older adults exhibit greater motor output variability, which impairs their movement control, compared with young adults. This age-associated amplification in motor output variability seems to be related to impaired visual feedback processing and/or transformation of noisier descending drive to the spinal motoneuron pool or an altered synergistic activation of the antagonistic muscles. This shortcoming in motor control exhibited by older adults can however be circumvented with adequate training and low amount of visual feedback. These results suggest that the adaptability of the aging central and peripheral nervous systems can be augmented by incorporating appropriate visual feedback manipulations. Sensory

information is processed centrally by various supra-spinal centers, and the results from our study provide evidence suggesting that for older adults visual feedback processing is an important limitation in the control of movement and short term adaptations when learning fine novel motor tasks.

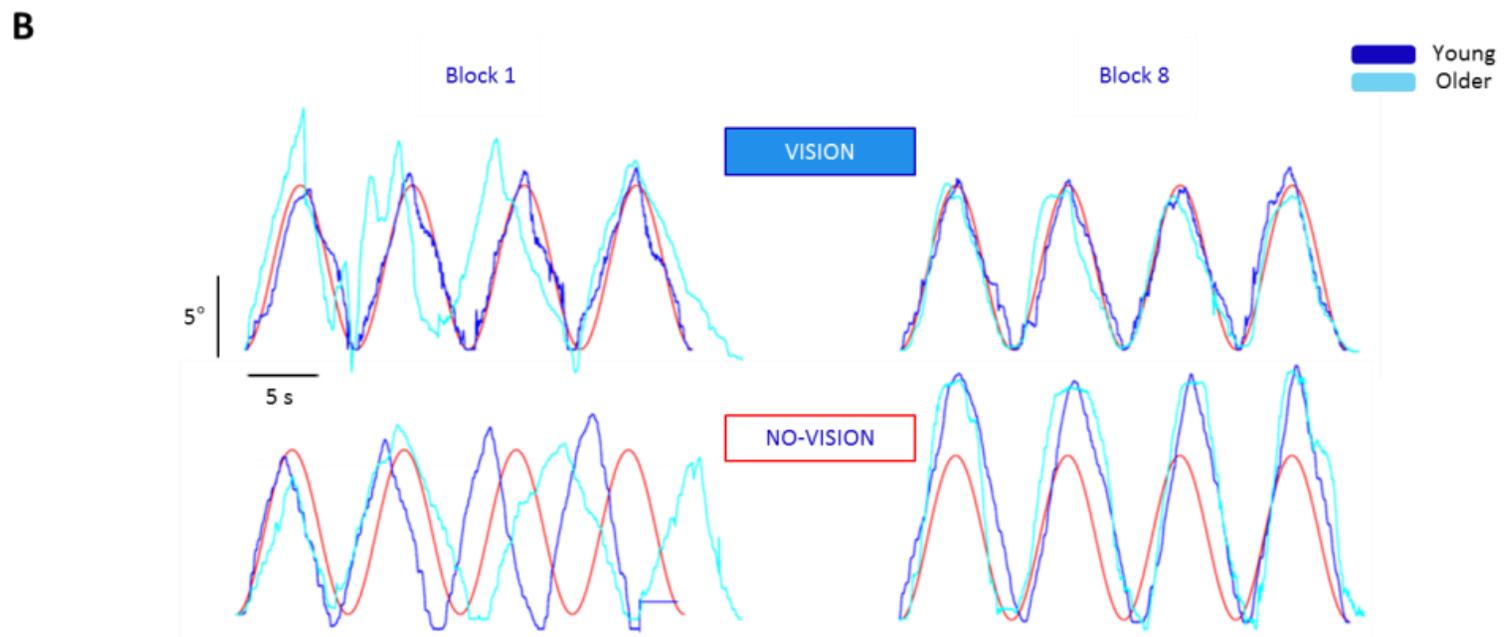
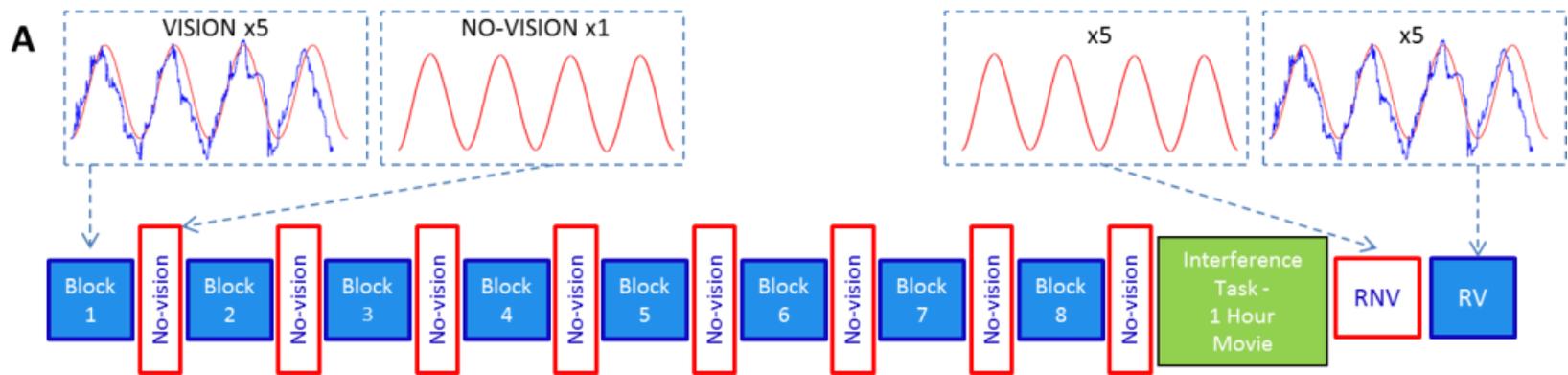


Figure 2-1. Experiment 1 - protocol and experimental conditions..

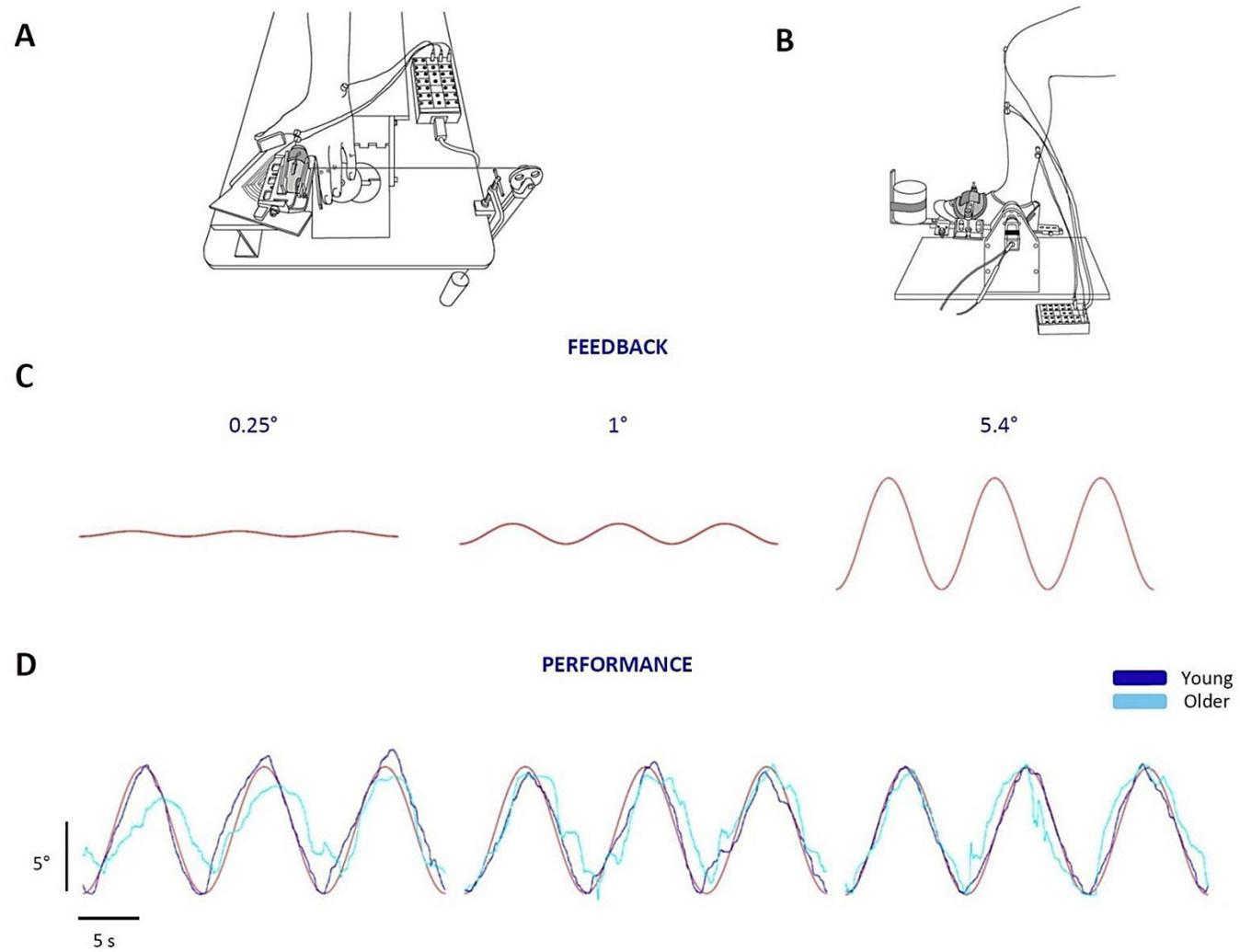


Figure 2-2. Experiment 2 - setup and conditions..

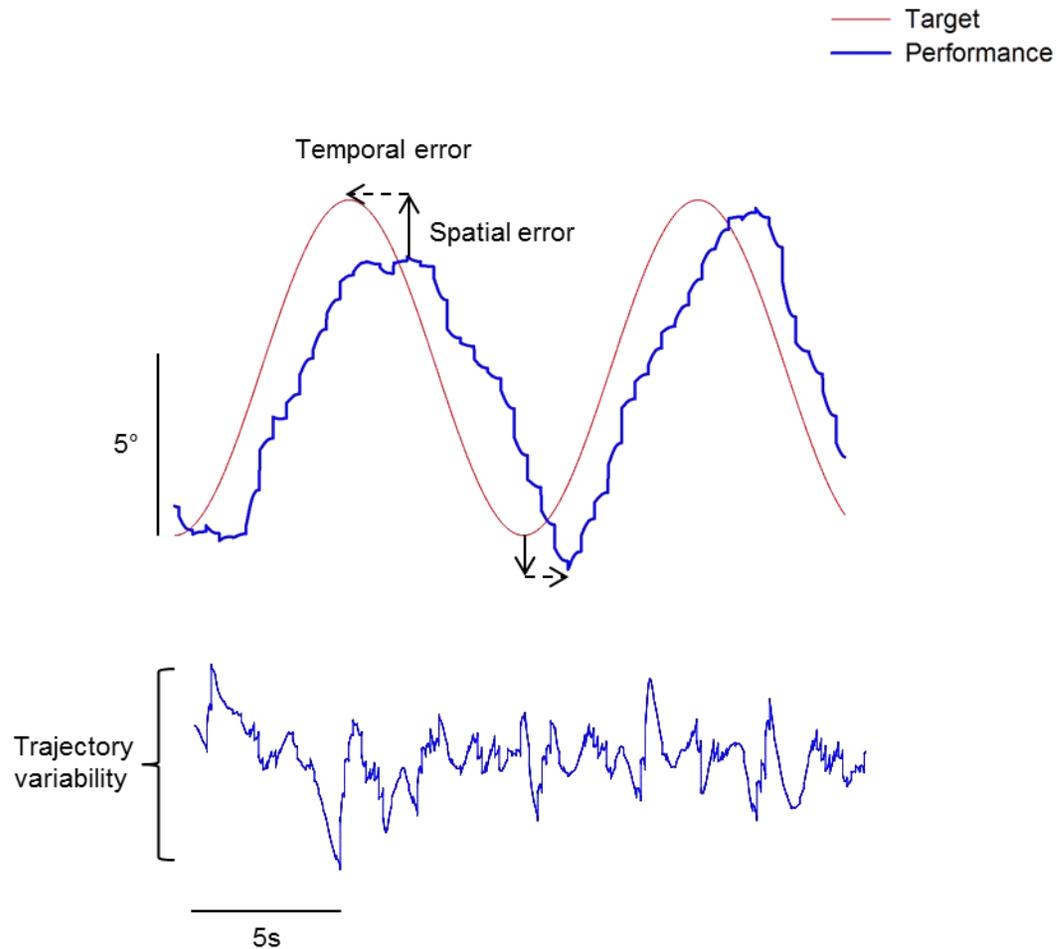


Figure 2-3. Quantification of movement errors and variability. Movement errors were quantified as the root mean squared error of the subject's performance from the template, spatial error as the shortest peak-to-peak distance in position between the performance and the template and temporal error as the shortest peak-to-peak distance in time between the performance and the template. *Bottom trace:* Movement variability was quantified as the SD of the detrended trajectory after filtering the task frequency of 0.12 Hz from the subject's performance.

