Postural motor learning and the effects of age on practice-related improvements in compensatory posture control

by

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AUTHOR'S DECLARATION

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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ABSTRACT

The purpose of this thesis was to examine the capacity for acquisition and retention of practice-related improvements in compensatory posture control and the nature of postural motor learning among healthy young and older adults repeatedly exposed to continuous surface motion via a translating platform. Although much research has been conducted to examine the strategies adopted by the central nervous system to control posture in response to external perturbations, the learning capabilities of this system have remained relatively unexplored. Many of the studies that have explored practice-related changes in balance performance have focused on short-term adaptations to highly predictable stimuli.

Borrowing from implicit sequence learning paradigms, we developed two experimental protocols to examine postural motor learning for a compensatory balance task in an environment with limited predictability. Applying key principles of motor learning to our experimental design including retention intervals and a transfer task enabled us to draw conclusions about the permanency and specificity of the observed changes. Our investigations revealed practice-related changes in the motor organization of posture control. In young adults, a shift in the complexity of the control strategy occurred which lead to improvements in spatial and temporal control of the COM. In contrast, a majority of older adults persisted with a simplified control strategy which restricted improvements in COM control. Importantly, despite control strategy differences, the two groups showed comparable rates of improvement in almost all outcome measures including measures of trunk stability and temporal COM control. Longer-term retention of behavioural changes provided evidence for learning in young adults. Similar maintenance of improvements was observed for some outcome measures in older adults. Where significant losses in performance occurred in this group, retention was evident in the rapid reacquisition of performance to the level of proficiency achieved in original practice.

Based on these results, we concluded that age affected the adapted control strategy but not the capacity for postural motor learning. Further, regardless of age or protocol, the pattern of postural perturbations did not influence acquisition of a strategy of stability and thus, we concluded that postural motor learning under the current conditions was non-specific, that is, it did not involve sequence-specific learning. These results provide important insight into the generalized nature of compensatory postural motor learning and subsequently, into the potential for positive transfer of balance skill to other balance tasks.

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DEDICATION

This thesis is dedicated to my husband Rob whose unwavering support and personal sacrifice has given me great strength, to my mom whose perspective has kept me grounded, and to my dad whose quiet encouragement echoed loudly when I needed it most.

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Chapter 1

GENERAL OVERVIEW

1.1 BACKGROUND

Much research has been conducted to examine the strategies adopted by our central nervous system (CNS) to control posture in response to external perturbations. This research has largely aimed to characterize CNS control in response to varying features of perturbations and/or the sensory environment and to describe age or disease-related changes in this control. Very early reports suggested that compensatory postural control resulted from reflex-like responses to sensory stimuli but more recent studies have demonstrated that the CNS can modify these postural responses in an adaptive, context dependent manner based on prior experience and expectation (Nashner 1976; Horak et al. 1997). Despite experimental evidence that complex balance control is centrally organized (see Horak and Macpherson 1996 and Jacobs and Horak 2007 for reviews) and that experience plays a critical role in balance performance (Horak et al. 1997), the learning capabilities of this system have remained relatively unexplored. A majority of studies that do explore experience-related changes focus on short-term adaptations to highly predictable stimuli and fail to document a) the permanency necessary to demonstrate learning (Schmidt and Lee 1999) or b) the generalizability of the adaptive response. As such, previous work limits our understanding of the central nervous systems' capability for strategy development and coordination under conditions of extended practice, as would occur when performers are aiming to learn or relearn a balance skill.

Of the studies that have explored adaptive compensatory postural responses to perturbed stance, most of the work has described responses to discrete perturbations such as nudges or sudden movements of the support surface (see Horak et al. 1997 for review). Much less work has examined responses to continuous perturbations such as those experienced while standing on a boat or riding the subway; conditions which require continuous postural regulation rather than transient balance recovery (Maki and Ostrovski 1993). Researchers who have begun to examine adaptive responses to continuous perturbations have focused on constant amplitude and frequency displacements of the support surface (Corna et al. 1999; Buchanan and Horak 2001; Ko et al. 2001; Ko et al. 2003) in which the disruptions to balance are highly predictable. Further, studies examining the effects of age on compensatory postural responses have reported age-related declines in posture control (Horak et al. 1989; Tang and Woollacott 2004) but varied support for adaptive postural responses in older adults (Woollacott et al. 1986; Hocherman et al. 1988; Stelmach et al. 1989; Bugnariu and Sveistrup 2006).

Based on previous research, it is currently not known how the CNS adapts to continuous perturbations with limited predictability, which regulatory features in the perturbation environment are extracted by learners to improve performance, and whether or not age affects the capacity to improve compensatory balance control. In this thesis, we examined the nature of and capacity for longer-term changes in compensatory posture control under less predictable conditions than those that have been studied to date and explored the effects of age on postural motor learning.

1.2 RELEVANCE AND SIGNIFICANCE

Humans are frequently faced with challenging perturbations in their environment which require complex balance control to maintain stability. Often these perturbations are unpredictable in magnitude, timing, or occurrence, and therefore it is important to understand how the CNS organizes motor systems under conditions with limited predictability. Secondly, interventions designed to improve balance control rely on the assumption that balance can be improved with practice (Shupert and Horak 1999) and indeed, multidimensional exercise programs designed to improve balance control have demonstrated positive change in clinical tests of balance performance (Shumway-Cook et al. 1997; Baker et al. 2007; Howe et al. 2007; Shumway-Cook and Woollacott 2007, p 279). Since motor learning is an integral part of rehabilitation however, the design and implementation of balance training programs could be further improved with a greater understanding of postural motor learning, particularly in 1) older adults who have a higher incidence of postural instability (Tang and Woollacott 2004) and 2) in external perturbation conditions since inadequate postural responses to displacements of the body's centre of mass (COM) under these conditions account for a majority of falls (Horak et al. 1997).

Each year, approximately 30% of community-dwelling adults aged 65 or older fall at least once and the incidence increases to approximately 40% for people 80 years or older or living in long-term care facilities (Tang and Woollacott 2004). According to Health Canada, Division of Aging and Seniors (2003), these falls account for 65% of all injuries in this group. Unless the incidence of falls and fall-related injuries can be reduced, older adults will continue to suffer from injuries, decreased mobility, and reduced independence, and the economic costs will continue to escalate in response to an aging population. According to a scientific review issued by Health Canada in 2001, balance training was a component of most programs in which there was a statistically significant reduction in falls (Branswell 2001). To optimize the link between balance training and reduced fall incidence, it is necessary to understand how postural coordination strategies change with practice and to determine older adults' capability for longer-term improvement in balance control.

