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4. Aging and neuromuscular adaptations with practice

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Abstract. Numerous studies have demonstrated that aging can impair motor control and accuracy. Because in the next thirty years the number of working Americans over the age of 65 will almost triple, it is important to determine whether such impairments can be minimized with practice. In this chapter, we will review recent studies which demonstrate that the aging nervous system can adapt to task demands with practice and improve motor performance almost to that of young adults. Furthermore, we will discuss the neuromuscular mechanisms that contribute to the motor adaptations from the single motor unit to multi-muscle activity, which appear to be different for young and older adults.

Introduction

The ability to learn new motor skills and adapt to new demands across the lifespan is a fundamental component for survival. Nonetheless, aging results in significant biological changes and consequently impairments in motor performance. The core of this chapter reviews scientific evidence which

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demonstrate that the ability of older adults to adapt and learn new motor tasks is compromised due to an impaired motor output. Furthermore, this chapter will discuss the neural mechanisms that may contribute to the impaired ability of older adults to adapt to new motor tasks and the effect of training to improve their motor adaptability. Understanding how the healthy aging neuromuscular system learns to adapt and accomplish accurate movements when it is impaired by greater motor output variability [1,2] is crucial for the following reasons: 1) It can weaken the ability even of healthy older adults to adapt to changing environments and consequently compromise their independence and health. 2) The aging population will increase dramatically in the next 30 years and in some developed nations (e.g. USA) may comprise 25% of the workforce [3,4].

1. Aging, motor-output variability, and accuracy

The actions produced by a voluntary muscle contraction vary within a trial (trajectory variability) (Figure 1A) and from trial to trial (end-point variability) (Figure 1B) [5,6]. Theoretically, motor-output variability is assumed to be *noise* superimposed on the motor command at any level of the nervous system [7]. The functional significance of motor output variability is that it can impair the ability of humans to perform accurate movements [8].

Older adults often exhibit an inability to move smoothly and accurately during activities of daily life [9-12]. Experimental evidence suggest that older

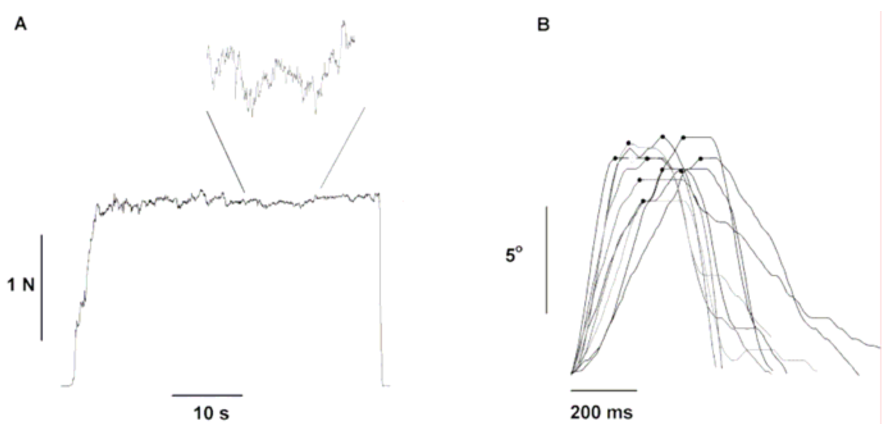

Figure 1. Within-trial and trial-to-trial motor output variability. The recording in the left (A) demonstrates the involuntary variability in the force output despite the efforts of a young adult to exert a constant isometric contraction with no variations. This variability is dominated by low-frequency oscillations (inset). The recording to the right (B) demonstrates the trial-to-trial variability during goal-directed movements exerted by a young adult. It is evident from the 10 trials graphed that variability exists across trials for both the spatial and time components of movement.