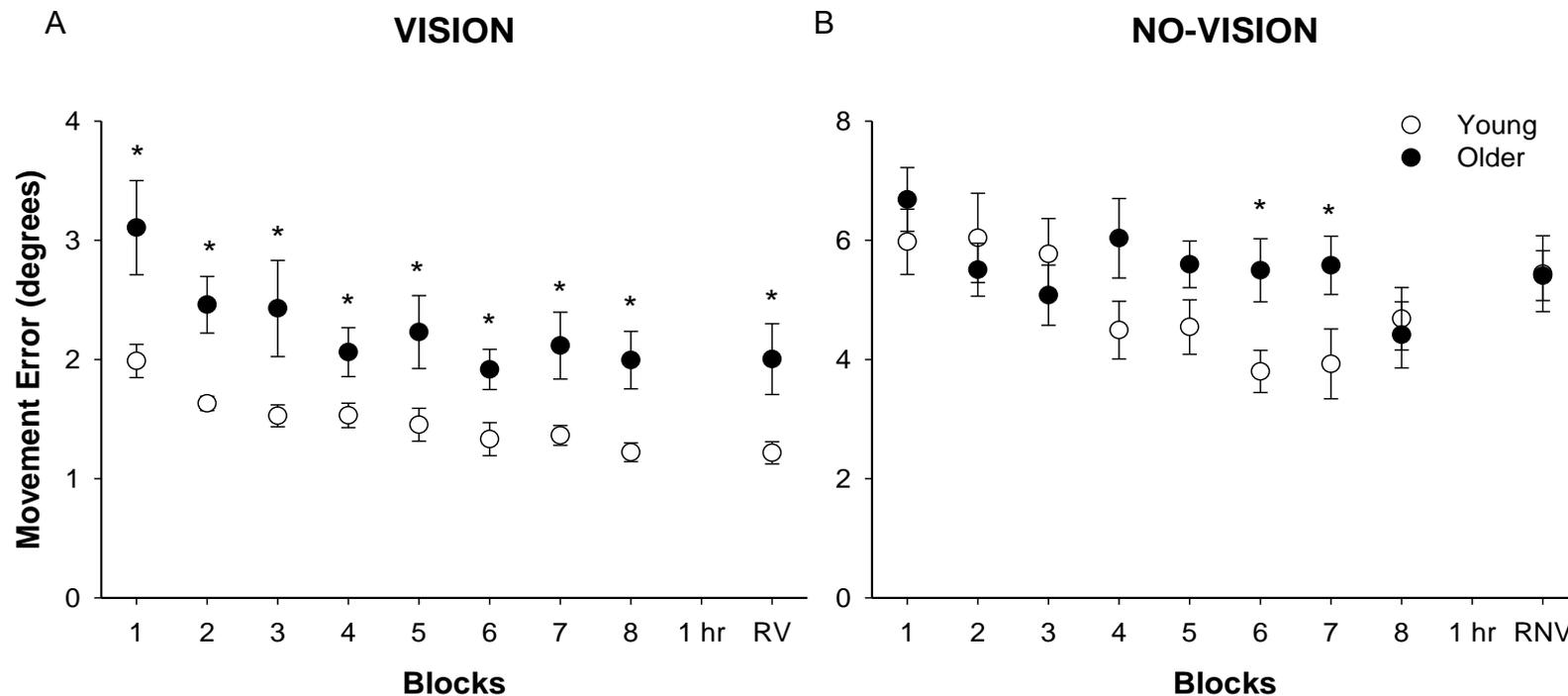


Figure 2-4. Practice and movement error. A. Average movement error for blocks of 5 vision trials across the 58-trial protocol (including retention trials). Practice improved (#) movement error in both young and older adults in the first 5 blocks of trials (30 trials). Point of inflection for both age groups was around the fifth block, which indicated most of the practice induced improvements in movement error occurred during the first 30 trials, and remained constant for trials 31-58. Old adults exhibited significantly greater (*) movement error compared with young adults across all trials. B. Average movement error for no-vision trials across the 58-trial protocol. Age-associated differences in movement error during the vision trials were eliminated with the removal of trajectory feedback. Older adults exhibited significantly (*) greater error compared with younger adults only during block 6 and 7.

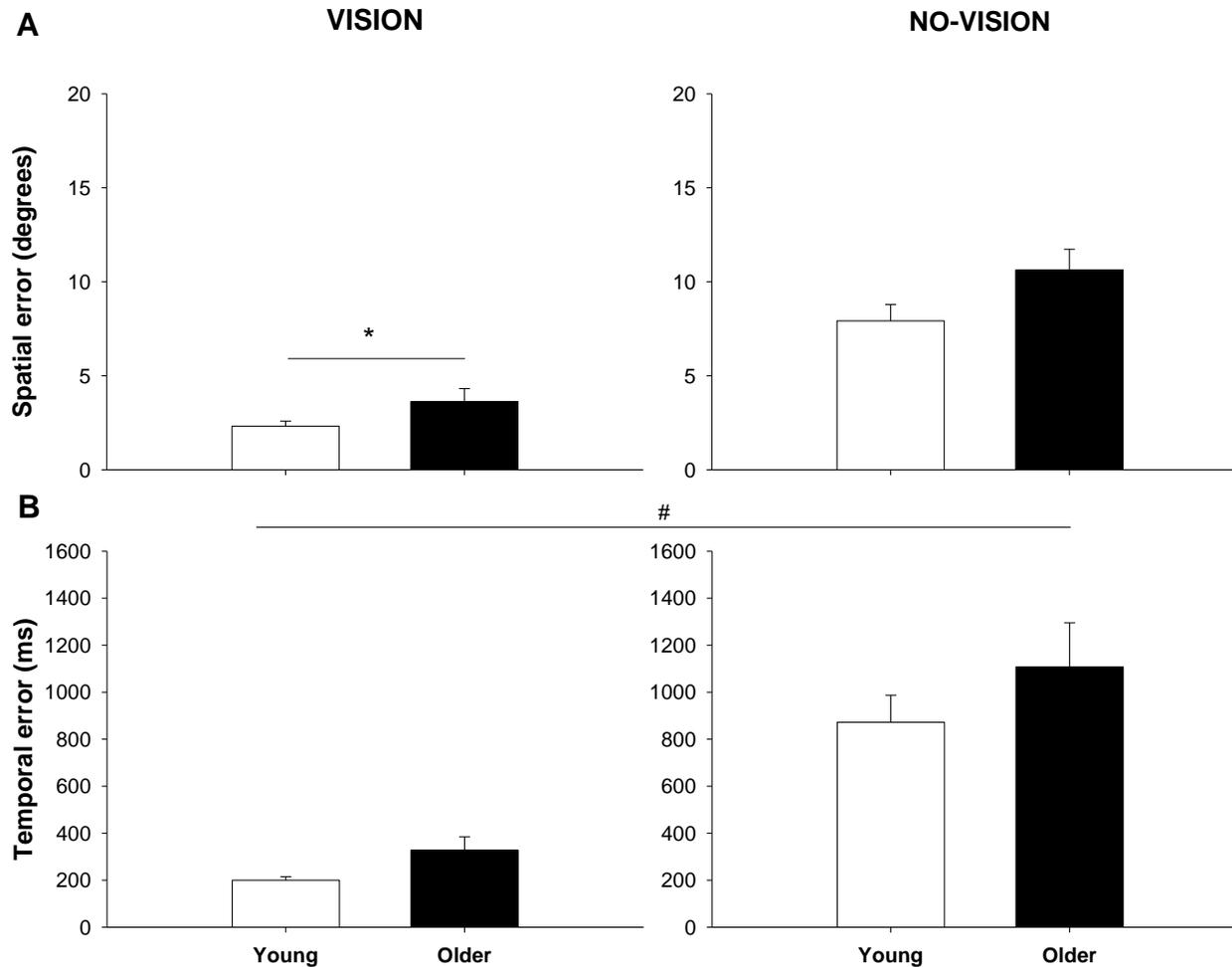


Figure 2-5. Age-associated differences in spatial and temporal errors with visual feedback. Average spatial and temporal error during vision (left column) and no-vision (right column) conditions. A. Older adults exhibited significantly (*) greater spatial error compared with younger adults only during the vision trials. These age-associated differences were eliminated with the removal of trajectory feedback during the no-vision trials. B Subjects exhibited significantly (*) lower temporal error compared during the vision trials compared with no-vision trials.

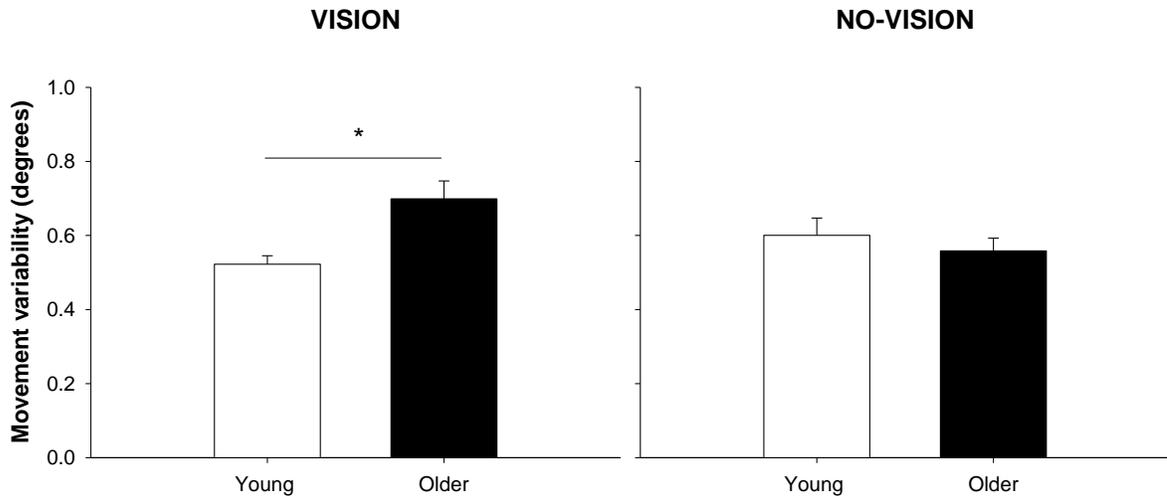


Figure 2-6. Age-associated differences in movement variability with and without visual feedback. *Left panel:* Older adults exhibited significantly (*) greater movement variability compared with younger adults only during the vision trials. These age-associated differences were eliminated during the no-vision trials (*Right panel*).

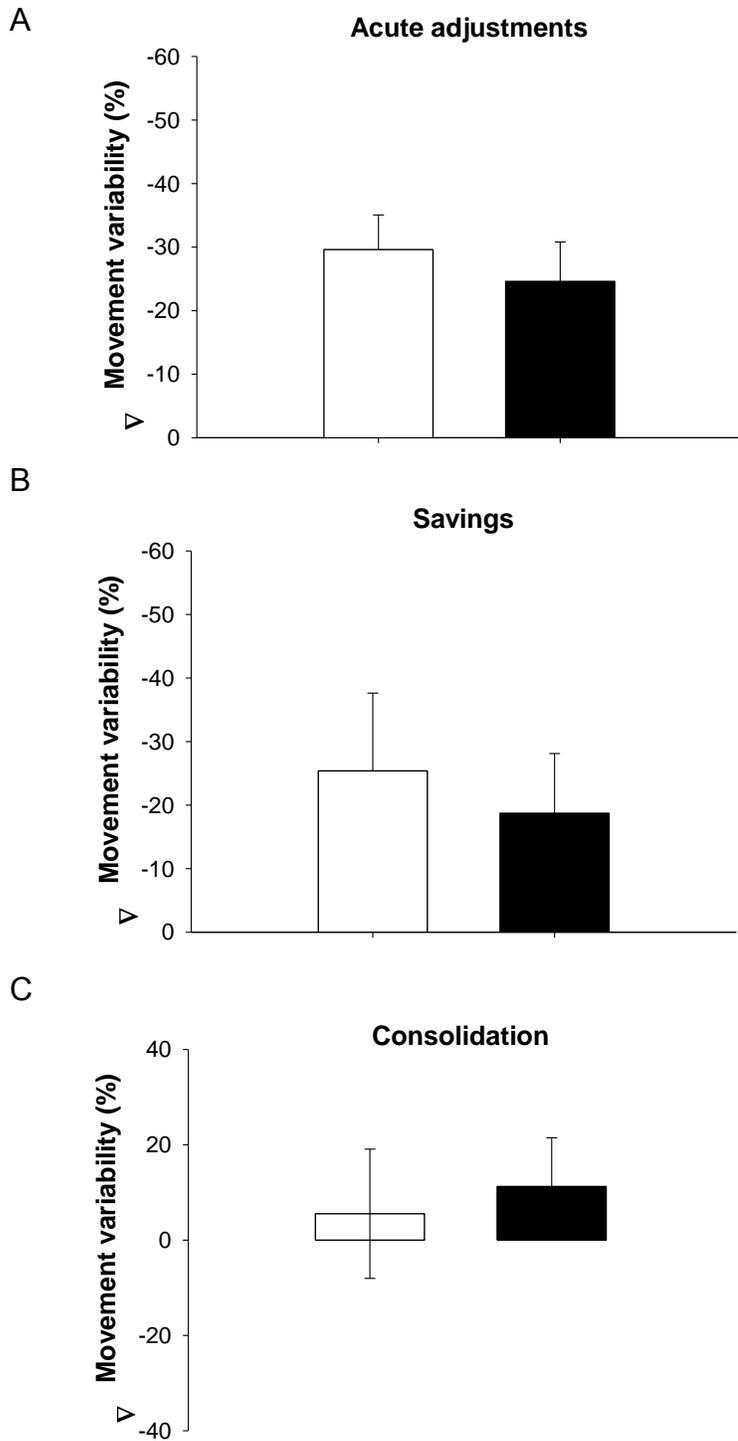


Figure 2-7. Short-term adaptations in movement variability during practice trials. The findings for A. Acute adjustments; B Savings; and, C. Consolidation suggested that there were no age-associated differences in the movement variability. Findings were the same for movement error.