1.3 MAIN OBJECTIVES

Together, the studies in this thesis explored balance control in response to continuous perturbations with limited predictability in healthy young and older adults. The main objectives of this thesis were to a) further characterize compensatory postural responses following a mechanical perturbation to stability by quantifying responses to variable amplitude oscillations of the support surface and b) to understand older adults' capacity for longer-term, practice-related improvements in whole-body coordination under conditions requiring continuous, postural regulation.

Four specific questions were addressed in this thesis:

1. What changes in the motor organization of postural control occur as a performer becomes more familiar with a continuous compensatory posture control task and do these changes reflect learning?
2. If yes, what is the nature of this learning? Do observed improvements reflect general or specific learning?

3. Does aging affect the ability or the strategy used to learn in this environment?
4. Did the protocol adopted in early studies of this thesis influence the nature of postural motor learning?

We hypothesized that changes in posture control strategy would occur with repeated exposure to the variable amplitude balance task and that these changes would be maintained following a retention interval, providing evidence for postural motor learning. We expected that this capacity for change would be reflected in smaller amplitudes of COM displacement, a shift in temporal control of COM indicative of an anticipatory mechanism of control, and changes in lower limb joint motion suggestive of CNS attempts to improve efficiency. Finally, we hypothesized that postural motor learning would be general rather than specific in both young and healthy older adults for both protocols established in this thesis.

Chapter 2

REVIEW OF THE LITERATURE

This literature review provides an overview of studies conducted to examine compensatory postural control and the flexibility of these triggered responses in young and healthy older adults. It also provides evidence supporting the need to explore postural motor learning in older adults.

2.1 POSTURE CONTROL DURING PERTURBED STANCE

Posture control during stance can be defined as the ability to maintain the COM within the base of support of the feet (Tang and Woollacott 2004). Disturbances to the COM can result from voluntary movements (e.g. arm raise, rising to toes) or external perturbations (e.g. being pushed, moving the support surface). If the destabilizing event can be anticipated as in the case of a voluntary movement or a known external perturbation (Nardone and Schieppati 1988; McChesney et al.. 1996; Hocherman et al. 1988) the nervous system can use predictive control of balance (i.e. anticipatory postural adjustments) to reduce or avoid large COM displacements and reduce the need for corrective responses (Hocherman et al. 1988; Pavol and Pai 2002). The challenge imposed on the CNS when an external perturbation is unpredictable is to interpret and integrate information about the nature of the disturbance from visual, vestibular, and somatosensory inputs in a timely manner and generate an appropriate compensatory response (Horak and MacPherson 1996; Frank and Patla 2003; Massion and Woollacott 2004). If a perturbation becomes predictable through repeated exposure to the same destabilizing event, the nervous system can integrate anticipatory postural adjustments with compensatory postural responses (Dietz et al. 1993; Schieppati et al. 2002).

A common method of inducing a perturbation involves using a translating or tilting (rotating) support surface to displace the COM relative to the base of support. These surface perturbations mimic a slip, trip, or the acceleration/deceleration of a moving object and provide insight into CNS mechanisms for the control of upright stance (Tang and Woollacott 2004). Early research using the translating platform predominantly explored responses to transient perturbations such as a single forward shift of the platform (see Horak et al.. 1997 for review) while more recently, investigators have used repeated forward/backward shifts of the platform to induce a continuous perturbation (Diener et al. 1986; Hocherman et al. 1988; Woollacott et al. 1988; Kleiber et al. 1990; Dietz et al. 1993; Maki and Ostrovski 1993; Buchanan and Horak 1999; Corna et al. 1999; Buchanan and Horak 2001; Ko et al. 2001; Schieppati et al. 2002; Ko et al. 2003; De Nunzio et al. 2005; De Nunzio et al. 2006; Bugnariu and Sveistrup 2006). In almost all continuous perturbation studies, the characteristics of platform motion (i.e. frequency/amplitude) have been constant, producing a predictable disturbance. Such perturbations (repeated transient or continuous) enable greater preplanning of responses than when the disturbance is unpredictable (Nashner 1976; Hocherman et al. 1988). In studies using continuous, ‘unpredictable’ perturbations, randomness has been achieved using constant amplitude motion of the platform with changes in frequency every 10-50 cycles of platform motion (Maki and Ostrovski 1993; Berger et al. 1992; Dietz et al. 1993; Bugnariu and Sveistrup 2006), or random presentation of trials generated from a few predetermined amplitude and frequency combinations but held constant within a given trial (Ko et al. 2001). No study has examined continuously varied perturbation characteristics within a trial.

2.2 TRANSIENT POSTURAL RECOVERY VERSUS CONTINUOUS POSTURAL REGULATION

Three characteristic strategies (defined as the weightings of sensory inputs, organization of postural responses, and activation of these responses) occur in response to *transient* horizontal perturbations and these strategies are implemented by a variety of muscle synergies (Horak and Macpherson 1996). The ankle strategy is observed in response to slow, small perturbations on a firm even surface or when the goal of the task is to maintain vertical alignment of the legs and trunk (Horak and Nashner 1986; Horak and Macpherson 1996; Massion and Woollacott 2004). The characteristic muscle activation pattern for the ankle strategy is a distal-to-proximal sequence from ankle to thigh on the same dorsal or ventral aspect of the body (Nashner 1983). The hip strategy occurs when it is difficult to produce ankle torque (i.e. in response to large or rapid perturbations and on short support surfaces) (Horak and Nashner 1986; Horak and Macpherson 1996; Massion and Woollacott 2004). Muscle activation patterns for the hip strategy occur in a proximal-to-distal sequence (Nashner 1983). Horak and Macpherson (1996) propose that the ankle and hip strategies represent extremes of a response continuum and more commonly a combination of these strategies is adopted. The third strategy is to take a step and is used when the goal is to maintain vertical trunk orientation. It is most often seen in older adults (Tang and Woollacott 2004), for large/fast perturbations or in response to a perturbation that a participant has never experienced (Horak and Macpherson 1996). In healthy young adults, the ankle strategy is often used as the first response to a destabilizing force (Nashner 1983; Horak and Nashner 1986).