adults exhibit reduced ability to control the force and timing of a muscle contraction. For instance, during constant isometric contractions or slow movements with various limbs, it is generally accepted that the trajectory variability (within-trial) is greater for older adults compared with young adults, especially for intensity levels lower than 20% of maximum [2,5,6,13-21]. These age-associated impairments appear to be even greater and more consistent across intensities for end-point variability. For example, when young and older adults contracted the knee extensors on an isokinetic device and aimed to match parabolic force-time targets ranging from 5% to 90% of maximum at 200 ms, older adults exhibited significantly greater end-point variability in peak force, impulse, time-to-peak force, and impulse duration [22,23]. Interestingly, the older adults exhibited the most variability in the *temporal characteristics* of movement (time-to-peak force, impulse duration). Similar results during different tasks have been demonstrated for movements with the index finger [2] and arm [24]. Furthermore, recent findings show that during aiming isometric [1] and anisometric contractions [1,25] older adults exhibit greater trajectory and end-point variability, especially for the temporal characteristics of the contractions (Figure 2). Furthermore, these

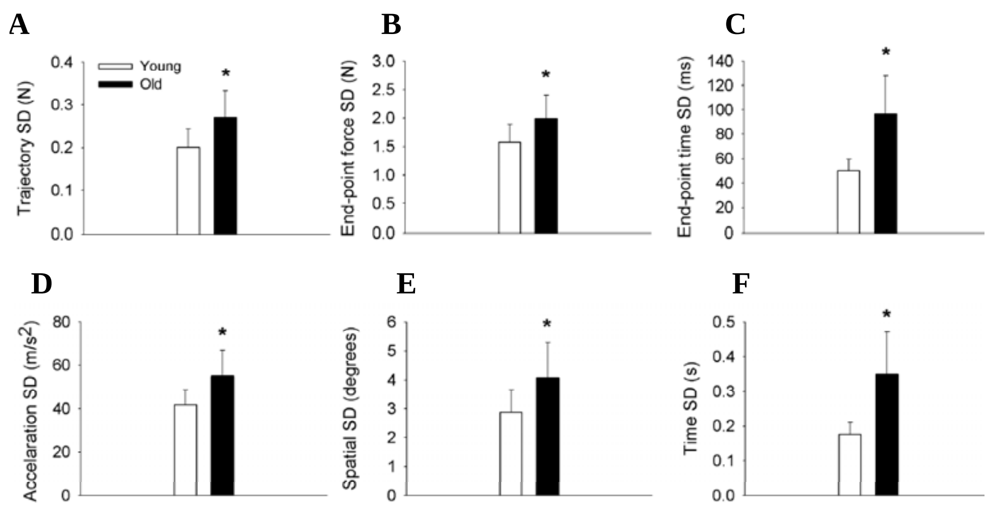

Figure 2. Aging amplifies motor output variability, especially for the timing of the contraction. The top row shows a comparison between young and older adults for motor output variability of the index finger during isometric contractions of the first dorsal interosseus muscle, whereas the bottom row shows similar measurements during anisometric (movement) contractions of the first dorsal interosseus muscle (movement). Each bar shows the mean ± confidence interval of the trajectory variability (A, D), peak force (B) or spatial variability (E), and time to peak force variability for the first 40 trials (C, F). These results indicate that motor output variability is greater for older adults compared with young adults, especially for the timing of the contraction. Data from Christou et al. (2007a) [1] and Christou et al. (2007b)[30].

findings indicated that both forms of motor output variability are strongly associated with end-point error in force, space, and time. This evidence extends to multi-joint aiming [26] and continuous [27-29] tasks. During aiming tasks [26], older adults compared with young adults exhibited impaired accuracy and greater movement variability. Therefore, heightened levels of motor-output variability may predispose older adults to adapt different neuromuscular strategies to learn, retain, and transfer novel motor tasks with accuracy.

2. Aging and motor learning

Learning novel motor tasks includes both acute and long-term adaptations of the nervous system. Acute adaptations refer to the initial neural and motor output adjustments with exposure to a novel motor task, whereas long-term adaptations refer to a) the ability to ***retain*** the learned task (performance at a different time) and b) the ability to ***transfer*** what has been learned to new conditions and variations of the same task [31-33]. The acute and long-term adaptations are associated with different changes in activity within higher centers [34-36]. For example, Floyer-Lea and Matthews (2005) [34] showed that initial learning of an isometric task induced the greatest improvements in performance and was associated with decreases in activity in the prefrontal, parietal, and cerebellar cortex, and increases in the cerebellar dentate nucleus, putamen, and thalamus. In contrast, long-term learning of a motor task was associated with adaptations in the contralateral somatosensory and motor cortex and the putamen. Hikosaka et al. (2002) [35] interpret these initial practice-induced adaptations in higher centers to be associated with the process of learning a new motor task explicitly, which involves spatial improvements (initial learning) followed by fine tuning of the motor system to further improve motor performance (long-term implicit learning).