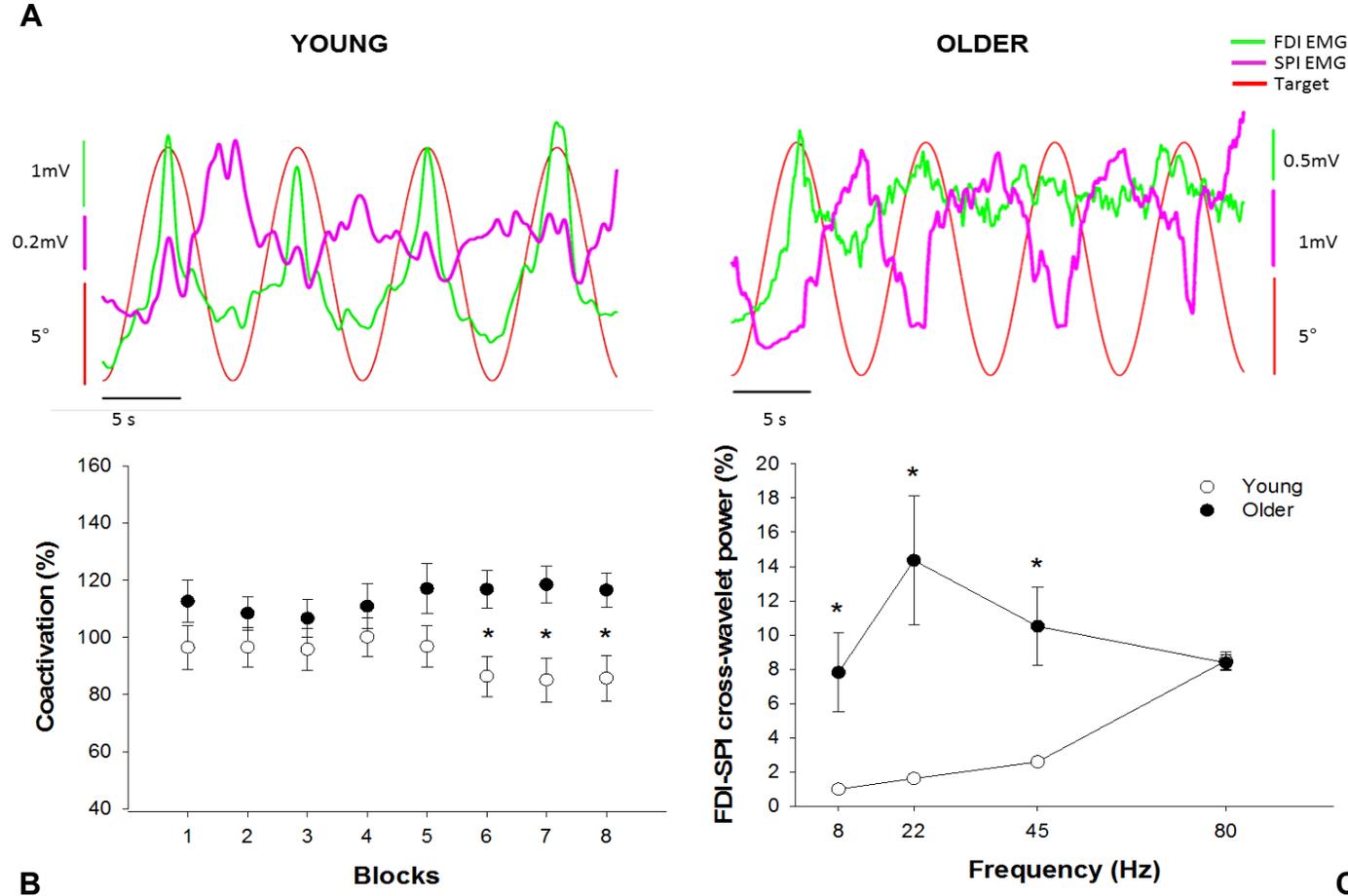


Figure 2-8. Antagonistic EMG activity in young and older adults. A. Representative figure showing FDI (green) and SPI (pink) activity with respect to the target sinusoid (red) across a single trial for young (left panel) and older (right panel) adults. B. Average coactivation of antagonistic muscles for blocks of 6 practice trials across the training session. Older adults exhibited significantly (*) greater coactivation compared with younger adults from blocks 6-8. C. Average normalized cross-wavelet spectrum from 5-100 Hz. Older adults exhibited significantly (*) greater power from 5-60 Hz exhibiting differential modulation of the descending drive to the antagonistic muscles compared with young adults.

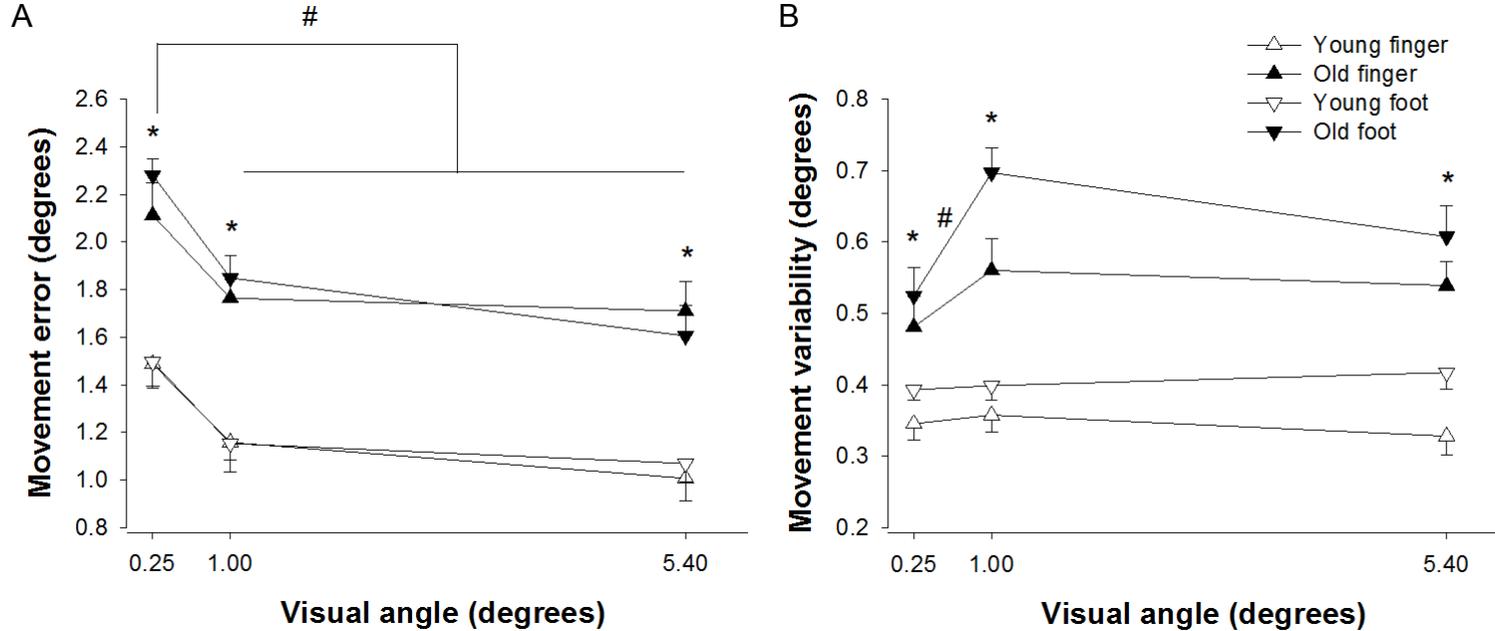


Figure 2-9. Movement error and variability during different visual feedback conditions. A. The total movement error produced by young (dark blue triangles) and older (light blue triangles) adults at three different visual angles (0.25°, 1°, and 5.4°) with the finger (triangle up) and foot (triangle down). The total movement error at the 0.25° was significantly (#) higher than 1° and 5.4°. Older adults exhibited significantly greater (*) movement error when compared with young adults across all visual angles regardless of the effector used. B. Older adults exhibited significantly greater (*) movement variability when compared with young adults across all visual angles regardless of the effector used. Furthermore, older adults exhibited significantly (#) lower movement variability at 0.25° when compared with variability at 1° visual angle.

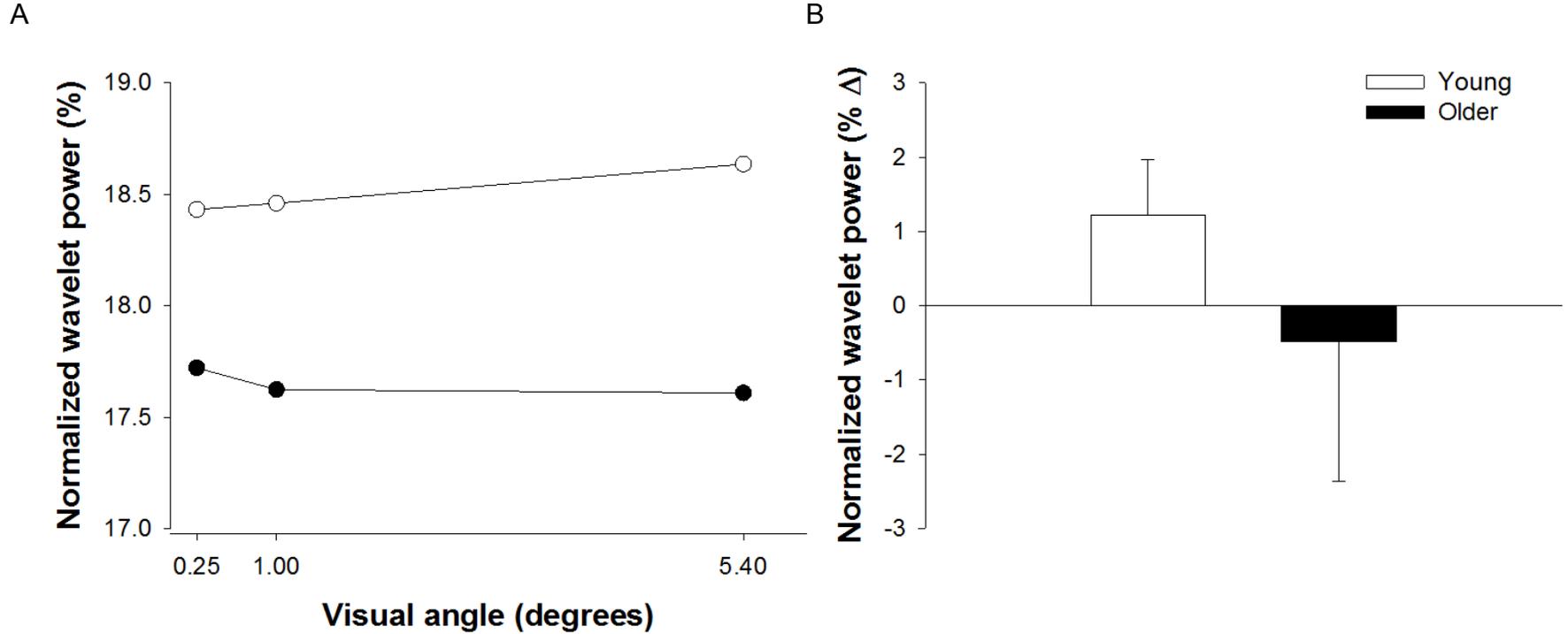


Figure 2-10. Visual feedback gain and agonist muscle activity. Visual gain influenced the modulation of the descending drive to the agonist muscles differentially in young (open symbols) and older (filled symbols) adults. A. Normalized agonist EMG power from 5-100 Hz across three different visual gains (0.25°, 1°, and 5.4°) in young and older adults. B. % change in normalized EMG power from 5-100 Hz from 5.4° to 0.25° for young and older adults.

CHAPTER 3 TRAINING WITH LOW-GAIN VISUAL FEEDBACK ENHANCES MOTOR LEARNING IN OLDER ADULTS

Motor learning consists of the acquisition of the task with practice and transfer (generalization) of the acquired behavior to newer and different tasks (Schmidt and Lee 2011). Theoretically, the central nervous system learns to perform new tasks with accuracy by minimizing motor output variability (Wolpert and Ghahramani 2000). Task acquisition is associated with the continuous updating of the motor command leading to reinforcement and further reduction of motor output variability with sustained practice (Wolpert et al. 2011). Amplified motor output variability during acquisition can negatively influence updating of the motor command for subsequent movements (Harris and Wolpert 1998).

Numerous reports suggest that older adults exhibit impairments during the acquisition compared with young adults (Christou 2009; Harrington and Haaland 1992; Howard and Howard 1997; Seidler 2007a). The primary mechanisms proposed to explain the impairment in acquisition include altered motor planning (Shea et al. 2006) and compromised visual feedback processing (McNay and Willingham 1998; Seidler 2006). The evidence for motor planning suggests that an inability to plan and organize movements into sub-sequences in older adults; hence they do not learn sequential movements as well as young adults (Shea et al. 2006). Our findings from Experiment 1 (Chapter 2) suggest that the aging differences in short-term adaptations accompanying practice are not accounted for by motor planning but rather due to amplified motor output variability. This amplification in motor output variability is caused by impairments in the visual feedback processing, which was confirmed by the findings from Experiment 2. Specifically, the age-associated differences in motor output variability were

exacerbated with greater amount of visual feedback (medium and high gains). Findings from force control studies have demonstrated that the amount of visual feedback (e.g. gain) interacts with the ability of older adults to perform motor tasks. Increasing the gain of the visual feedback amplifies motor output variability only in older adults but not young adults (Kennedy and Christou 2010; Sosnoff and Newell 2006; Tracy et al. 2007). Taken together, impaired visual feedback processing and amplified motor output variability are major mediators of motor performance deficits in older adults.

Although older adults demonstrate the ability to improve motor performance with practice, their inability to match the performance of young adults further suggests that task acquisition may be impaired (Christou et al. 2007a). Nonetheless, there is limited evidence whether these impairments extend to the transfer of learning. It is unclear if older adults can share components of the practiced task to newer and different tasks (transfer) (Onuskhko et al. 2012; Seidler 2007a). Collectively, amplified motor output variability due to impaired visual information processing with magnified visual feedback would inhibit/impair motor learning. On the contrary, training with reduced visual feedback will improve motor learning in older adults. Therefore, the purpose of this study was to investigate whether low- or high-gain visual feedback would facilitate acquisition and transfer of novel motor tasks in older adults. Part of the findings have been reported in abstract form (Baweja et al. 2012).

Methods

Participants. Thirty older (71.7 ± 6.2 years; 16 women) and ten young adults (23.8 ± 5 years; 5 women) volunteered to participate in this study. All subjects reported being healthy without any known neurological problems, and were not using any medications known to influence neuromuscular function. Additionally, all subjects were

right-handed (Oldfield 1971) and right-footed (Elias and Bryden 1998) according to standardized surveys, and had normal or corrected vision. The Institutional Review Board at the University of Florida approved the procedures. All subjects provided written informed consent before participation in the study. Subjects were divided into training (20 older adults) and control groups (10 young & 10 older). The training group was further randomly split into older adults who trained with high-gain ($n = 10$) and low-gain ($n = 10$) visual feedback.