For stance on a *continuously* (predictable) translating platform, postural patterns emerge based on translation frequency (Buchanan and Horak 1999; Corna et al. 1999; Buchanan and Horak 2001; Ko et al. 2001). At very slow frequencies, participants ride the platform (Buchanan and Horak 1999; Ko et al. 2001). As translation frequency increases, participants first adopt an ankle strategy (Ko et al. 2001) and then shift toward fixing their head and trunk in space (> 0.9 Hz) (Buchanan and Horak 1999; Ko et al. 2001). Comparisons of postural responses to transient versus continuous perturbations do reveal differences in control strategy which have been attributed to the need for transient balance recovery versus continuous postural regulation (Diener et al. 1986; Maki and Ostrovski 1993). Participants tend to lean further forward for continuous versus transient perturbations (Hocherman et al. 1988; Berger et al. 1992; Dietz et al. 1993; Maki and Ostrovski 1993). Maki and Ostrovski (1993) also report that levels of co-contraction differ between perturbations types. In their study, increased co-contraction was most prevalent for responses to forward transient and large continuous perturbations. The differences in response strategies between transient and continuous perturbations may be influenced by the contributions of each sensory system to the balance response; the somatosensory system is dominant for transient perturbations (Diener et al. 1988; Horak et al. 1990) while visual and vestibular information also contribute to compensation for slow, continuous perturbations (Diener et al. 1986; Dietz et al. 1989).

Peripheral sensory information alone does not determine the patterns of activity of a compensatory postural response (Diener et al. 1988; Horak et al. 1997). Results from platform translation studies demonstrate that compensatory postural responses to applied perturbations are context-dependent, driven by characteristics of platform motion (i.e. magnitude/velocity/frequency) (Diener et al. 1988, Buchanan et al. 1999, Ko et al. 2001), support condition (Horak and Nashner 1986), instruction (e.g. keep feet in place) (Burleigh and Horak 1996), central set (i.e. the modification of automatic motor responses based on expectation of a stimulus) and task goals (Tang and Woollacott 2004; Horak and Macpherson 1996). Based on these and similar findings, it is thought that certain aspects of compensatory postural responses (i.e. selection of spatial-temporal patterns) may be determined in advance by central mechanisms (i.e. predetermining a plan for action) while other aspects (e.g. activation of the central program, magnitude of the response) are influenced by sensory inputs (Gurfinkel et al. 1976; Diener et al. 1988; Hocherman et al. 1988).

2.3 COMPENSATORY POSTURAL ADAPTATIONS

Evidence has shown that CNS can employ successful adaptive control to deal with postural challenges. This adaptive control has been defined as a “set of sensory, cognitive, and motor processes associated with practice, training, or experience that result in temporary changes in behaviour” (Bhatt 2006, p. 61). The effect of experience on postural responses to repeated *transient* perturbations is exhibited as decreases in the gain of antagonist muscle responses (Woollacott et al. 1988; Horak et al. 1989), and adoption of a ‘pre-lean’ in the direction of predicted sway (Horak et al. 1989) for platform translations. For upward tilt of the support surface in which a CNS response to stretch of the gastrocnemius actually worsens backward body tilt, successive trials result in a decrease in gastrocnemius activity and a corresponding decrease in backward sway (Nashner 1976). A subsequent change in task condition demonstrates that postural control strategies are selected in advance of the movement based on "central set" because perturbations imposed after a change in condition (e.g. narrow to normal support surface) do not elicit a new strategy immediately; rather, transition occurs over several trials (Nashner 1976; Horak and Nashner 1986; Hansen et al. 1988). Patients with cerebellar lesions are unable to scale responses appropriately to repeated platform translation (Horak and Diener 1994) and patients with Parkinson's disease have difficulty switching set in response to changes in perturbation conditions (Schieppati and Nardone 1991; Horak et al. 1992; De Nunzio et al. 2007).

Repeated exposure to *continuous*, constant amplitude-frequency translations results in stronger couplings between joint motions, reductions in phase lag between body and platform motion (Ko et al. 2003) and shifts from feedback to feedforward control (Hocherman et al. 1988; Dietz et al. 1993). Adaptations to stepwise increases in frequency during continuous, constant amplitude-frequency translations occur as gradual transitions between characteristic postural patterns (Buchanan and Horak 2001). The adapted postures occur in as few as three to five cycles (Berger et al. 1992; Dietz et al. 1993; Corna et al. 1999; Bugnariu and Sveistrup 2006).

When a series of transient perturbations is less predictable, motor responses tend toward a default value corresponding to a medium sized perturbation (Horak et al. 1989) or to a size appropriate to withstand the largest perturbation (Beckley et al. 1991). The default response choice has been attributed to the degree of predictability and the level of risk. In situations that are highly unpredictable and/or present a substantial risk of falling, participants are reported to adopt a more conservative response that accounts for the largest possible perturbation (Beckley et al. 1991). Pavol and Pai (2002) propose that the long-term goal of the CNS in unpredictable conditions is to acquire an ‘optimal’ movement strategy that decreases the likelihood of losing balance and reduces dependence on reactive responses to maintain balance.

2.4 EFFECT OF AGEING ON ADAPTIVE POSTURE CONTROL

There is considerable evidence to support increased incidence of postural unsteadiness with advancing age (see Horak et al. 1989; Tang and Woollacott 2004; Horak et al. 2006 for reviews). Studies designed to examine age-related changes in postural control have provided evidence to suggest that declines in stability may result from unique combinations of impairments to sensory and/or motor components of posture control (Horak et al. 1989; Horak 2006). Studies of older adults’ responses to external perturbations have revealed delayed onset latencies of the postural muscles compared to young adults (Woollacott et al. 1986) and impaired scaling of postural responses to the magnitude of the perturbation (Shupert and Horak 1999). Studies have also shown that older adults demonstrate general decreases in the magnitude of postural responses (but longer duration) and impairments in the sequencing of muscle synergies, displaying temporal reversal and longer co-activation periods in their postural responses to horizontal displacements of the support surface (Tang and Woollacott 2004).