The literature on aging and motor learning is limited to sequence learning tasks requiring older adults to press response buttons with the fingers. The findings are mixed with some studies indicating no age differences in sequence learning [37,38] and other studies, from the same group, demonstrating age-associated impairments in learning sequential motor tasks [39]. A recent study by Seidler [40] demonstrates that although the accuracy of joystick aiming movements with the wrist was impaired in older adults compared with young adults, the rate of learning the task was similar between the two age groups. However, when a visuomotor perturbation was imposed (rotation of the visual feedback at 30 and 45 degrees) the ability of older adults to adapt was significantly impaired compared with that of young adults. Retention of these movements with the original feedback condition indicated no significant differences between young and older adults.

In contrast, other researchers demonstrate that when young and older adults perform sequential movements (movements that require to follow sequences of targets) with the elbow flexor and extensor muscles, the rate of learning the task (quantified as the duration to perform the task) is slower for older adults compared with young adults [41]. Furthermore, older adults had an impaired retention of the task 24 hours later (Figure 3A).

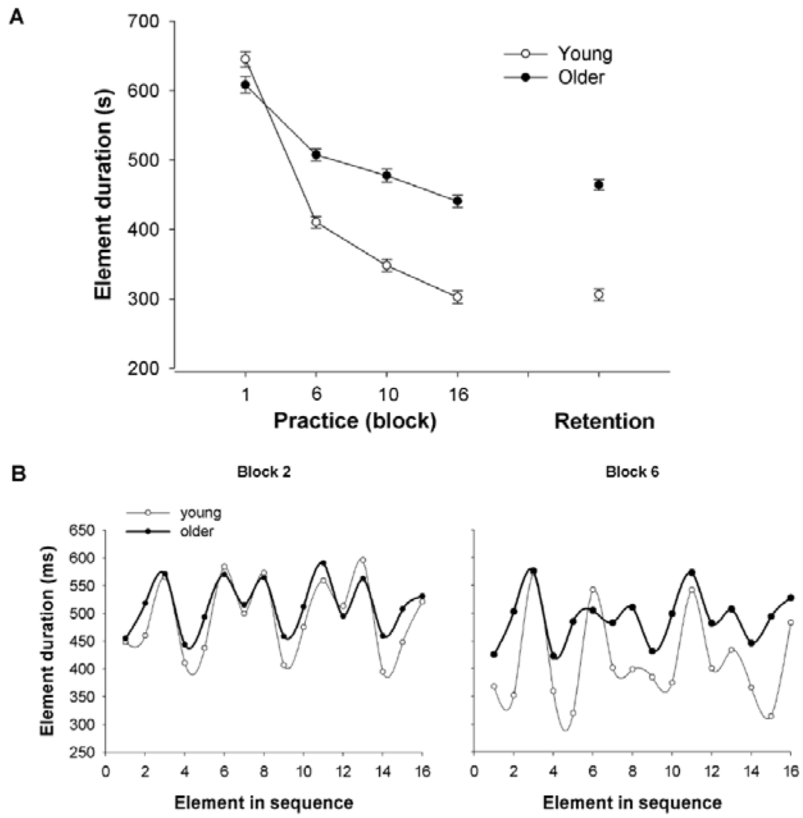

Figure 3. Age-associated differences in learning sequential movements with the elbow flexor muscles. Each point is the mean ± standard error of 10 repetitions of the sequence for 8 young and 8 older adults. Element duration (Y axis) refers to the time it took subjects to perform the sequential task. Although both young and old adults improved significantly with practice of the task (3A), the practice-associated improvements were greater for the young adults. Thus older adults exhibited impaired motor learning compared with young adults. Retention of the sequential task 24 hours after the practice session indicated that young adults retain the task better than older adults. Figure 3B shows representative sequence structure from one young and one older adult at blocks 2 and 6. It is evident that young and older adults organize the sequence differently, which may be responsible for at least some of the age-related deficits with learning the movement. These findings demonstrate that motor learning is impaired in older adults compared with young adults possibly due to different structuring of the sequence. Data from Shea et al. (2006) [41].