Experimental arrangement. Each subject was seated comfortably facing a 30 inch computer screen with a native resolution of 2560 x 1600 pixels (Apple Cinema Display, Apple Inc., Cupertino, CA, USA) that was located 1.5 m away at eye level. The monitor was used to display the sinusoidal target and movement produced by the ankle and index finger. All subjects affirmed that they could see the contents of the feedback on the display clearly. The experimental sessions and training were performed with the non-dominant ankle. Subjects were seated comfortably in an upright position with the left hip flexed at 90° and abducted by $\sim 10^\circ$. The knee joint was also flexed at $\sim 90^\circ$. The left ankle was secured in a customized ankle device that isolated the movement of the ankle to the dorsiflexion and plantar flexion plane (Figure 2-1B). For movements with the index finger during the second experimental session, the left arm was abducted by 45° and flexed to $\sim 90^\circ$ at the elbow. The left forearm was pronated and secured in a specialized air pillow (Versa Form TM, AB Germa, Sweden). The thumb, middle, ring, and fifth fingers of the left hand were restrained with metal plates and there was approximately a right angle between the index finger and thumb. Only the left index finger was free to move. The left index finger was placed in an adjustable finger orthosis

to maintain extension of the middle and distal interphalangeal joints and was abducted 5° from the neutral position (Figure 2-1A).

Measurement of limb movement. Movement of the foot was produced by dorsiflexion of the left ankle over a 10° range of motion (90-100°) about the left talocrural joint. The movement of the ankle was measured with a low-friction potentiometer (SP22G-5K, Mouser electronics, Mansfield, TX, USA) that was located directly lateral to the fibular malleolus. Movement of the index finger was produced by the abduction-adduction over a 10° range of motion (5-15°) about the second metacarpophalangeal joint. The abduction–adduction movement of the index finger was measured with a low-friction potentiometer (SP22GS-5K, Mouser electronics, Mansfield, TX, USA) that was located directly under the metacarpophalangeal joint. The position signals were sampled at 1 kHz with a Power 1401 data acquisition system (Cambridge Electronic Design, Cambridge, UK) and stored on a computer.

Measurement of muscle activity. The Tibialis Anterior (TA) muscle is involved significantly when dorsiflexing and plantar flexing with the foot in this experimental setup (Kwon et al 2012). Activation of the TA muscle was recorded with one pair of Ag-AgCl sintered fixed-wire surface electrodes (8mm diameter, model E220N, In Vivo Metric, Healdsburg, CA, USA) and taped on the skin distally to the innervation zone (Hermens et al. 2000). The reference electrode was placed over the patella. The recording electrodes were placed in line with the muscle fibers. The center-to-center distance between the two electrodes of a pair was 15 mm.

The first dorsal interosseous (FDI) muscle is involved significantly when abducting and adducting the index finger in this experimental setup (Christou and Enoka 2010).

FDI muscle activity was recorded with a pair of Ag-AgCl sintered fixed-wire electrodes (4 mm diameter, model E220N-LS, In Vivo Metric, Healdsburg, CA, USA) and taped on the skin distally to the innervation zone (Homma and Sakai 1991). The reference electrode was placed over the ulnar styloid. The EMG signals were amplified (x 2000) and band pass filtered at 3-500 Hz (Grass Model 15LT system, Grass Technologies, West Warwick, RI, USA). EMG signals were sampled at 2 kHz with a Power 1401 A/D board (Cambridge Electronic Design, UK) and stored on a personal computer.

Experimental procedures. Each subject participated in a familiarization session and two experimental sessions (see Figure 3-1 for a schematic of the experimental protocol). During the familiarization session, subjects received written and oral descriptions of the project, watched a visual demonstration of the protocol, and were given 3-5 practice trials of the experimental task. Additionally, during the familiarization session older subjects were informed whether they were invited to participate in the control or training groups for the study. The two experimental sessions were separated by a 2 week period of the unloaded visual feedback training.

For the pre-test (day 1), each subject performed the following procedures: 1) maximal voluntary contractions (MVC) with the tibialis anterior muscle (dorsiflexion of the ankle); 2) 5 sinusoidal movement trials at three different visual angles (0.25°, 1°, and 5.4°; randomly assigned and blocked at every visual angle); and, 3) repeat MVC with the tibialis anterior muscle to assess the level of fatigue. During the post-test (day 14), to test generalizability (transfer) of the training, subjects also performed the same tasks with the ipsilateral index finger. For this session, subjects performed the following procedures: 1) maximal voluntary contractions (MVC) with the first dorsal interosseous

(abduction of the index finger) and tibialis anterior muscles; 2) 5 sinusoidal movement trials with four different visual feedback conditions (no-vision, 0.25°, 1°, and 5.4°; randomly assigned and blocked at every feedback condition); and, 3) repeat MVC with the first dorsal interosseous and tibialis anterior muscles to assess the level of fatigue; and 4) repeat 1 through 3 with the index finger or ankle depending on which joint was tested first (counter-balanced).

MVC task. Subjects were instructed to exert maximal force with ankle dorsiflexion and index finger abduction. MVC force was measured with a one-dimensional force transducer (Model-41 Precision Low Profile Load Cell, Honeywell International Inc., Columbus, Ohio, USA). Subjects were instructed to increase the force from baseline to maximum over a 2 s period and maintain the maximal force for about 4 s. Five such recordings were made or until two of the maximal trials were within 5% of each other. Each subject was given at least 60 s rest between consecutive trials. The maximal voluntary contraction (MVC) force was quantified as the average force over 3 s (constant part) of the highest trial. MVC's were performed to test whether the training protocol induced any strength gains in the subjects at the end of two weeks (change in ankle strength from pre- to post-training experimental sessions).

Sinusoidal task. A custom-written program in Matlab® (Math Works™ Inc., Natick, Massachusetts, USA) was used to provide the targeted movement and visual feedback condition (0.25°, 1°, and 5.4°). The subjects had to match a position-time sinusoidal target with amplitude of 10° and a frequency of 0.6 Hz (18 cycles per trial of 30 s). Subjects were given 15 s between trials and 3 minutes between visual angles. The target was provided as a red sine in the middle of the screen and the movement of

the subjects as a blue line progressing with time from left to right (Figure 3-2).

Dorsiflexion of the ankle and abduction of the index finger corresponded to the blue line going up on the screen. Plantar flexion of the ankle and adduction of the index finger corresponded to the blue line going down on the screen. All movements were completely unloaded and subjects were asked to match the sinusoidal target as accurately and as smoothly as possible.

Visual feedback gain manipulation. Visual feedback gain was manipulated by varying the visual angle. The use of visual angle to manipulate visual feedback gain ensures that the amount of visual feedback provided is the same across subjects (Vaillancourt et al. 2006b). Visual angle (degree) was quantified as the inverse tangent of the height of the character (height of the sinusoidal template in meters) divided by the distance from the feedback monitor (meters):

$$\alpha = \tan^{-1}\left(\frac{h}{d}\right)$$

Where, α is the visual angle, h is the height of character (sinusoidal template) and d is the distance of the eye from the computer screen. This can be achieved by manipulating the ordinate scale of the feedback and the seating distance from the feedback monitor. Because the distance to the monitor was kept constant throughout the experiment, we varied visual angle by manipulating the ordinate scale of the target area.

Unloaded visual feedback training. Participants in the training groups were divided in to low-gain (0.25°) and high-gain (5.4°) training groups. Subjects completed training by practicing the sinusoidal target with the same setup as in the experimental session. The training session consisted of 4 sets of 15 trials for a total of 60 trials per

training session. On average, each training session lasted ~60 min. Subjects trained a total of five times every other day (days 3, 5, 7, 9 and 11) after the first experimental session (day 1). All subjects in the training groups completed 15 trials x 4 blocks x 5 practice sessions, for a total of 300 practice trials.

Data Analysis

Movement error and variability

Data were analyzed from the second sine wave after the start of the trial until the eighteenth sine wave (completion of the task) to prevent any variation due to initial adjustments. Movement error was quantified in three ways: 1) total movement error as the root mean square error (RMSE) between the target and the position-time sinusoid created by the subject; 2) temporal error (milliseconds; ms) as the horizontal absolute error between the peaks and crests of the subject position-time sinusoid and the target (see Figure 2-3); and, 3) spatial error (degrees) as the vertical absolute error between the peaks and crests of the subject position-time sinusoid and the target (see Figure 2-3). For the no-vision condition (test of transfer), movement error was quantified as the difference in power at peak frequency between the subject's movement and target template (0.6 Hz; Figure 3-6A). This was done because subjects had no reference of their performance relative to the target during these trials and attempted to reproduce it out of memory. Smaller difference in the magnitude of the power at 0.6 Hz would indicate that subjects learned and memorized the spatial and temporal parameters of the sinusoidal target with practice.

Prior to further data analysis, the movement signal was filtered with a 4th-order (bi-directional) Butterworth filter using a 0.3-0.8 Hz band-stop to filter out the task frequency from the subject's performance. Movement variability was quantified as the standard

deviation (SD) of the detrended movement trajectory. The dependent variables for movement error were the RMSE, spatial and temporal errors. The dependent variable for movement variability was the SD of performance trajectory.

Task specific agonist EMG burst index

The EMG activity of the tibialis anterior and first dorsal interosseous muscles was recorded during the MVCs and the two experimental sessions. The interference EMG of the tibialis anterior and first dorsal interosseous muscles was rectified and smoothed using a fourth-order Butterworth filter with a low-pass cut-off frequency of 5 Hz (Figure 3-2). This filter was used to identify the agonist EMG bursts during the movement (Christou et al. 2007a). The EMG burst index (%) was quantified as the proportion of power in the EMG bursts from 0.5-0.75 Hz versus the power in the whole signal from 0-5 Hz:

$$\text{Task Specific Agonist EMG burst} = \left(\frac{\text{Power } 0.5 - 0.75 \text{ Hz}}{\text{Power } 0 - 5 \text{ Hz}} \right) \times 100$$

An increase in the magnitude of the power from 0.5-0.75 Hz with practice would indicate rhythmical EMG burst activity around the task frequency of 0.6 Hz.

Motor learning

Acquisition. To investigate motor learning during acquisition we examined the movement errors and variability across practice for the two training groups with the following: 1) acute adjustments – values from practice day-1 block-1 to practice day-5 block-4; 2) savings – values of block-1 across 5 days of practice; and, 3) consolidation – the percent change in values between block-4 of the previous day vs. block-1 on the next day. The percent change for each variable was quantified as:

$$\text{Percent } \Delta = \left(\frac{\text{Values } B1_{\text{next day}} - \text{Values } B4_{\text{previous day}}}{\text{Values } B4_{\text{previous day}}} \right) \times 100$$

Practice-induced motor adaptations. Practice-induced motor adaptations in movement errors, variability and EMG burst activity were computed as the difference score between pre- and post-test performance values:

$$\text{Practice induced adaptations} = \left(\frac{\text{Values}_{\text{post-test}} - \text{Values}_{\text{pre-test}}}{\text{Values}_{\text{pre-test}}} \right) \times 100$$

Transfer. To test whether low- or high-gain visual feedback training facilitated greater generalizability in older adults, during the post-test older adults also performed the task with the ipsilateral index finger. Transfer was examined by comparing performance values of the three different groups of older adults during the index finger tasks.

Statistical Analysis

Acquisition

Acute adjustments. A mixed three-way ANOVA (2 training groups x 5 practice days x 4 blocks/day) with repeated measures on practice days and blocks compared total movement error, spatial error, temporal error and movement variability for the two training groups.

Savings. A mixed two-way ANOVA (2 training groups x 5 block-1 for each practice day) with repeated measures on practice blocks compared total movement error, spatial error, temporal error and movement variability for the two training groups.

Consolidation. A mixed two-way ANOVA (2 training groups x 5 days) with repeated measures on the changes per day compared total movement error, spatial error, temporal error and movement variability for the two training groups.

Practice-induced motor adaptations. A mixed three-way ANOVA (3 groups (Old training, old control, young control) x 2 experimental sessions (pre-test and post-test) x 3 visual feedback gains) with repeated measures on experimental sessions and visual feedback gains compared total movement error, spatial error, temporal error, movement variability for the three groups.

Transfer

A two-way ANOVA (3 groups x 3 visual feedback gains) with repeated measures on visual feedback gains (0.25°, 1°, and 5.4°) compared the total movement error, spatial error, temporal error and movement variability of the three groups of older adults (high-gain training, low-gain training and older control). A one-way ANOVA compared the movement error and variability of the three groups of older adults for the no-vision condition (memory test).

Regressions

Multiple linear regression analyses (stepwise) were used to examine the contribution of practice-induced adaptations in MVC, spatial error, temporal error, movement variability and agonist EMG burst to the change in RMSE between pre- and post-training experimental sessions. Additional models were used to determine the contributions of movement variability during practice and agonist EMG burst to the movement error at transfer. Any subjects that exhibited values outside $\pm 3SD$ were excluded as outliers (all subjects in this manuscript exhibited values within $\pm 3SD$). The relative importance of the predictors was estimated with the part correlations (part r), which provide the correlation between a predictor and the criterion, partialling out the effects of all other predictors in the regression equation from the predictor but not the criterion (Green and Salkind 2002).

Analyses were performed with the PASW® 18.0 statistical package (SPSS Inc., Chicago, IL, USA). Post-hoc tests (with Bonferroni correction) were used to determine effects within the groups of subjects. Group-related differences in all variables were analyzed using t-tests for independent samples. The alpha level for all statistical tests was 0.05. Data are reported as means \pm SD within the text and as means \pm SEM in the figures.

Results

Strength

The MVC of the young and older adults was similar ($P = 0.7$) at pre-test (young vs. old: 133.7 ± 43.9 vs. 118.1 ± 47.5 N) and post-test (young vs. old: 141.1 ± 23.1 vs. 125.6 ± 52.9 N). To determine whether our training protocol induced any increments in muscle strength over the two-week period, we compared the tibialis anterior MVCs of the pre- and post-training sessions recorded before beginning the experimental sessions. The tibialis anterior MVCs did not change significantly ($P > 0.1$) from pre- to post-training sessions in all groups of subjects. Specifically, the tibialis anterior MVC before the pre- and post-training experimental sessions were: young adults: 133.7 ± 43.9 vs. 141.1 ± 23.1 N, older adults training group: 127.6 ± 51.1 vs. 131.3 ± 52.1 N and older adults control group: 98.8 ± 33.8 vs. 98.9 ± 29.7 N. Therefore, any differences in movement accuracy and variability between the groups of subjects were not related to the strength of the subjects.