Research examining the effects of age on the ability to adapt to external perturbations provides some support for the maintenance of a flexible posture control system but evidence for the ability of older adults to generate adaptive postural responses is not conclusive. A study designed to examine the ability of older adults to adapt to repeated, *transient* rotational perturbations demonstrated that older adults were able to attenuate undesirable muscle activity with repeated exposure (Woollacott et al. 1986). Studies by Woollacott and Manchester (1993) and Bugnariu and Sveistrup (2001) however, report that anticipatory control mechanisms are disrupted with age as examined by muscle onset latencies in response to transient horizontal perturbations. Stelmach et al. (1989) report that older adults did not exhibit functional adaptations to small rotational perturbations, showing increased rather than decreased postural sway with repeated exposure. This variability in the adaptive capacity of older adults in response to external threats to balance is also evident in studies of *continuous* perturbations. Results of some experiments exposing older adults to continuous, predictable oscillations of the support surface have revealed that age does not affect participants' ability to adapt as demonstrated by leg muscle activation in anticipation of the turnaround point (Hocherman et al. 1988) but that there is considerable inter-subject variability in the postures used to maintain balance (Hocherman et al. 1988; Nardone et al. 2000). In these studies, the general response indicates that older adults 1) adopt a rigid movement strategy; aiming to minimize changes in ankle position rather than changes in centre of mass (Hocherman et al. 1988; Wu 1998), and 2) aim to stabilize their head. The authors speculate that the dominant use of a ride strategy in this population results from older adults' need for a secure balance strategy that does not depend on accurate timing of muscle activation necessary for stabilizing the trunk

(Hocherman et al. 1988). A recent study by Bugnariu and Sveistrup (2006) however, reported that older adults do not adapt to continuous oscillations of the support surface (i.e. do not demonstrate anticipation of the turnaround point of the platform) and can not adapt as well as young adults to increases in translation frequency (as evidenced by smaller stability margins for greater periods of time). Fujiwara et al. (2007) also reported a general decline in adaptability to floor oscillation with advancing age among older adults who underwent short-term practice. Together, these findings suggest that there is an age-related decline in the flexibility of the posture control system in responding to external perturbations but that the capacity to adapt is not completely lost.

2.5 POSTURE CONTROL AND MOTOR LEARNING

Motor learning is defined as "a set of processes associated with practice or experience leading to relatively permanent changes in the capability for movement" (Schmidt and Lee 2005, p 302). Rehabilitation programs aimed at improving balance control are based on principles of procedural motor learning such as variability of practice, augmented feedback, etc. Procedural learning represents one of two systems of human learning, characterized by retention of performance improvements that are unavailable to awareness (implicit) and distinguished from the declarative system which supports learning and retention of facts or events; knowledge that is explicit or verbalizable (Willingham et al. 1989; Magill 1998). Magill (1998) proposed that knowledge acquired during procedural learning includes the critical, regulatory features of the environment (as characterized by Gentile 1972) that can assist in determining how the body must move to achieve the task goal. Understanding a) *if* relatively permanent improvements in compensatory balance control occur and if so, b) *what* regulatory features in the environment are important and c) *how* these features are learned is important given the critical differences between compensatory postural tasks and the voluntary motor tasks typically used to examine procedural learning.

The studies examining adaptive posture control together with current views which support the involvement of higher-level structures such as the basal ganglia, cerebellum, and cortex in compensatory postural control (Horak and Macpherson 1996; Horak and Diener 1994; Jacobs and Horak 2007) provide support for CNS capacity to make permanent changes in balance behaviour. This possibility is further supported by everyday observations of improvements in balance control during the learning of complex motor skills (e.g. skiing). Of the few studies which have studied balance skill acquisition in adults, most have used voluntary posture tasks (Shea et al. 2001; Caillou et al. 2002; Gauthier et al. 2008). These studies have reported positive effects of postural training on the performance of novel balance tasks. Most of these studies however, have restricted assessment of learning to performance outcome (e.g. RMS error of stabilometer motion (Shea et al. 2001)), limiting our understanding of how changes in control strategy are used to produce skilful performance. Caillou et al. (2002) is among the few studies that have examined practice-related changes in body kinematics, revealing a reorganization of joint coordination with practice. Even fewer studies have examined the capacity for permanent, practice-related changes in compensatory balance control (Debu et al. 1989). Ko et al. (2001, 2003) demonstrated that practice on a continuously translating platform led to more coordinated motion of the limbs and torso and increased use of the passive, inertial forces generated by the platform. These changes persisted across days providing evidence for learning

(Schmidt and Lee 1999) but the platform movements in this study were highly predictable, limiting the external validity of the results.

In a characteristic task designed by Nissen and Bullemer (1987) and adapted by others (Willingham et al. 1989; Reber and Squire 1994) to investigate implicit motor learning, a light appears in one of four positions on a display screen and participants are required to press one of four response keys corresponding to the position of the light. These studies have demonstrated that participants who are exposed to a repeating sequence of light cues show a greater reduction in reaction time than those who are exposed to random sequences despite lack of awareness of the repetition. Studies using this paradigm in older adults consistently show learning of the sequence that is comparable to young adults (Willingham 1998).

A second experimental task used to demonstrate implicit sequence learning requires participants to visually track a waveform presented on a monitor with corresponding movements of a joystick (Pew 1974; Wulf and Schmidt 1997) or a stabilometer (Shea et al. 2001). In each trial, the middle segment of the waveform is repeated but participants are not informed of this feature (Fig. 2.1).

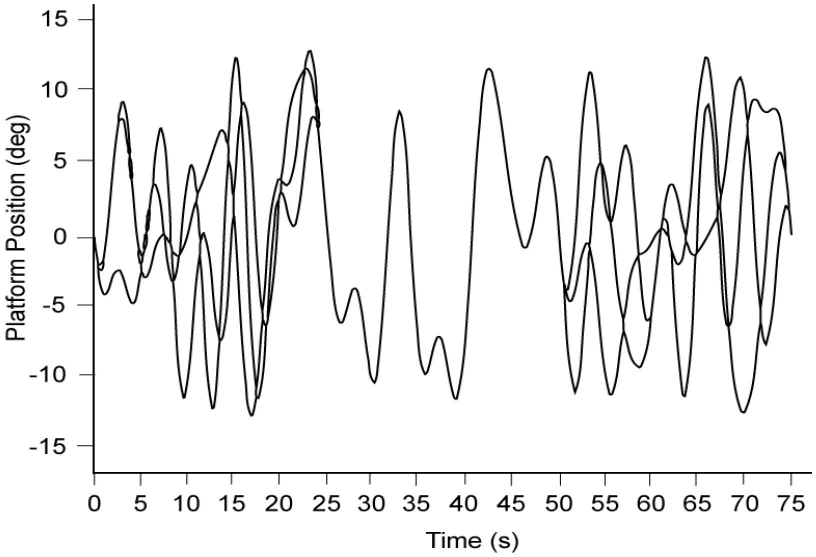

Fig. 2.1: An overlap of two trials representing the target waveform and illustrating the repeated middle segment (taken from Shea et al. 2001)

These studies reveal that participants show greater accuracy on repeated versus random segments of the waveform despite being unable to verbalize knowledge of any regularities in the target waveform. That is, participants do not modify their behaviour on the basis of reportable knowledge about environmental regularities. Studies of older adults exposed to tracking tasks have reported a slower rate of improvements in accuracy in these tasks relative to young adults (Willingham 1998). According to Nissen and Bullemer (1987), differential improvements in performance for repeated sequences primarily reflects sequence-specific knowledge rather than more general characteristics of the task because 1) if a random sequence is presented after a period of training, reaction time increases substantially and 2) training on a random sequence yields minimal reduction in reaction time. The results presented here demonstrate that performance improvements can occur in the absence of factual knowledge about regularities in the environment and that these improvements can be very specific.