Analysis of the sequence structure indicated that older adults did not organize their motor output into sub-sequences as effectively as the young adults (Figure 3B). Furthermore, recent findings suggest that the ability of older adults to acquire new aiming motor skills with the index finger is compromised [1]. Older adults were less accurate than young adults in the force and time domains during the initial trials of the task due to altered agonist-antagonist muscle activity and greater motor-output variability. Thirty-five practice trials improved force and time end-point accuracy for both age groups. Older adults became as accurate as young adults for the force but not for the time parameter of the target (Figure 4). Time accuracy remained different even after 100 practice trials primarily due to an alternative timing between the agonist and antagonist muscle activity. In addition, the adjustments in motor-output variability associated with the initial improvements in end-point accuracy differed for young and older adults. Finally, there is evidence that when older adults practiced a finger task

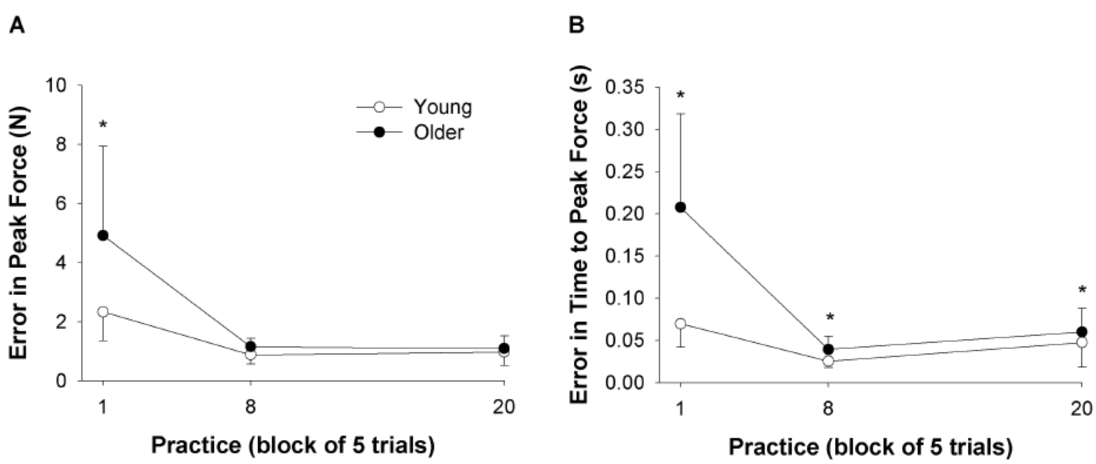

Figure 4. Practice improves force but not time accuracy of older adults to that of young adults. Average force and time end-point error for blocks of 5 trials (blocks 1, 8, and 20 are shown) across the 100-trial protocol [1]. A) Practice improved force end-point error in both young (62%) and older (77%) adults in the first eight blocks of trials (40 trials). B) Practice improved time end-point error in both young (64%) and older (81%) adults in the first eight blocks of trials (40 trials). The point of inflection for both age groups was around the eighth block, which indicated most of the practice-induced improvements in end-point error occurred during the first 40 trials, and remained constant for trials 41-100. Older adults exhibited significantly greater force and time end-point error compared with young adults in the first two blocks of trials. Furthermore, older adults exhibited greater time end-point error compared with young adults for trials 41-100 (blocks 9-20). These findings demonstrate that despite their large improvements with practice, older adults exhibit impaired time accuracy following 100 practice trials. Data from Christou et al. (2007) [1].

for a longer time (6 weeks), they reduced the variability in their movement trajectory, which was associated with a standardized manual dexterity task [25]. Overall, it appears that learning new complex motor tasks is impaired in older adults either due to a noisier output or due to altered way of structuring the motor output.