Motor Learning – Acquisition

The purpose of this analysis was to determine whether low-or high gain visual feedback training could facilitate better acquisition in older adults. Therefore, we analyzed the dependent variables on the practice days between the two training groups.

Only the significant training group and practice session main-effects and training group x practice session interactions are of interest and will be presented.

Acute-adaptations

Both the training groups exhibited similar ($P > 0.2$) overall movement error, spatial error, temporal error, and movement variability across the practice sessions. The practice session main effect was significant for the overall movement error ($P < 0.001$), spatial error ($P < 0.001$), temporal error ($P = 0.02$), and movement variability ($P < 0.001$) indicating that regardless of the training type both the training groups reduced their movement errors and variability with practice. Post-hoc tests indicated that most of the improvements occurred in the first three days of practice and then remained constant over the last two days (Figure 3-3). The training group x practice session interaction was not significant in all the variables ($P > 0.1$) indicating that with practice both training groups reduced their movement errors and variability at the same rate.

Savings

Both the training groups exhibited similar ($P > 0.1$) savings in overall movement error, spatial error, temporal error, and movement variability across the practice sessions. The practice session main effect was significant for the overall movement error ($P < 0.001$), spatial error ($P < 0.001$), temporal error ($P = 0.005$), and movement variability ($P < 0.001$) indicating that regardless of the training type both the training groups increased the savings of their movement errors and variability with practice. Post-hoc tests indicated that most of the savings occurred in the first two days of practice and then remained relatively constant over the next three days of practice. The training group x practice session interaction was not significant in all the variables ($P >$

0.1) indicating that with practice both training groups increased savings at the same rate.

Consolidation

Both training groups exhibited similar ($P > 0.5$) consolidation of overall movement error, spatial error, temporal error, and movement variability across the practice sessions. The practice session main effect was not significant ($P > 0.1$) for the overall movement error, spatial error, temporal error, and movement variability indicating that regardless of the visual feedback type both training groups exhibited similar reduction in their movement errors and variability with practice. The training group x practice session interaction was not significant in all the variables ($P > 0.1$) indicating that with practice both training groups reduced their movement errors and variability at the same rate.

Practice induced adaptations

There were no differences in performance due to the amount of visual feedback used during acquisition. Therefore, we combined both training groups to examine whether low-intensity training improved motor performance in older adults to the level of young adults. This was done by comparing the performance of the three groups (older training, older control and young control) of subjects from pre-test to post-test. Because practice-induced adaptations are of interest only significant group x experimental session interactions will be presented.

Movement errors. The group x experimental session interaction was significant for the overall movement error ($F_{2,37} = 12.14$, $P < 0.001$; Figures 3-3 and 3-4A), spatial error ($F_{2,37} = 11.56$, $P < 0.001$; Figure 3-4C) and temporal error ($F_{2,37} = 8.84$, $P < 0.001$; Figure 3-4D). Post hoc analysis of the interaction indicated that: 1) during the first experimental session both the groups of older adults exhibited significantly greater

movement errors compared with the young adults; 2) only the training group reduced their RMSE (~ 43%), spatial error (~ 45%), and temporal error (~ 84%) by the second experimental session compared with the young and older adults control groups; 3) during the second experimental session only the older adults control group exhibited significantly greater movement errors compared with the training and young adults groups; and 4) during the second experimental session older adults training group exhibited similar movement errors as young adults.

Movement variability. Similar to movement error measures, the group x experimental session interaction was significant for movement variability ($F_{2, 37} = 7.197$, $P = 0.002$; Figures 3-3 and 3-4B). Post hoc analysis of the interaction indicated that: 1) during the first experimental session both the groups of older adults exhibited significantly greater movement variability compared with the young adults; 2) only the training group reduced their movement variability (~ 35%) by the second experimental session compared with the young and older adults control groups; 3) during the second experimental session only the older adults control group exhibited significantly greater movement variability compared with the training and young adults groups; and 4) during the second experimental session older adults training group exhibited similar movement variability as young adults.

Motor Learning – Transfer to Hand

To test whether low- or high-gain visual feedback training with the foot facilitated greater transfer in older adults, we examined the performance of the three groups of older adults with the ipsilateral index finger.

Tests with visual feedback

Movement errors. The group main effect was significant for the overall movement error ($F_{2, 27} = 8.5$, $P = 0.002$; Figure 3-5A), spatial error ($F_{2, 27} = 3.3$, $P = 0.05$; Figure 3-5B) and temporal error ($F_{2, 27} = 3.6$, $P = 0.04$; Figure 3-5C). Post hoc analyses indicated that only the low gain training group exhibited significantly lower movement errors compared with the control group. The groups x task interactions were not significant for any of the measures.

Movement variability. The main-effects and interactions were not significant.

Test with no-vision (memory)

Movement error. The group main effect approached significance ($P = 0.08$; Figure 3-6B) suggesting that only the training groups were able to match the spatial and temporal characteristics of the target template compared with the older control group.

Movement variability. The main-effects and interactions were not significant.

Predicting the Practice-Induced Adaptations in Movement Error

The older adults in the training groups exhibited lower movement errors and variability following the low-intensity training and matched the performance of young adults at post-test. Furthermore, there were no strength gains over the two weeks and young and older adults exhibited similar MVCs. Therefore, multiple linear regression models were used to determine the following: 1) the contribution of spatial error, temporal error, movement variability and EMG burst activity to the practice-induced improvements ($\% \Delta$) in movement error; 2) the contribution of tibialis anterior strength (MVC) to the practice-induced improvements ($\% \Delta$) in movement error and variability.

The change in RMSE from pre- to post-test was predicted (Figure 3-7) by the spatial error ($R^2 = 0.69$, $P = 0.001$), movement variability ($R^2 = 0.73$, $P = 0.001$) and

tibialis anterior EMG burst activity ($R^2 = 0.25$, $P = 0.001$). Furthermore, the strength of the subjects was not associated with the changes in overall movement error ($R^2 = 0.03$, $P > 0.1$) and variability ($R^2 = 0.06$, $P > 0.1$). The correlation matrix for the movement errors, variability and EMG measures is presented in Table 3-1. The individual correlations suggest that improvements in RMSE were strongly associated with reductions in spatial error ($r = 0.83$, $P < 0.001$) and movement variability ($r = 0.85$, $P < 0.001$). In contrast, improvements in RMSE were moderately associated with reduction in the temporal error ($r = 0.5$, $P = 0.001$) and an increase the tibialis anterior burst activity ($r = -0.48$, $P = 0.001$). These findings suggest that the improvements in movement errors were associated the reductions in spatial error, temporal error and movement variability and an increase in the rhythmic burst activity of the tibialis anterior. Furthermore, the improvements in movement errors and variability were not associated to changes in the strength of subjects.

Prediction of Performance at Transfer

On average, the low-gain training group exhibited better transfer to the hand compared with the high-gain training group. Hence, multiple regression models were used to determine the following associations on transfer performance for the training groups: 1) the contribution of movement variability during practice sessions to the movement error at transfer; 2) the contribution of agonist (FDI) EMG burst activity to the movement errors and variability at transfer.

The movement variability during practice days predicted (Figure 3-8 left panel) the movement error ($R^2 = 0.55$, $P < 0.001$) and variability at transfer ($R^2 = 0.71$, $P < 0.001$) with the index finger tasks. This analysis indicates that subjects who practiced with lower motor-output variability exhibited better transfer to the hand. The FDI burst activity

predicted (Figure 3-8 right panel) the movement error ($R^2 = 0.3$, $P = 0.012$) and movement variability ($R^2 = 0.48$, $P = 0.001$) at transfer for the training groups. These findings suggest that subjects with more rhythmic FDI burst activity around the target frequency exhibited lower movement error and variability with the index finger movements at transfer.

Discussion

The purpose of this study was to investigate whether low- and high-gain visual feedback could be used as interventions to facilitate acquisition and transfer of novel motor tasks in older adults. The 2 week unloaded visual feedback training reduced ankle movement variability of older adults to the level of young adults regardless of the visual feedback gain used during training. The novel finding of the present study, however, was that training with low-gain visual feedback enhanced the transfer of learning to the ipsilateral index finger. Furthermore, subjects who exhibited lower ankle movement variability during practice demonstrated lower movement errors and variability during transfer with the index finger. Collectively, our findings demonstrate that for older adults amplified motor output variability during practice and compromised visual feedback processing are important limitations in learning novel motor tasks.

Motor Learning - Acquisition

Based on the findings from studies on learning with visuo-motor rotations (McNay and Willingham 1998; Seidler 2007a; 2006) and the influence of visual feedback gain on force control (Kennedy and Christou 2010; Sosnoff and Newell 2006; Tracy 2007a; Vaillancourt et al. 2003), we expected that older adults would exhibit greater impairments during acquisition with high-gain visual feedback due to impairments in visual information processing. Contrary to our expectation, regardless of the visual

feedback gain older adults from both training groups reduced their ankle movement errors and variability at the same rate (Figure 3-3). The time course of these improvements was similar to that reported by previous training studies involving the abduction of the index finger and dorsiflexion of the ankle (Kornatz et al. 2005; Patten and Kamen 2000). For example, Kornatz et al (2005) observed that with two weeks of light-load training older adults reduced their movement variability, but there were no further improvements in motor performance with the subsequent four weeks of strength training (Kornatz et al. 2005). Similarly, Patten and Kamen (2000) reported that older adults reduced their motor output variability with two weeks of practicing a sinusoidal force task with ankle dorsiflexion (Patten and Kamen 2000).

Numerous studies have reported that amplified motor output variability is indicative of a noisier descending drive to the spinal motor neuron pool (Christou and Enoka 2011; Moritz et al. 2005; Poston et al. 2008). The minimum variance hypothesis also suggests that less noisy (variable) trajectories as an effect of practice are associated with lesser end-point variance and greater accuracy (Harris and Wolpert 1998). The strong associations between the practice induced improvements in movement variability and movement error in our data are indicative of this view (Figure 3-7). Furthermore, older adults in the training groups reduced their movement errors and variability within the first three practice sessions and demonstrated relatively consistent performance for the following days (Figures 3-3). It has been suggested that the rapid initial improvements during acquisition occur primarily due to reduction in errors relative to the target (Floyer-Lea and Matthews 2005). Once the learner matches the average performance to the target, subsequent adjustments are associated with the reduction in the variability of

performance (reinforcement; (Wolpert et al. 2011)). Previous training studies have shown that older adults reduce motor-output variability with practice of goal-directed tasks (Christou et al. 2007a), anisometric tasks (Kornatz et al. 2005) and force modulation tasks (Voelcker-Rehage and Alberts 2005). Our findings are consistent with these and suggest that the aging nervous system exhibits remarkable neuroplasticity in adapting to novel motor tasks.

It is also likely that the practice-induced improvements in movement errors and variability in our study are due to an improved ability of the nervous system to activate the involved muscles. Only the older adults who participated in the training group changed their agonist EMG burst pattern to increase muscle activation around the target frequency. These changes in the EMG burst pattern parallel the practice-induced adaptations in movement errors and variability only for the training group from pre- to post-test experimental sessions (Figure 3-4). The observed associations between the practice induced adaptations in movement error and agonist EMG burst activity were weak ($R^2 = 0.25$, $r = -0.49$; Figure 3-8, Table 3-1). This effect could be masked by experimental limitations such as surface EMG recordings and unloaded movements. Nevertheless, these findings are indicative of a change in the activation signal to the spinal motor neuron pool with practice which contributes to the improvements in movement errors. Previous training studies in older adults have reported similar observations in agonist muscle activity with practice. For example, age-associated differences in trajectory and force variability can be reduced with two weeks practice and are accompanied with lowering of the agonist muscle's motor unit discharge rate variability in older adults (Kornatz et al. 2005; Patten and Kamen 2000). Similar findings

have been reported when young and older adults practiced goal-directed contractions. With practice young adults shortened the timing between agonist-antagonist muscle activation, while older adults exhibited a prolongation in this timing primarily due to modulation of the agonist muscle (Christou et al. 2007a). Collectively, these findings indicate that the neural adjustments in the agonist muscle activation contribute towards the practice-induced improvements.

Motor Learning – Transfer to Hand

A novel finding of our study was the subjects who trained with low-gain visual feedback exhibited better transfer to the ipsilateral index finger (Figure 3-5). These findings suggest that although the type of visual feedback does not seem to influence task acquisition, it influences the persistence and generalizability of the acquired behaviour. Previous behavioral findings on transfer of learning provide mixed results. One set of studies on sequence learning and visuo-motor adaptations suggest that older adults demonstrated similar performance as young adults during transfer (McNay and Willingham 1998; Seidler 2007a). In contrast, recent findings from our lab suggest that transfer of learning is impaired in older adults and it is influenced by the motor output variability during practice. In this study, the training groups were divided into: Easy and Hard training. Subjects who trained with the easy task exhibited lower motor output variability during practice and better performance (lower errors) during the transfer tasks compared with subjects in the hard training group (Onuskhko et al. 2012). These findings suggest that the ability to transfer information from the acquired tasks is influenced by the amplitude of variability and type of practice. Findings from our study show that only the low-gain training group exhibited lower errors compared with the control group that did not train (Figure 3-5). In terms of visual feedback it is likely that

low-gain feedback simplified the task for older adults. That is, with low-gain subjects only had sufficient information about the global spatial and temporal location of their performance with respect to the target sinusoid. With high-gain subjects were not only given high resolution information regarding their spatial and temporal errors but also movement variability. This promotes the sharing attentional demands for visuo-motor corrective strategies alongside motor learning during the high-gain training. On the contrary, low-gain visual feedback enhanced motor learning by reducing the cognitive load for visuo-motor corrections and allowed the subjects to prioritize attentional demands on motor learning strategies.