Chapter 3

COMPENSATORY POSTURAL ADAPTATIONS DURING CONTINUOUS, VARIABLE AMPLITUDE PERTURBATIONS REVEAL GENERALIZED RATHER THAN SEQUENCE-SPECIFIC LEARNING

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3.1 OVERVIEW

We examined changes in the motor organization of postural control in response to continuous, variable amplitude oscillations evoked by a translating platform and explored whether these changes reflected implicit sequence learning. The platform underwent random amplitude (maximum ± 15 cm) and constant frequency (0.5 Hz) oscillations. Each trial was composed of three 15-second segments containing seemingly random oscillations. Unbeknownst to participants, the middle segment was repeated in each of 42 trials on the first day of testing and in an additional seven trials completed approximately 24 hours later. Kinematic data were used to determine spatial and temporal components of total body centre of mass (COM) and joint segment coordination. Results showed that with repeated trials, participants reduced the magnitude of horizontal body COM displacement, shifted from a COM phase lag to a phase lead relative to platform motion and increased correlations between ankle/platform motion and hip/platform motion as they evolved from an ankle strategy to a multi-segment control strategy involving the ankle and hip. Maintenance of these changes across days provided evidence for learning. Similar improvements for the random and repeated segments, however, indicate that participants did not exploit the sequence of perturbations to improve balance control. Rather, the central nervous system (CNS) may have been tuning into more general features of platform motion. These findings provide important insight into the generalizabilty of improved compensatory balance control with training.

3.2 INTRODUCTION

During many of our daily activities, we are exposed to continuous threats to balance such as those experienced while standing on a moving bus, in which the perturbations are variable or unpredictable. Researchers have begun to examine responses to continuous, externally-imposed disturbances by exposing participants to constant amplitude, sinusoidal movements of the support surface (Dietz et al. 1993; Corna et al. 1999; Nardone et al. 2000; Buchanan and Horak 2001; Ko et al. 2001; Ko et al. 2003). Results have demonstrated that these conditions provide an opportunity for the CNS to integrate predictive postural adjustments with automatic responses (Dietz et al. 1993; Schieppati et al. 2002) and that this predictive control occurs in as few as three to five oscillations (Bugnariu and Sveistrup 2006). Findings also suggest that compensatory postural coordination patterns emerge based on instructions given to participants (to adopt a particular strategy), and the dynamics of platform motion (Buchanan and Horak 2001, Ko et al. 2001; Schieppati et al. 2002). At slow frequencies of translation, participants choose to 'ride' the platform with very little motion in the lower limb joints while at fast frequencies, participants fix their head and trunk in space by increasing joint motion at the ankle and hip (Buchanan and Horak 1999).

To date, all of the studies that have explored continuous perturbations using a moving support surface have used highly predictable translations. Environmental challenges faced in cyclical tasks such as walking however, are often unpredictable in the magnitude of an imposing perturbation and tasks such as skiing or standing on a moving bus can be unpredictable in both magnitude and timing. We know from observation of these everyday tasks that it is possible to improve stability with practice but because the disruptions are less predictable, the central nervous system (CNS) cannot adapt in the same way that it does to the constant amplitude/frequency perturbations that have been examined experimentally. In order to begin understanding how balance control is learned under less predictable conditions and to characterize the evolution of the balance response with practice, we exposed participants to variable amplitude/constant frequency surface translations using a methodology designed to explore implicit sequence learning.

In implicit sequence learning tasks, performers learn to produce serial responses to sequentially presented stimuli (as in playing the piano) unintentionally and without explicit awareness of the regularities in these stimuli. This type of learning is often studied using variants of the serial reaction time (SRT) task introduced by Nissen and Bullemer (1987) or upper limb tracking tasks (Pew 1974; Wulf and Schmidt 1997; Magill 1998). In these studies, a fixed sequence of stimuli evokes responses from participants that are faster, more accurate, or less variable than exposure to random series of stimuli, even though participants are unaware of sequence regularities. In 2001, Shea et. al. reported that implicit sequence learning also occurred for a complex, whole body task requiring participants to track a waveform on a computer screen with corresponding movements of their centre of pressure. The postural movements in this study were voluntary allowing the CNS to compare predicted outcomes (as signaled by efference copy or predicted sensory consequences) with the actual outcome of the movement as a form of predictive learning that would not occur if participants were responding to a series of externally imposed disturbances. Further, evidence for implicit sequence learning is based primarily on visuomotor tasks (e.g. mirror tracing, serial reaction time tasks) although many skills, particularly those involved in posture control, do not require visuomotor transformation.

It has been shown that postural responses are affected by the predictability of the disturbance and task goals (Horak et al. 1997). It is presently not known if implicit sequence learning would occur for postural tasks involving externally-imposed perturbations in which the primary goal is to maintain upright stance and not necessarily to predict and follow platform motions. Under these conditions, it is possible that learning may be non-specific. Studies of upper limb SRT tasks have provided evidence for non-specific improvements (Wulf and Schmidt 1997; Magill 1998; van der Graaf et al. 2004). The mechanism for these improvements has been attributed to learning how to respond (i.e. how to associate motor responses to stimuli) in order to optimize the procedure for completing the task successfully.