3. Practice protocols to constrain motor output variability and improve learning

There is significant evidence that brain plasticity is operational in older adults, which suggests that training can potentially stimulate the brain of older adults to develop alternative strategies and minimize the age-associated impairments in motor performance that are caused by structural changes [42]. As expected, motor learning occurs with physical practice of a task in older adults. These improvements appear to be associated with reductions in the variability of motor output but not due to increases in strength. For example, Kornatz et al. (2005) [25] demonstrated that 2 weeks of training with a light load (10% maximum) reduced trajectory variability of the index finger when older adults learnt to lift and lower a light load with precision. Subsequent practice with a heavier load (70% maximum; strength training) for 4 weeks did not have any significant effect on the performance of the task, indicating that older adults benefitted primarily from light-load steadiness training. In addition to the specific task that was practiced, the steadiness training transferred to a standardized manual dexterity task (Purdue Pegboard).

The disassociation between improvements in strength and improvements in variability has been shown by other studies, which indicate similar improvements in motor output variability achieved with low- or high-intensity strength training of the first dorsal interosseous [25] and of the knee extensors [43]. Furthermore, longitudinal studies found that strength training the knee extensors improved strength but did not improve fluctuations in motor output [44]. In contrast, training protocols that emphasized muscle coordination and skill improved the consistency of motor output in various muscle groups [45-47] but this improvement was not associated with increases in strength. For example, when older adults practiced Taiji for a few months, they improved both strength and motor output variability of the knee extensors. However, the improvements in strength and force variability were not associated (Figure 5), which indicates that practice of coordinated movements with the upper and lower body can be transferred into a single-joint task (knee extension). Overall, these results suggest that practice protocols that emphasize coordination of movement can minimize motor output variability and transfer to new tasks, most likely via neural adaptations.

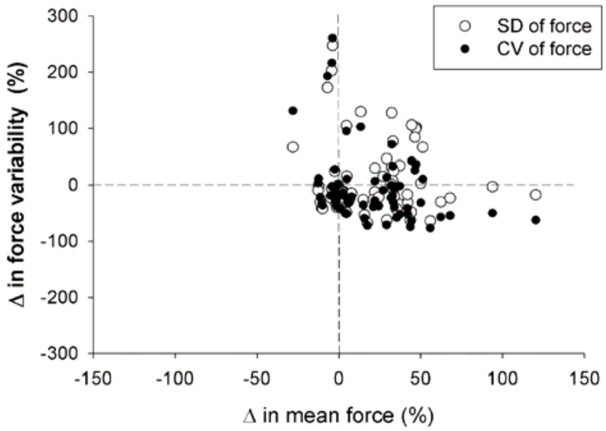

Figure 5. Taiji training and force variability in older adults. Sixteen older adults underwent Taiji training and ten older adults served as the control group [45]. Older adults that participated in the Taiji training increased strength (X axis; values above 0 for change in mean force) and decreased force variability (Y axis; values less than 0 for change in SD and CV of force), whereas the control group did not change significantly for either measurement (Y axis; most values above 0 for change in SD and CV of force). Nonetheless, the improvements in force variability were not associated with the increases in strength. These findings indirectly suggest that Taiji, an unconstrained activity, increased strength and reduced motor output variability in older adults most likely by improving the interaction of the involved agonist and antagonist muscles.

4. Neuromuscular mechanisms that can impair motor learning in older adults

Neurophysiological changes that accompany aging include alterations in various structures of the brain [42], death of cortical motor neurons [48], and spinal alpha motor neurons [49,50], as well as, the slowing of the signal transmitted from the corticospinal and reflex pathways to the motor neurons [51]. These changes may alter the planning and execution of the motor command and consequently alter the precision of the motor output [8]. Because the motor unit is the final common pathway of higher centers to the muscle, these age-associated changes at higher centers and consequent impairments in the motor output should be evident in the discharge characteristics of motor units [6,52]. The following two neuromuscular mechanisms can potentially explain the greater variability in older adults and potentially impair their ability to learn novel motor tasks with accuracy:

Motor unit discharge rate variability

The variability of motor unit discharge has been shown to be related to synaptic noise [53]. It has been suggested that the summation of motor unit discharge rate variability is the cause of motor output variability in humans [8]. Computer simulations indicate that increasing the variability of motor unit discharge (CV of discharge rate) amplifies the force fluctuations within a trial [6,54]. Consistent with the simulations, experimental findings have shown that the increased fluctuations in the movement trajectory exhibited by older adults are associated with an increased variability of motor unit discharge [15,25]. Furthermore, recent findings that combine experimental measurements and simulations provide direct evidence that the variability of motor unit discharge is a major determinant of force variability [54,55]. Finally, the variability of motor unit discharge in older adults has been associated with a functional manual dexterity task. Specifically, the practice-induced decreases in the CV of motor unit discharge during movements with the index finger improved the ability of older adults to perform better with the Purdue Pegboard task [25] (Figure 6).