It is likely that the distinct regions of the brain involved in processing low- and high-gain visual feedback (Coombes et al. 2010) differentially influence the learning of the task. Findings from imaging studies report selective age-associated degeneration of the dorso-lateral prefrontal (Raz et al. 1997) and ventral visual cortex (Park et al. 2004) which would account for the poorer performance at transfer exhibited by high-gain training group. These areas of the cortex have been implicated in the planning of motor actions (Heuninckx et al. 2008) and visual guidance of movement with high-gain (Blumberg and Kreiman 2010; Coombes et al. 2010). The regions of activation during low-gain information transmission are the bilateral V3 and V5 in the visual cortex and the ventral premotor cortex (Coombes et al. 2010). The V3 and V5 are believed to be a part of the dorsal visual stream with direct projections to the parietal cortex (Goodale and Milner 1992) and play a role in the processing of global motion (Braddick et al. 2001). Therefore, the distinct neural networks and differential processing of visual information may mediate the dissimilarities in the acquisition and transfer found in our

study. Taken together these findings suggest that: 1) there is dissociation between the decline of cortical white and gray matter and motor performance deficits with aging; 2) neural networks involved in the control and sensory guidance of movements differentially interact with motor learning in older adults; and 3) training protocols targeting specific neural networks could potentially enhance sensorimotor learning. Future research needs to evaluate the aging nervous system's ability for sensorimotor plasticity by evaluating changes in the cortico-motor representations that occur with motor learning.

In conclusion, we found that age-associated amplification in motor output variability can be improved with practice to the level of young adults. Practice emphasizing lower motor output variability is beneficial to motor learning which is most evident at transfer. It seems that impaired visual feedback processing contributes to compromised transfer of learning in older adults. This limitation in motor learning exhibited by older adults can, however, be circumvented with adequate training and low amount of visual feedback. These results suggest that the motor learning in the aging nervous system can be augmented by incorporating appropriate visual feedback manipulations with adequate practice.

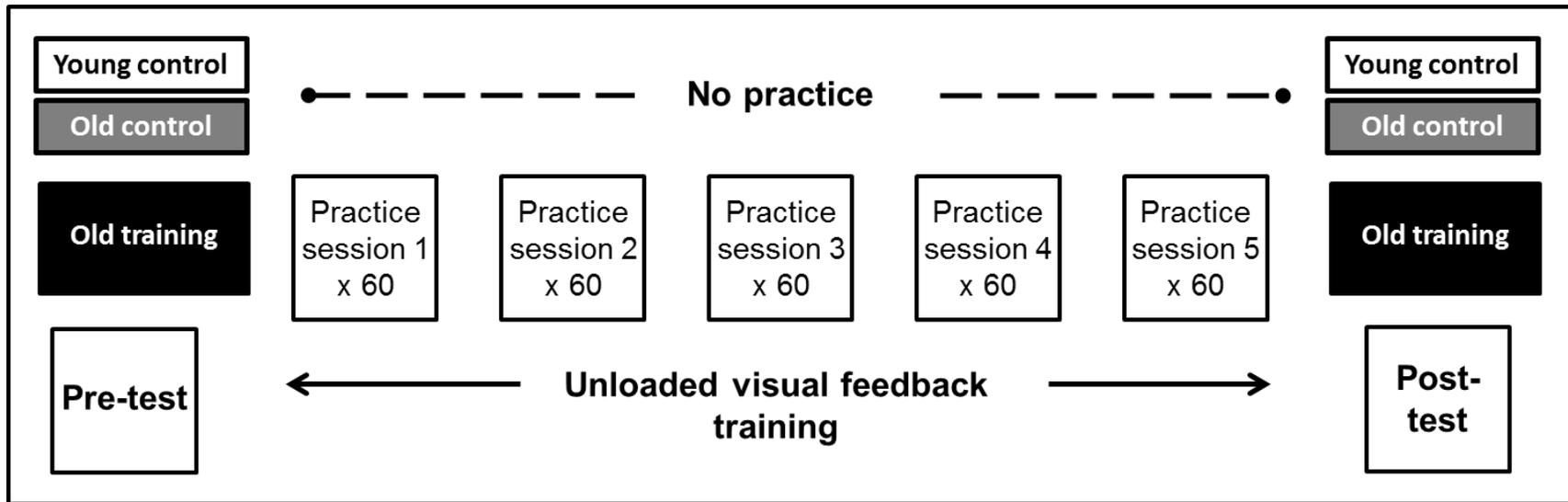


Figure 3-1. Experimental Protocol. Subjects were divided into one training (20 older adults) and two control groups (10 young & 10 older). The training group practiced unloaded ankle dorsi-plantar flexion movements for 5 sessions (x 60 trials) over 2 weeks. Maximal voluntary contraction (MVC) and agonist muscle activity from the tibialis anterior was recorded at the beginning (pre-test) and end (post-test) of the training.

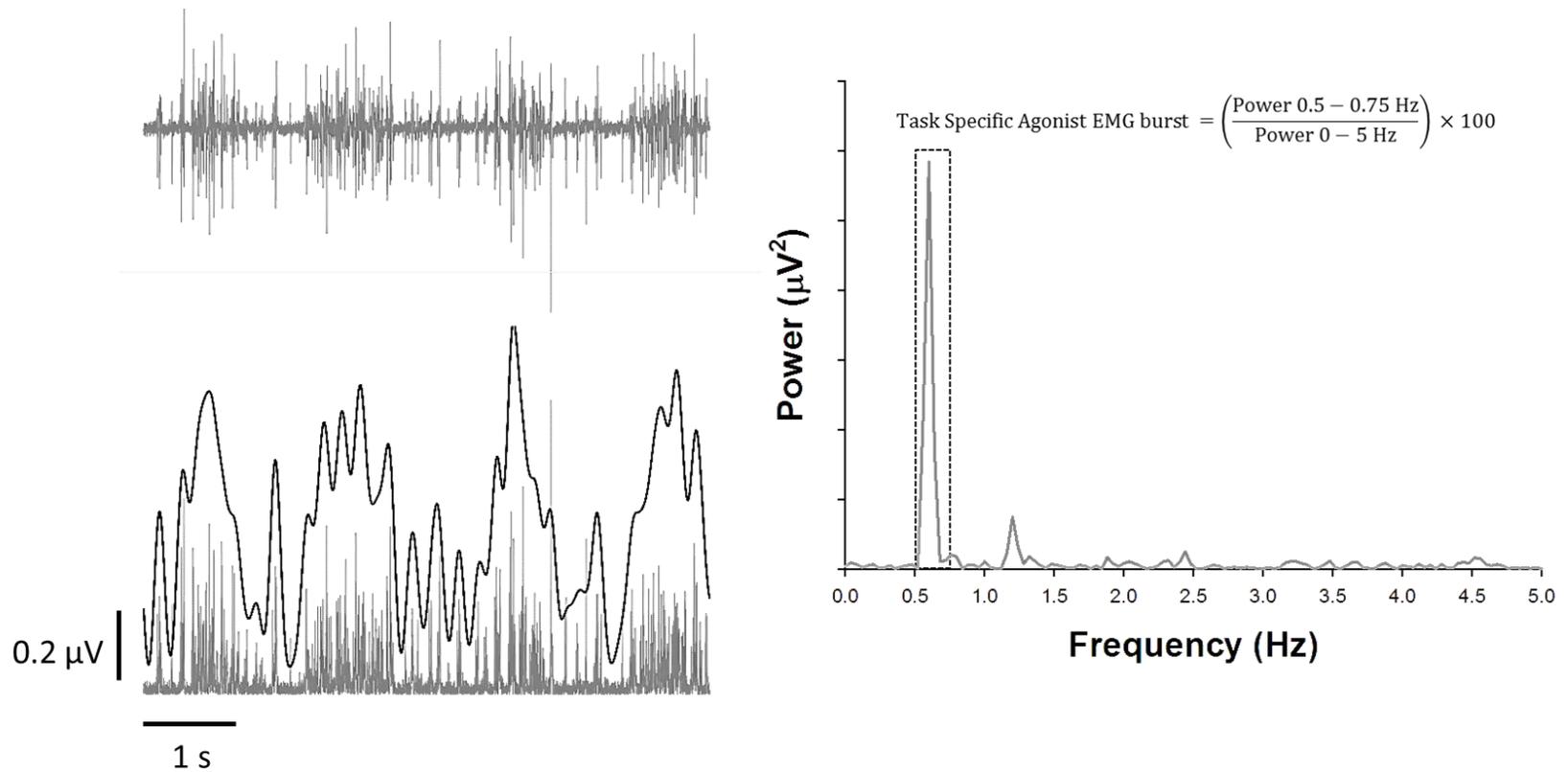


Figure 3-2. Quantification of task specific agonist EMG burst activity. The interference EMG of the tibialis anterior and first dorsal interosseous muscles was rectified and smoothed using a fourth-order Butterworth filter with a low-pass cut-off frequency of 5 Hz. This filter was used to identify the agonist EMG bursts during the movement around the task frequency of 0.6 Hz. The EMG burst index (%) was quantified as the proportion of power around the task frequency (0.5-0.75 Hz) versus the total power in the EMG signal from 0-5 Hz.

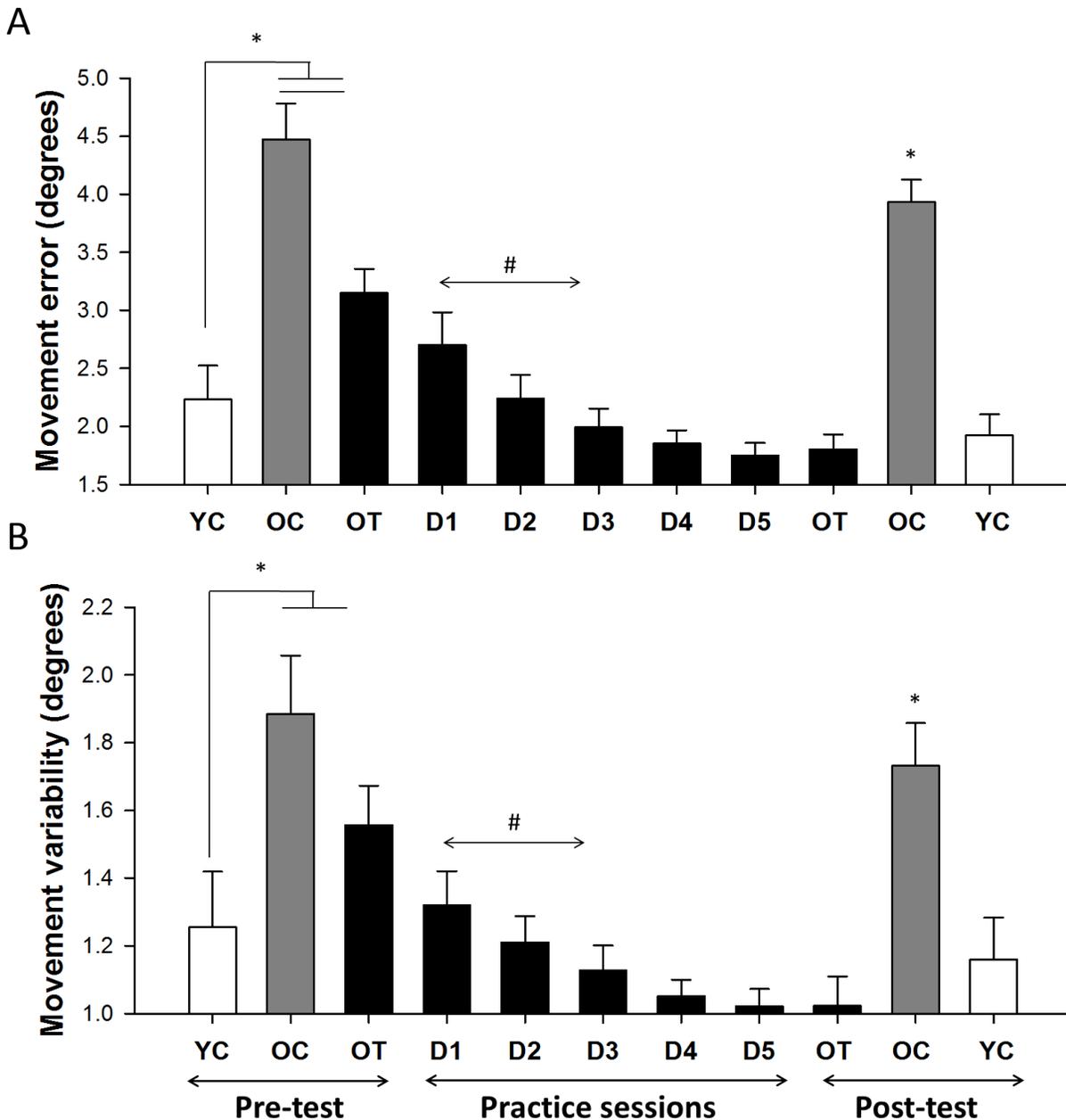


Figure 3-3. Acute and practice induced adaptations in movement error and variability. During the pre-test both the old training (black bars) and old control (grey bars) groups of older adults exhibited significantly (*) greater movement error (A) and variability (B) compared with the young adults (white bars). Most of the improvements with training occurred in the first three days of practice (#) and then remained relatively consistent. During the post-test the older adults training group exhibited similar movement errors and variability as young adults.