The primary goal of this study was to determine how participants learn to improve balance when exposed to continuous perturbations that are less predictable than those that have been studied to date. Learning would be demonstrated by improvements in postural stability assessed in both spatial and temporal dimensions through increased centre of mass (COM) displacement control and lower limb joint coordination (spatial), and by shifts in the phase relationship between COM and platform motion from phase lag to phase lead (temporal). To ensure that performances are not driven by temporary variables such as motivation or fatigue, these improvements must be maintained after the retention interval

(Schmidt and Lee 1999). Based on the current paradigm, participants could improve by a) learning general characteristics of surface motion, b) tuning in to the specific sequence of platform translations, or c) engaging in both specific and non-specific learning to improve balance control. If improvements were driven by non-specific learning, participants would demonstrate equal improvements in postural stability for both random and repeated sequences. If participants engaged in implicit sequence learning, they would demonstrate a greater rate of improvement in postural stability for the repeated sequence. The second goal of the study was to understand the organizational changes in compensatory postural coordination patterns with repeated exposure to a continuous, variable amplitude perturbation to determine whether experience should be considered an important factor influencing the postural coordination pattern that is used to maintain balance.

3.3 MATERIALS AND METHODS

3.3.1 Participants

Twelve healthy adults (six males, six females) aged 19-29 (mean 24.3 ± 2.8 years) volunteered to participate (Protocol A). Following initial analysis of the data, an additional ten healthy adults (five males, five females) aged 22-34 (mean 29.4 ± 3.4 years) completed a modified subset of trials (Protocol B). All participants successfully completed two clinical tests of balance (30-second one legged stance, one legged stance with eyes closed) and provided informed consent prior to data collection. The methods used in the study were approved by the Oregon Health and Science University Institutional Review Board and by the Office of Research Ethics at the University of Waterloo (ORE #12479).

3.3.2 Task and Procedures

Participants wore an industrial safety harness and stood on a hydraulically driven, servo-controlled platform that could be moved horizontally forward and backward. A series of platform translations was elicited to generate a continuous perturbation that oscillated at a fixed frequency of 0.5 Hz and variable amplitude ranging from ± 0.5 to 15 cm. The combination of fixed frequency and random amplitude translations also resulted in random velocities of motion.

Protocol A: Random Amplitudes and Velocities

Trials were composed of three, 15-second segments containing seemingly random oscillations; however, the middle segment included a sequence of platform movements that occurred in every trial. Participants were not informed about the repeated nature of the middle segment. Combined, the three segments produced a 45-second trial (Fig. 3.1). Oscillation magnitudes were pseudo-randomly generated from a pool of amplitudes with the constraint that an oscillation at the start of a new segment could not differ by more than 8 cm from the preceding oscillation. This criterion was incorporated to ensure smooth transitions between segments. Participants were instructed to maintain balance while standing with eyes open, arms crossed at the chest and to avoid stepping if possible. Testing consisted of six blocks of seven trials with a 2-minute rest period between blocks. Participants returned for a seven-trial retention test approximately 24 hours following practice to examine a) whether learning had occurred and b) whether the repeated segment was learned more effectively than the random segment.

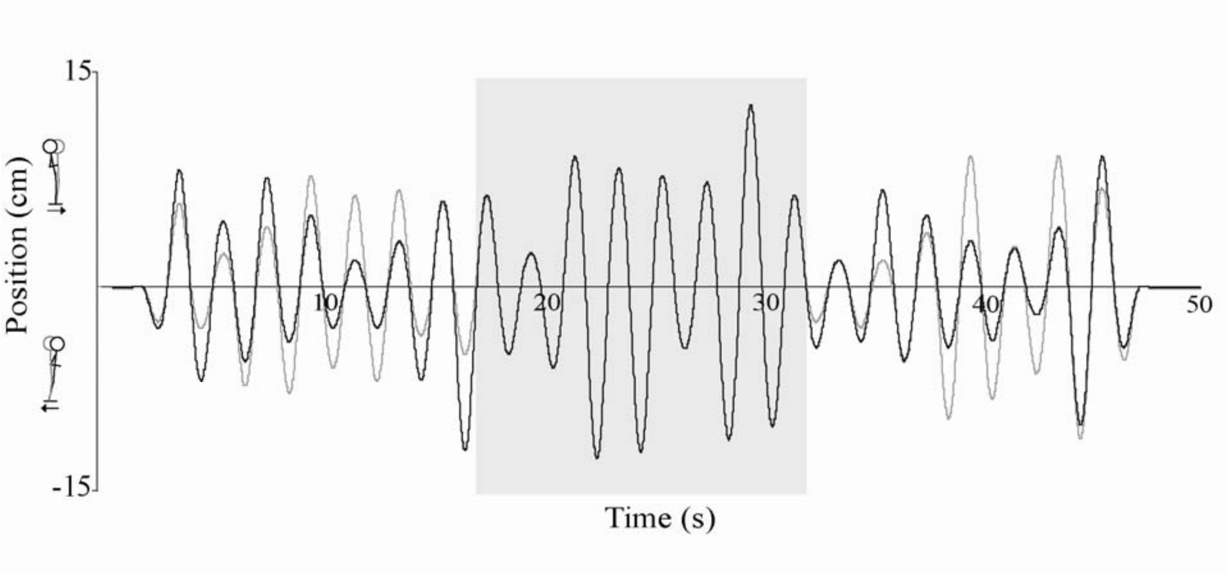

Fig. 3.1: An example of variable amplitude platform motion (range +/- 15 cm). The plot represents an overlay of two trials illustrating the repeated and random segments. The repeated segment is denoted by the area shaded in grey.

Protocol B: Matched Amplitudes and Mean Velocities

The random segments in Protocol B were generated from a pool of the 15 amplitudes that defined the repeated segment to ensure that the mean amplitude and velocity of platform translation were the same across segments. There were no restrictions on the direction of translation in the random segments; a forward translation in the repeated segment could appear as an oscillation in the forward or backward direction in a random segment. Again, no information was given to participants about the regularities in this segment. Participants were instructed to maintain balance and avoid stepping if possible while standing with eyes open and arms crossed at the chest. Testing consisted of seven trials.

3.3.3 Data Recording

A Motion Analysis System (Santa Rosa, Calif., USA) with six cameras captured three-dimensional spatial coordinate information about body segment displacements and the movement of the platform. Reflective markers were placed bilaterally on the following landmarks: head of the fifth metatarsophalangeal, lateral malleolus, lateral femoral condyle, greater trochanter, acromion process, and lateral mandibular joint. Markers were also placed on the platform. Data were sampled at 60 Hz and low pass filtered using a 2nd order, dual pass Butterworth filter with a cut-off frequency of 5 Hz. The position of the centre of mass (COM) of each body segment in the antero-posterior (AP) direction was calculated using the kinematic data and anthropometric data provided by Winter (1990). Whole body COM position (in space) in the AP direction was derived from the weighted sum of the individual segment COM locations. Ankle, knee and hip joint angles were calculated from adjacent segments.