The variability of motor unit discharge is rhythmical and has been attributed to the oscillatory input from higher centers to the motor neuron pool [16,56-60]. Recent findings demonstrate that older adults exhibit greater low-frequency oscillations in motor unit discharge (< 5 Hz) compared with

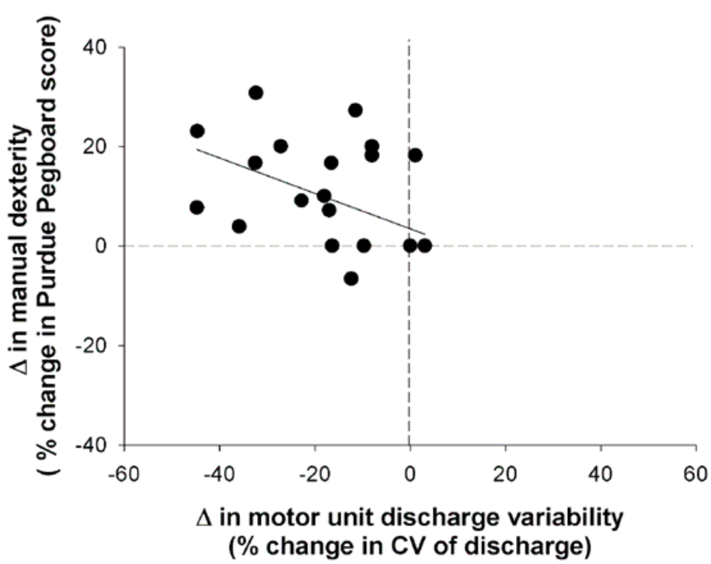

Figure 6. Functional significance of single-joint movement practice. The improvements in manual dexterity (Y axis; Purdue Pegboard score) were associated with declines in the variability in motor unit discharge rate (14B; X axis; $r^2 = 0.26$). Each point denotes the average value obtained from 1 subject for all trials and experimental sessions for the shortening and lengthening contractions [25]. These findings demonstrate that the practice-induced adaptations in single motor unit recordings with training transfer to more clinically and functionally relevant task performance, such as standardized manual dexterity tasks.

young adults [58], which emphasizes that the shared input to motor neurons differs between the two age groups. In addition, young and older adults exhibit different modulation of single motor unit discharge [61,62]. The variability in motor unit discharge, therefore, appears to be a major contributor to the fluctuations observed in the movement trajectory and can potentially impair the ability of older adults to learn a new motor task.

Agonist-antagonist muscle activation

There is evidence that adaptations to the antagonistic muscle activity can lower the trajectory variability and consequently improve the accuracy of goal-directed movements. An increase in the concurrent activity of the antagonist relative to the agonist muscles (coactivation) can increase joint stiffness and damping [63-65] and consequently reduce the fluctuations in a movement trajectory [66]. A number of recent findings indicate that coactivation is modulated during various interventions and can influence the accuracy of goal-directed movements. For example, coactivation increases when the stability of the limb is disturbed [64], when movement speed increases [67], and when target size is reduced during aiming movements [66]. Alternatively, improvements with practice may reflect changes in the triphasic pattern of muscle activation [68-73]. Numerous studies demonstrate that muscle activation during aiming movements, include an initial activation of the agonist muscles to accelerate the limb towards the target followed by activation of the antagonist muscle to brake the displacement of the limb and then coactivation of the agonist and antagonist muscles to position the limb [1,68-70,72-75]. In this scheme, the nervous system can adjust both the amplitude and the timing of the agonist and antagonist muscle activity to minimize the end-point error relative to the target.