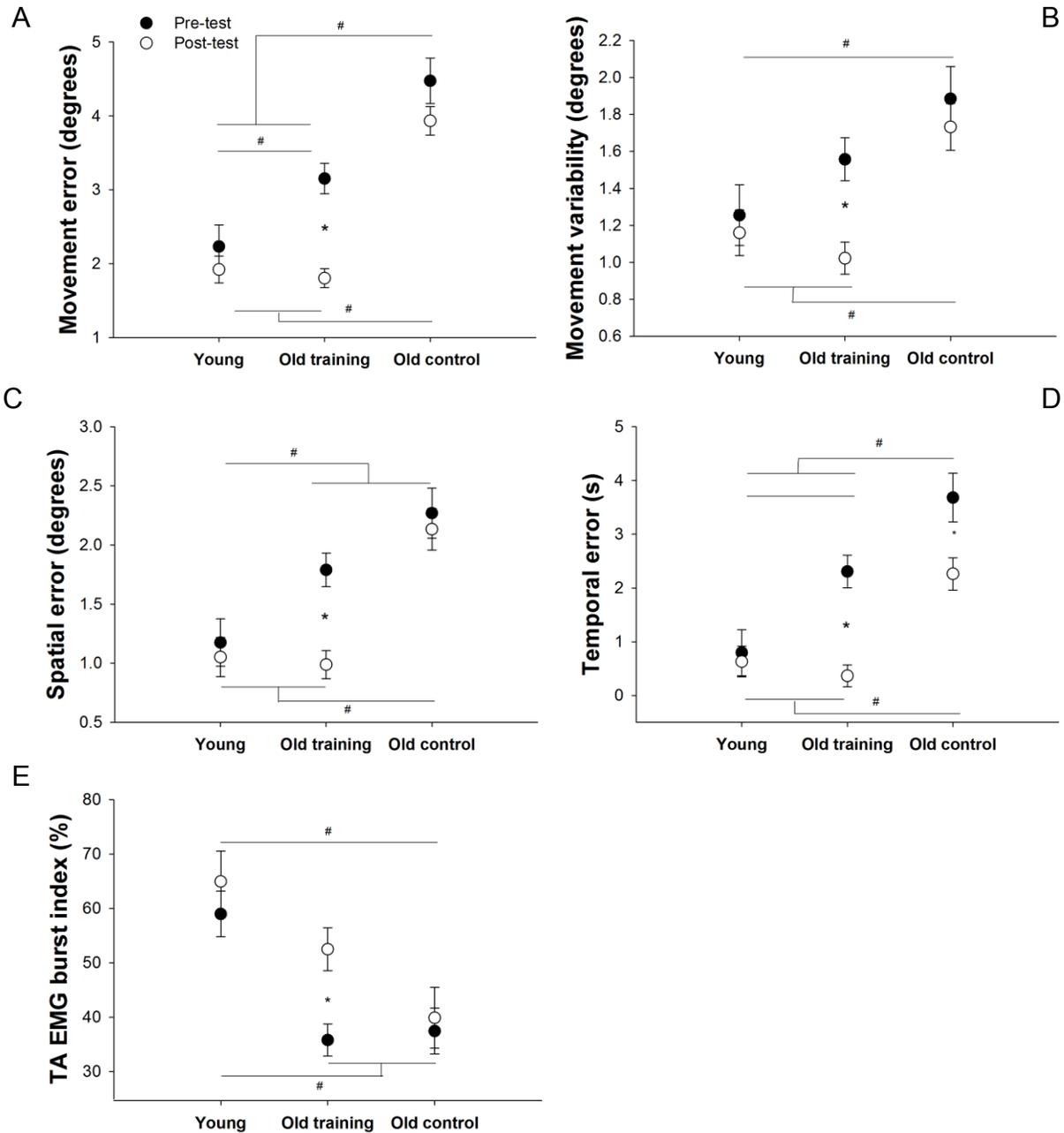


Figure 3-4. Practice induced adaptations in movement errors, variability and agonist EMG bursts. Only the training group significantly (*) reduced their (A) movement error by ~ 43%, (B) movement variability by ~ 35%, (C) spatial error ~ 45%, and (D) temporal error (~ 84%) by post-test compared with the young and older adults control groups. During pre-test all the older adults exhibited significantly (#) greater movement errors and variability compared with young adults. During the post-test the older adults training group exhibited similar movement errors and variability as young adults. Furthermore, only the older adults training group significantly (*) increased the (E) TA EMG burst activity (~ 48%) around the task frequency by post-test.

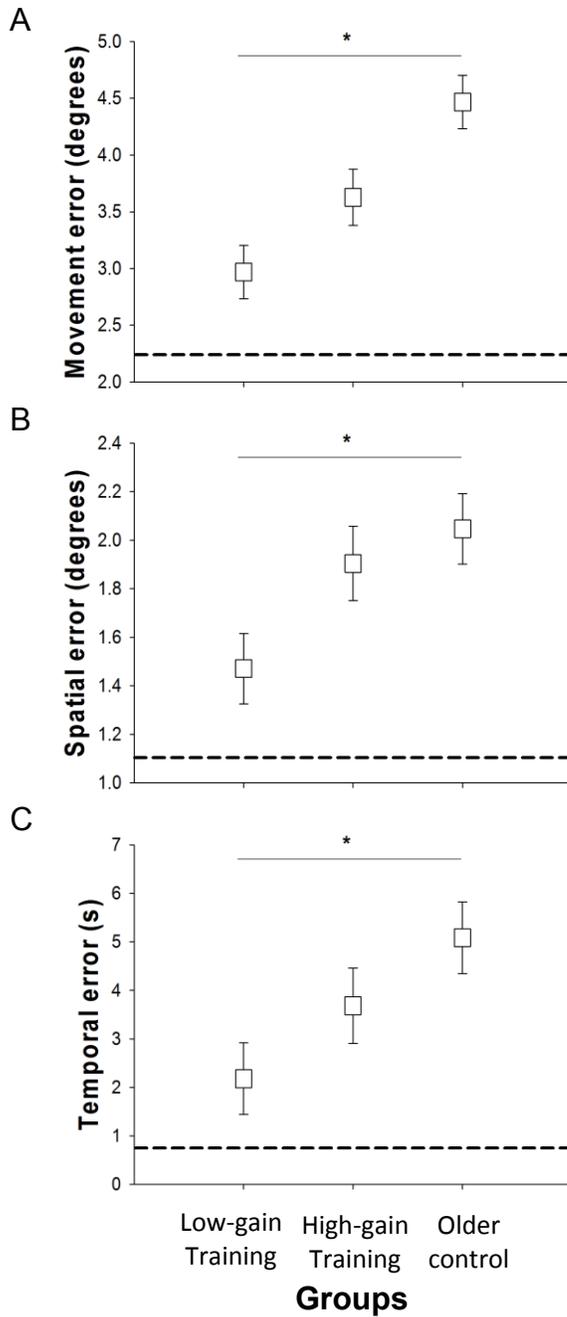


Figure 3-5. Transfer – movement errors with visual feedback. Only the low-gain training group (LGT) exhibited significantly (*) lower movement error (A), spatial error (B) and temporal error (C) compared with the high-gain training (HGT) and older adults control (OC) groups. The dashed line represents the average performance of the young adults control group.

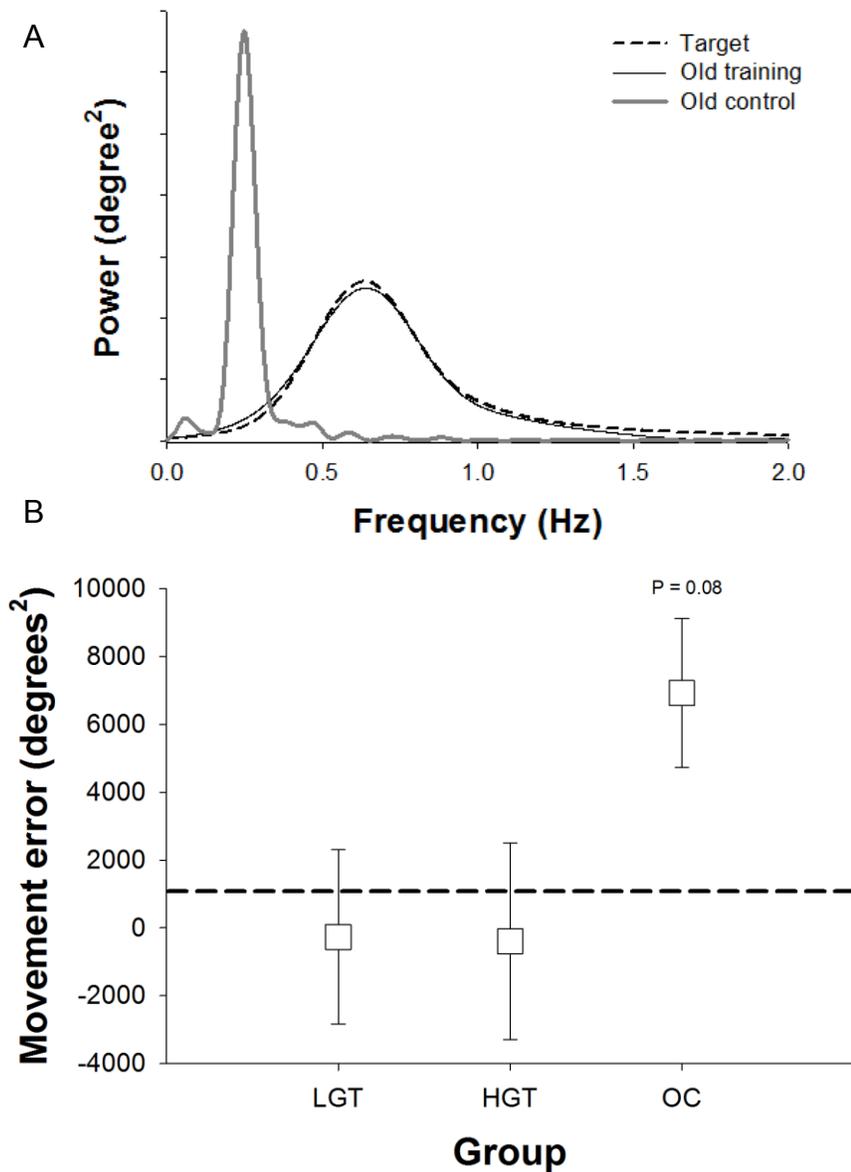


Figure 3-6. Transfer to hand – movement error with no-visual feedback. A: Movement error was quantified as the difference in power at peak frequency between the subject's movement and target template (0.6 Hz). This was done because subjects had no reference of their performance relative to the target during these trials and attempted to reproduce it out of memory. The dashed line represents the power of the template. The black line represents the power in the performance of an old training subject and the grey line represents the power in performance of an older control subject. B: The group main effect approached significance ($P = 0.08$) suggesting that only the training groups were able to match the spatial and temporal characteristics of the target template compared with the older control group when asked to trace the target out of memory. The dotted line represents the average performance of the young adults.

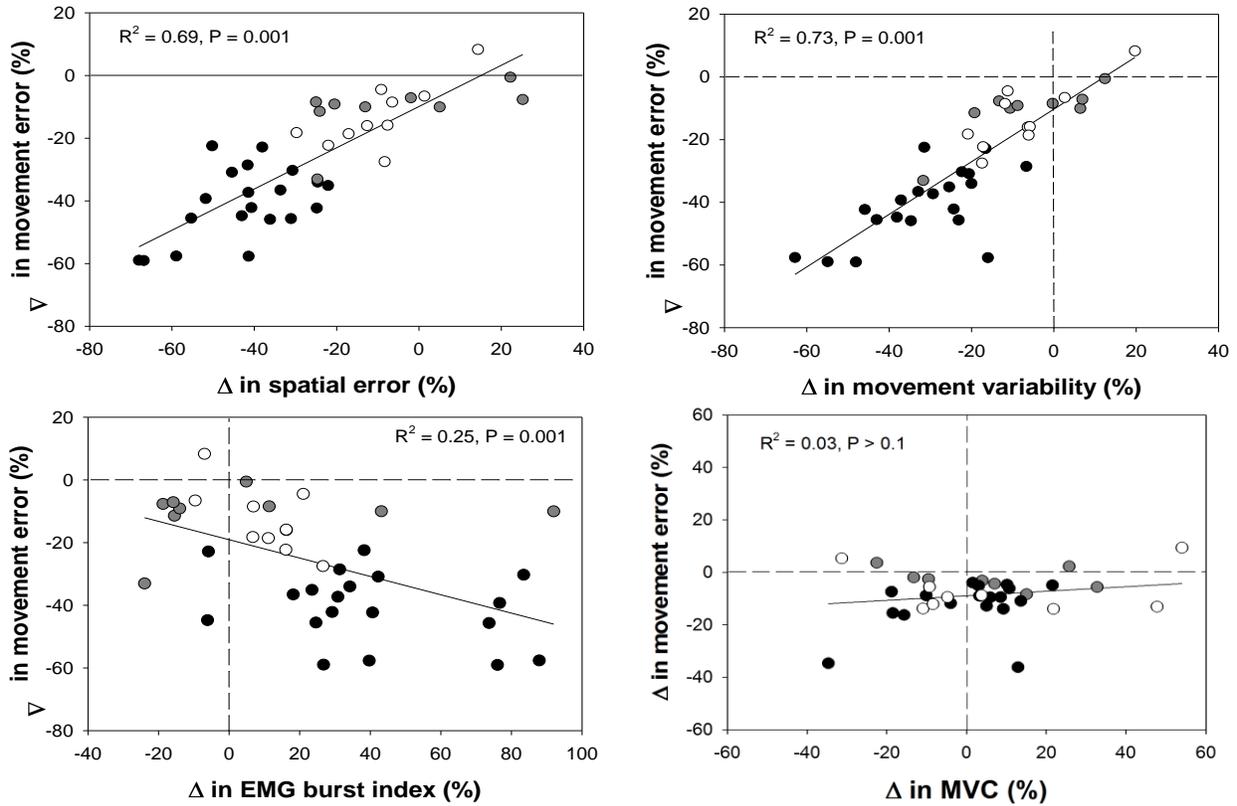


Figure 3-7. Predictions of practice-induced adaptations in movement error. The change in RMSE from pre- to post-test was predicted by the reductions in spatial error ($R^2 = 0.69, P = 0.001$; *top left*), movement variability ($R^2 = 0.73, P = 0.001$; *top right*). In contrast, reductions in movement error as associated with an increase in the tibialis anterior EMG burst activity ($R^2 = 0.25, P = 0.001$; *bottom left*). Changes in the strength of the subjects was not associated with the changes in overall movement error ($R^2 = 0.03, P > 0.1$; *bottom right*).

Table 3-1. Correlation matrix for the practice induced adaptations in movement errors, variability and EMG activity.