3.3.4 Outcome Measures

Mean gain of the COM (COM peak displacement/platform peak displacement) and relative phase of the COM (COM time peak/platform time peak) were derived as the primary outcome measures. The ratio of maximum COM displacement to maximum platform displacement was calculated for each peak and valley event during platform motion and these values were averaged for each segment within a trial to determine mean gain and mean gain variability. Theoretically, a COM gain of 1.0 would correspond to equal displacements of the platform and COM in space (similar to the ’ride’ strategy described in

Buchanan and Horak 1999) and would occur if participants were following platform motion. Small COM gain was considered improved balance control as participants stabilized their COM in space (Buchanan and Horak 1999). Relative phase was calculated using the time values of the peaks to compute a point estimate of maximum COM relative to maximum platform position on a cycle-by-cycle basis (Zanone and Kelso 1992). These values were averaged for each segment within a trial to determine mean relative phase and relative phase variability. Additional outcome measures included mean gain variability and mean relative phase variability of the COM, and correlations between platform motion and lower limb hip, knee, and ankle joint angles. We considered increased phase leads of COM relative to platform motion as an indication of improved predictive control and changes in correlation between joint kinematics and platform motion as evidence for changes in postural control strategy. We also correlated the change in COM phase with the change in COM gain from early to late training to examine whether changes in gain were driven by changes in phase. When inspected, all COM phase changes ranged from 6.66º to 14.59º (mean = 10° ± 2.74) with the exception of two participants whose phase change was greater than 1.5 standard deviations from the mean and therefore, were removed from this analysis. Finally, we calculated the RMS amplitude of platform motion for random and repeated segments to investigate whether platform characteristics accounted for behavioural performance.

3.3.5 Data Analysis

All variables were compared between segment two (repeated) and segment three (random) to for trials in which participants did not take a step. The first segment was omitted from the analyses to ensure that events induced by the onset of platform translation did not interfere with the investigation of sequence learning. In total, 40/588 trials were omitted from protocol A resulting from 16 steps taken in the repeated segment and 24 steps taken in the random segments. 3/70 trials were omitted from protocol B (2 steps repeated segment, 1 step random segments).

For Protocol A, the COM data were compared across blocks of trials on day one to explore acquisition performance. Joint angle data were compared during early (block 1) and late (block 6) training to examine the shift in control strategy with practice. The retention block on day two was compared to early (block 1) and late (block 6) training on day one for all variables to examine learning. Two-way (segment x block) repeated measures ANOVAs, conducted separately for acquisition and retention phases, were used for all statistical comparisons. For acquisition, primary outcome measures were analyzed in a 2 (segment) x 6 (block) ANOVA while a 2 (segment) x 2 (block) ANOVA was used to analyze the joint angle data. Retention performance was analyzed using a 2 (segment) x 3 (block) ANOVA. *Post hoc* analyses were conducted using Tukey's studentized range (HSD) tests unless otherwise noted. For correlational analyses, R values were transformed into z scores prior to statistical examination. For Protocol B, the COM data were analyzed in a 2 (segment) x 7 (trial) ANOVA. Post hoc analyses were conducted using paired t-tests with Bonferroni corrections. For all tests, an acceptable significance level was 0.05.

3.4 RESULTS

3.4.1 Protocol A: Random Amplitudes and Velocities

Acquisition Performance

Comparisons between random and repeated segments revealed that participants did not exploit the repeating sequence of perturbations to improve balance control. The analysis of mean gain indicated a significant interaction between segment and block ($F(5,55) = 5.35$; $p = 0.0004$; Fig. 3.2). Main effects analyses of training blocks for each segment type revealed that mean gain decreased for both repeated ($F(5,55) = 12.32$; $p < 0.0001$) and random ($F(5,55) = 7.34$; $p = 0.0001$) segments by an average of 15% (0.61 ± 0.14 to 0.51 ± 0.084) and 13% (0.66 ± 0.16 to 0.56 ± 0.10) respectively. Post hoc analyses revealed a significantly lower COM gain for the repeated versus random segment as early as block one ($p = 0.032$) but the difference in mean gain between segment types during late training was no greater than that during early training ($t(11) = -0.144$; $p = 0.89$). For both segments, gain values were less than 1.0, indicating that participants did not follow platform motion to maintain balance. Together these results suggest that the difference between repeated and random segment types occurred during very early exposures to the task but did not differentiate further with training.