There are at least two groups of observations that suggest coactivation can impair rather than improve the accuracy of goal-directed movements in older adults. First, increased coactivation, often observed in older adults [13,15,76,77], can impair the requisite ratio and timing of activation between the agonist and antagonist muscles during aiming tasks [78], reduce the targeted acceleration of the limb [79], and consequently influence the accurate displacement of the limb to match the target [80]. Second, coactivation decreases as practice improves the accuracy of a goal-directed movement [66,81]. Numerous studies propose that initial impairments in accuracy are primarily due to timing errors, such as the duration of the agonist muscle [69] and the latency of the antagonist relative to the agonist muscle peak activity [82]. Similarly, recent findings [1] indicate that practice

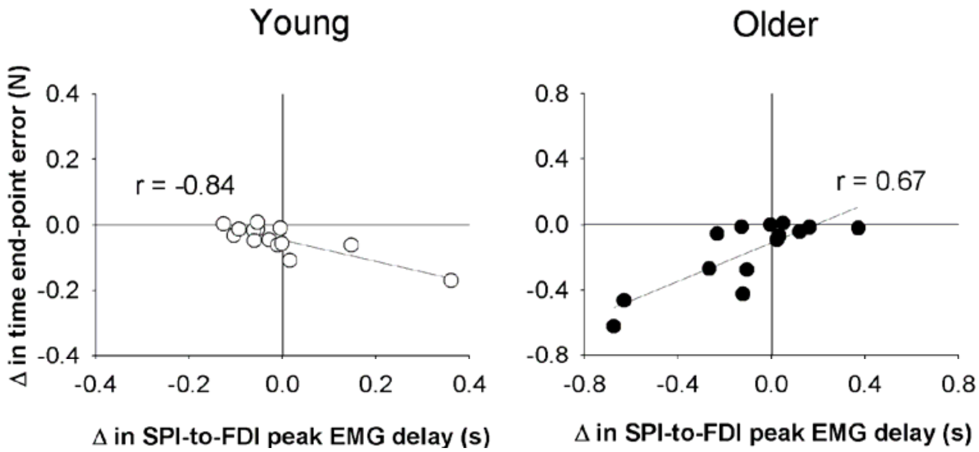

Figure 7. Different practice-induced adaptations in agonist-antagonist activation improve time end-point accuracy in young and older adults. This figure shows the association between the change in time end-point error with 35 practice trials and the change in the timing of the agonist-antagonist peak EMG for young and older adults [1]. The decrease of the time end-point error with practice for young adults was associated with lengthening of the delay between the SPI-to-FDI peak EMGs (*r* = –0.84), whereas the decrease of time end-point error in older adults was associated with shortening of the delay between the SPI-to-FDI peak EMGs (*r* = 0.67). These findings demonstrate that young and older adults organize agonist and antagonist muscle activity differently to improve motor performance with practice.

improves the accuracy of an isometric aiming task in older adults by shortening the duration of the agonist muscle activity and the time between the agonist and antagonist muscle activity, and reducing timing variability of the involved muscles across trials (Figure 7). Interestingly, young and older adults changed the relative timing between the agonist and antagonist muscle with practice differently. In particular, young adults increased the time between the peaks of the antagonist muscles, whereas older adults decreased the time between the peaks of the antagonist muscles. In addition to single-joint movements, older adults exhibit different neural activation strategies during multi-joint movements [29]. Thus, impaired activation of the agonist-antagonist motor neuron pool by the nervous system, such as the one typically observed in older adults, can impair precise and accurate motor performance.

5. Summary

Even healthy aging results in significant biological changes and consequently impairments in motor performance. The ability of older adults to adapt and learn new motor tasks appears to be compromised due to a noisier motor output and differential structure of the motor output. Neuromuscular mechanisms that can explain the impaired motor output in older adults include greater discharge rate variability of the motor units and an impaired activation of the antagonist muscles. Practice protocols that emphasize coordination of movement in older adults appear to minimize motor output variability and learning. These adaptations are independent of strength gains with practice and because such gains transfer to new tasks must occur via neural adaptations of the involved muscles. Finally, experimental findings demonstrate that young and older adults organize the neural activation of involved muscles differently to improve motor performance with practice. Despite the current evidence, it is clear that the literature on aging and motor learning lacks significant information such as long-term retention and transfer of motor skills to other conditions. This is important because the aging population will increase dramatically in the next 30 years and in some developed nations (e.g. USA) may comprise 25% of the workforce [3,4].

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