	Movement error	Spatial error	Temporal error	Movement variability	TA EMG burst
Movement error	1	0.827**	0.494**	0.854**	-0.483**
Spatial error		1	0.59**	0.806**	-0.366*
Temporal error			1	0.445**	-0.361*
Movement variability				1	-0.372**
TA EMG burst					1

** and * indicate significant Pearson correlation at $P < 0.01$ and $P < 0.05$ respectively.

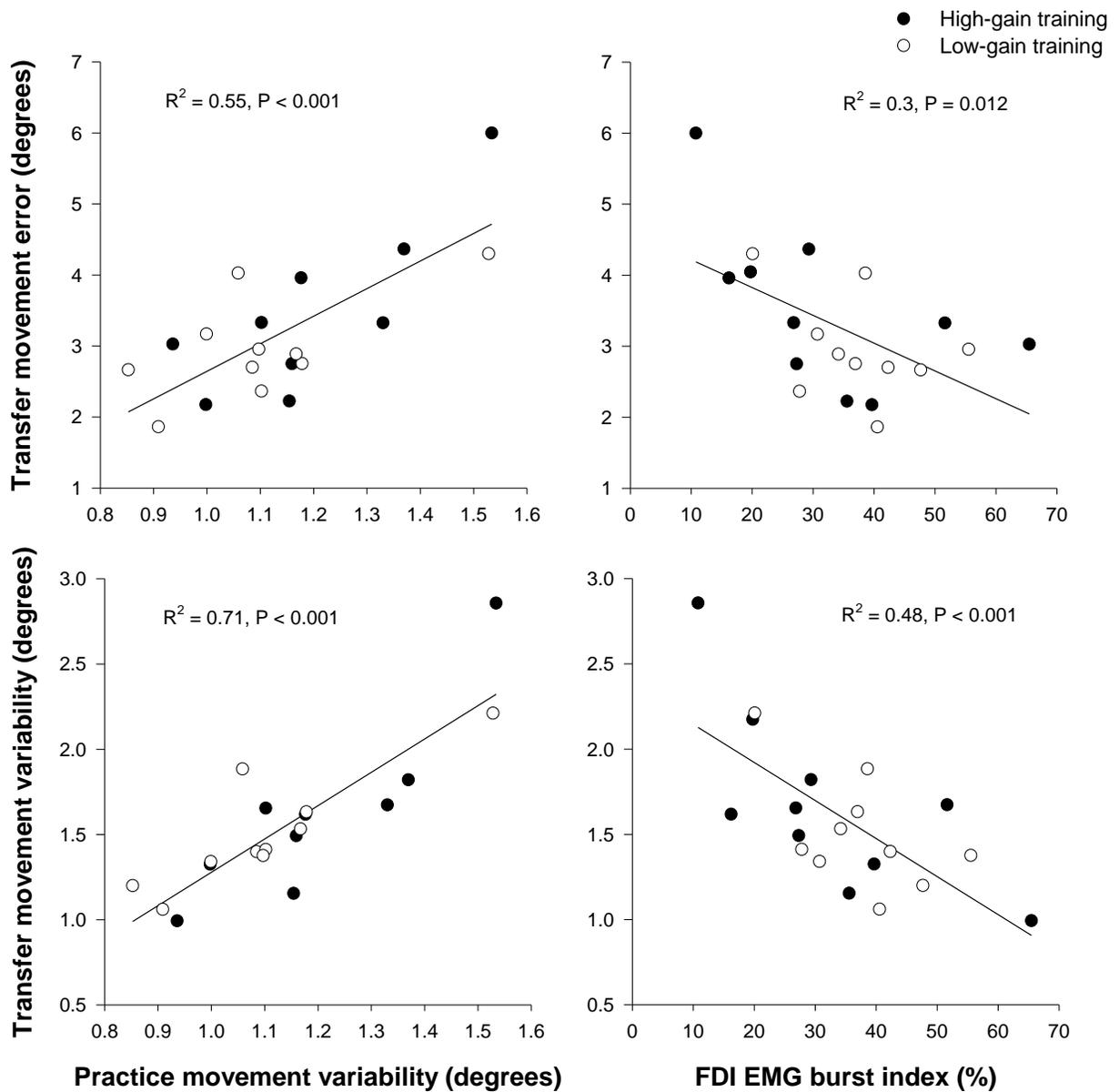


Figure 3-8. Prediction of performance at transfer. *Left panel:* The movement variability during practice days predicted the movement error ($R^2 = 0.55$, $P < 0.001$; *top*) and variability at transfer ($R^2 = 0.71$, $P < 0.001$; *bottom*) indicating that subjects who practiced with lower motor-output variability exhibited better transfer to the hand. *Right panel:* FDI burst activity predicted the movement error ($R^2 = 0.3$, $P = 0.012$; *top*) and movement variability ($R^2 = 0.48$, $P = 0.001$; *bottom*) at transfer for the training groups

CHAPTER 4 CONCLUSIONS

The purpose of this dissertation was to investigate whether different amounts of visual feedback can be used in training interventions to facilitate acquisition and transfer of novel motor tasks in older adults. Chapter 1 provided the background and rationale for the studies. It presented the importance of motor output variability and how its amplification due to deficiencies in visual feedback processing potentially mediates motor learning impairments in older adults. This was the core of the examination across three studies described in Chapters 2 and 3. The studies in Chapter 2 investigated the influences of motor planning and visual feedback processing in older adults during short-term adaptations. The major finding of the study was that compromised visual feedback processing but not motor planning mediated the age-associated deficiencies in motor performance. The impairments in motor performance were most evident with high-gain visual feedback. The study in Chapter 3 was designed to investigate the effects of low- and high-gain visual feedback training in augmenting acquisition and transfer in older adults. The data from this study suggested that the compromised visual feedback processing with high-gain negatively influenced motor learning in older adults, which was evident in the performance at transfer. In all, the findings from these experiments on motor control and learning in aging have theoretical and clinical implications for the aging population.

Aging and Processing of Visual Information

Vision is the primary source of sensory information that augments motor performance in humans (Carlton 1992; Slifkin and Newell 2000; Woodworth 1899). Recent evidence from our lab and others suggests that the amount of visual feedback

(e.g. gain) during performance interacts with the ability of older adults to perform motor tasks. Specifically, increasing the gain of the visual feedback amplifies motor output variability only in older adults but not young adults (Kennedy and Christou 2010; Sosnoff and Newell 2006; Vaillancourt et al. 2003; Welsh et al. 2007).

The visual control of movement was examined in Chapter 2 and the influence of visual feedback gain on motor learning in Chapter 3. The findings from these studies are suggestive of impairments in visual feedback processing in the aging nervous system. The processing of sensory information with and without feedback occurs through distinctly different neural networks (Goodale and Milner 1992). Furthermore, the cortical processing of visual feedback is gain dependent (Coombes et al 2010).

With the advent of high resolution imaging techniques, different networks for visual information processing have been suggested (Blumberg and Kreiman 2010; Coombes et al. 2010; Goodale and Milner 1992; Raz et al. 1997). These pathways connecting the prefrontal and visual cortices to the motor cortex have a strong impact on motor control. Furthermore, it is now documented that there is a structural and functional decline in specific regions of the aging central nervous system (for review see (Seidler et al. 2010)). The regions of interest to this study are: a) the dorso-lateral prefrontal cortex (DLPFC) and its connections with the primary motor cortex (M1) (Raz et al. 1997) which is involved in planning of motor actions for visual guidance of movement; 2) neurons in the ventral visual cortex (Blumberg and Kreiman 2010; Coombes et al. 2010; Park et al. 2004) associated with the transformation of high-gain visual information; 3) the cerebellar hemispheres (Heuninckx et al. 2008; Mattay et al. 2002) known for their role error based motor learning (Criscimagna-Hemminger et al. 2010); and 4) the

supplementary motor area (SMA) (Harada et al. 2009) which is associated with the internal guidance of movements, such as the performance of a sequence of movements from memory as opposed to visually guided movements (Shima and Tanji 1998).

Chapters 2 and 3 examined the motor performance of older adults across multiple levels of visual feedback gains and without feedback. The findings presented in Chapter 2 confirm that visual information processing is impaired in older adults. This impairment is evident with high-gain visual feedback as it exacerbates the age-associated differences in motor output variability. Interestingly, lowering the amount of visual feedback gain or completely removing it ameliorates these age-associated differences in movement error and variability. This data suggests that internal guidance of movement is affected to a lesser extent compared with visual guidance of movement in older adults. This is significant because the SMA is involved in the planning of movements. The lack of aging differences in movement planning observed in our study suggests no functional insufficiencies in the SMA or its connections to the premotor cortex (PMC) in older adults. Although the present set of studies did not examine the brain areas directly, further studies using brain imaging techniques are needed to examine these issues more closely.

The findings from Chapter 3 also relate to the roles of the prefrontal cortex and cerebellar hemispheres. For instance, the data showed that regardless of the visual feedback gain used for training older adults reduced their ankle movement variability to the level of young adults. Yet, on average only the low-gain training group demonstrated better transfer to the index finger. This finding reflects an interaction in the processing of visual information gain and motor learning. It is possible that the visuomotor deficits in

transfer for the high-gain group occur because the aging cerebellum is unable to keep up with the simultaneous demands of error correction and motor learning (Ghez and Fahn 1985). Together, the results from Chapters 2 and 3 suggest that neural pathways related to the DLPFC and its connections to the PMC are deficient in aging. This limits the ability of older adults to perform visually guided movements during high-gain and compromises motor learning.

In all, behaviorally older adults can learn novel motor tasks as well as young adults (Chapter 2 Experiment 1) and improve their movement errors and variability to the level of healthy young adults (Chapter 3). On the other hand, a decrease in structural cortical plasticity could be associated with motor learning deficits in older adults (for review see (Seidler et al. 2010)). This suggests that: 1) there is dissociation between the decline of cortical white and gray matter and motor performance deficits with aging; and 2) training protocols targeting specific pathways for sensory guidance of movement can enhance motor performance and learning. Another possibility is that the aging nervous system utilizes alternate pathways for acquisition and transfer of learning. Future research needs to evaluate the aging nervous system's ability for sensorimotor plasticity by evaluating changes in the cortico-motor representations that occur with motor learning.

Aging, Motor Output Variability and Motor Learning

Aging amplifies motor output variability and impairs the ability of older adults to perform motor tasks with accuracy (Christou 2010a). The findings presented in Chapter 2 confirm this and suggest that amplified motor output variability of the aging nervous system is driven by the constraints of the imposed task, greater visual feedback in the present study. Over the years, Wolpert and colleagues have suggested that amplified motor output variability during practice negatively influences updating of the motor

command for subsequent movements towards the same goal. Inversely, the central nervous system learns to perform new tasks with accuracy by minimizing motor output variability (Faisal et al. 2008; Harris and Wolpert 1998; Wolpert et al. 2011; Wolpert and Ghahramani 2000). The results from Chapter 3 directly demonstrate that the subjects who practice with lower motor output variability exhibited lower movement errors and variability during transfer. Therefore, confirming that amplified motor output variability negatively interacts with motor learning. Although older adults demonstrated the ability to improve motor performance with practice, their inability to match the performance of young adults suggests that motor learning may be impaired (Christou et al. 2007a; Seidler 2007b). The findings from Chapters 2 showed that regardless of the improvements with practice, older adults were not able to match the performance levels of young adults.

Transfer of learning is a useful assessment of motor learning because it reflects the learner's ability to share components of a learned skill to newer and different tasks (Schmidt and Lee 2011; Wolpert et al. 2011). It is an important component of motor learning as it renders a functional usefulness to practice. Recent findings from our lab suggest that transfer is influenced by the task difficulty during practice. Specifically, the level of difficulty during practice interacts with how well older adults learn and transfer the tasks (Onuskhko et al. 2012). The inability of the high-gain training group in Chapter 3 confirms this shortcoming of motor learning in older adults.

Overall, aging compromises multiple factors of motor learning. There are deficits in extraction of sensory information with aging, as shown by results from Chapter 2 and 3. As a result, the selection and execution of strategies is differentially compromised in

older adults, as demonstrated by the differences in performance at transfer between the low- and high-gain training groups. This necessitates the requirement to develop simple training paradigms that promote the effective use of visual information to lower motor output variability, and enhance motor learning in older adults.

Summary

The present investigation examined the influence of visual feedback gain on movement control and learning in older adults. Four main conclusions were drawn from these experiments. 1) Older adults exhibit greater motor output variability, which impairs their movement control and learning, compared with young adults. 2) Visual feedback processing is impaired in older adults and impairs motor performance, especially at high-gain. 3) The gain-dependent amplification of motor output variability differentially influences acquisition and transfer in older adults. 4) The age-associated limitation in motor learning can be circumvented with adequate training and lower amount of visual feedback. In sum, findings from the present studies have clinical implications in the understanding and development of rehabilitation protocols for aging and clinical populations.

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BIOGRAPHICAL SKETCH

Harsimran Baweja is an Indian Physical Therapist. He received his Ph.D. under the mentorship of Dr. Evangelos Christou in Applied Physiology and Kinesiology from the University of Florida in 2012. He has 8 peer reviewed publications in Experimental Brain Research, Journal of Motor Behavior, Muscle and Nerve, Human Movement Science and European Journal of Applied Physiology, and over 30 published abstracts. Harsimran's major projects during his doctoral studies focused on the influence of visual feedback manipulations on motor control and learning in young and older adults.

Harsimran has served as a reviewer for the Journal of Motor Behavior, Research Quarterly in Exercise and Sports, Neuroscience Methods, and Archives of Physical Medicine and Rehabilitation. In 2012, he received the Outstanding International Student award for his academic performance during his doctoral studies. He was also nominated for and won the 2012 Graduate Student Award for outstanding undergraduate mentoring from the Howard Hughes Medical Institute Science for Life program. Following his Ph.D. he continued his pursuit of science as a post-doctoral fellow with Dr. Robert Sainburg at the Pennsylvania State University in State College, Pennsylvania.

Harsimran received his bachelor's degree in Physical Therapy summa cum laude in 2005 from S.P. University (India). Prior to joining the Neuromuscular Physiology Lab with Dr. Christou in Jan 2008, he served at the Kashiba Children's Hospital and Bidada Sarvodaya Trust as a physical therapist for the Prosthetics and Orthotics department and Natural Calamities Management Team. He has also taught Biomechanics, Clinical Orthopedic Physical Assessment, Sports Injuries and Orthopedic Rehabilitation, and Motor Neuroscience at undergraduate and graduate levels at NTR University of Health

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Harsimran was born six miles from Taj Mahal; the younger of two sons to Alice and Gurcharan Baweja. In Jan 2010, Harsimran married his undergraduate sweetheart Niyati. He was a competitive swimmer and spring board diver at the National level in India from 1998-2000. In November 2000, he led the Indian Rowing Team U-19 in the IX Junior Asian Championships to the podium with a bronze medal. Harsimran is an avid motorcyclist and amateur photographer. He intends to finish his A-level sky-diving license on completion of his PhD.