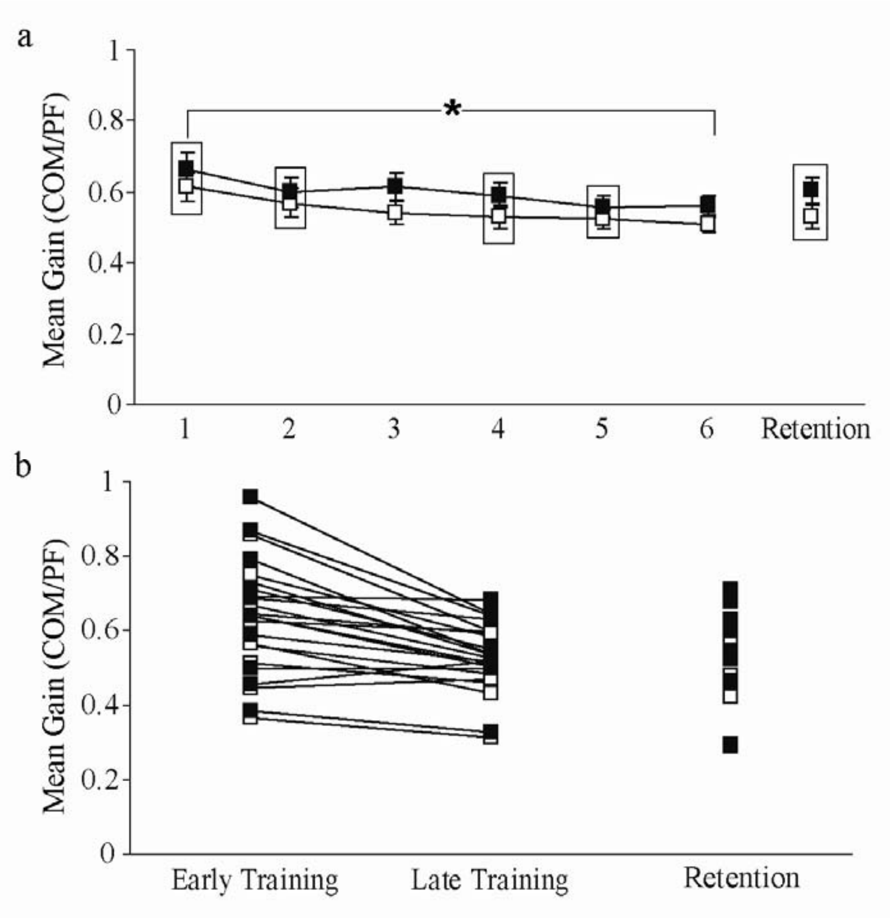

Fig. 3.2: a) Group changes in COM gain with training. Repeated segment performance is denoted by *white* squares. Random segment performance is denoted by *black* squares. Error bars represent standard error of the mean. Asterisks indicate significant differences between blocks while block outlines indicate significant differences between segment types ($p<0.05$). b) Individual changes in COM gain with training.

Analysis of mean gain variability (not shown) indicated a significant interaction between segment and training block ($F(5,55) = 6.39$; $p < 0.0001$). Main effect analyses of training block for each segment type revealed that the interaction was caused by fluctuation of the gain variability in the random segment only ($F(5,55) = 6.16$; $p = 0.0001$). Mean gain variability did not decrease for repeated ($p=0.40$) or random ($p = 0.052$) segments from early to late training.

In addition to changes in the magnitude of COM displacement, relative phase of the COM shifted from a phase lag (-10.26° ± 3.14) to phase lock (2.66° ± 7.69) for both repeated and random segments ($F(5,55) = 20.25$; $p < 0.0001$; Fig. 3.3), indicating that participants were able to improve predictive control of COM motion. Analysis of relative phase variability (not shown) indicated a significant interaction between segment and block ($F(5,55) = 3.89$; $p = 0.0043$). Main effect analyses of training block for each segment type revealed that phase variability decreased significantly for both repeated ($F(5,55) = 3.00$; $p = 0.018$) and random ($F(5,55) = 10.28$; $p < 0.0001$) segments with training. Post hoc analyses revealed that the repeated segment had significantly lower phase variability in block one only ($p = 0.017$). The correlation between change in COM phase and change in COM gain from early to late training was low for both repeated and random segments ($R^2 = 0.14$ and $R^2 = 0.41$ respectively) suggesting that the improvements in predictive control of COM motion did not determine improvements in COM gain.

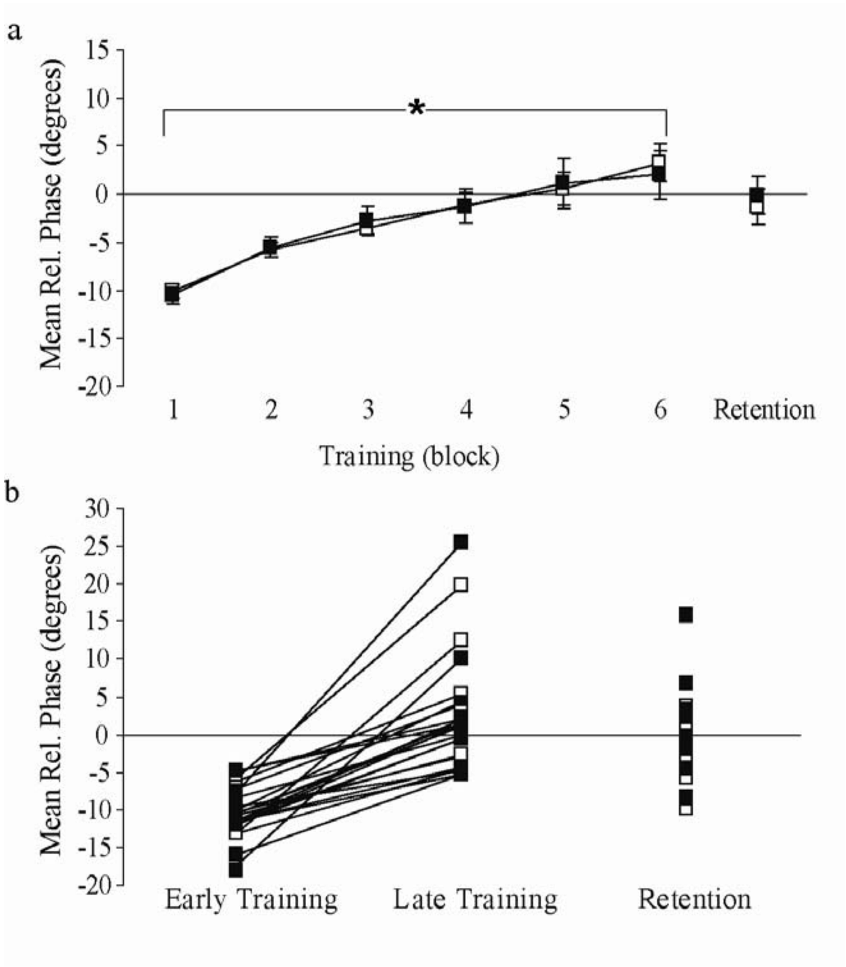

Fig. 3.3: a) Group changes in COM relative phase with training. Repeated segment performance is denoted by *white* squares. Random segment performance is denoted by *black* squares. Error bars represent standard error of the mean. Asterisks indicate significant differences between blocks ($p<0.05$). b) Individual changes in COM relative phase with training.

Joint angle correlations with platform motion demonstrated a change in postural coordination with training. Ankle angle correlations were negative and became stronger with training (F(1,11) = 10.97; p = 0.0069; Fig. 3.4). A main effect of segment type indicated that correlations were significantly stronger for the repeated segment (F(1,11) = 103.26; p < 0.0001). Knee angle was modestly correlated with platform motion but this relationship did not become stronger with training (F(1,11) = 0.26; p = 0.62). Inspection of the data revealed that the correlation was driven by six participants who adopted a flexed knee posture to maintain balance. Hip angle was not correlated with platform motion in early training but demonstrated an increase with practice (F(1,11) = 8.03; p = 0.016). Again, the repeated segment was more strongly correlated with platform motion than the random segment and this effect existed in both early and late training as evidenced by the main effect of segment type (F(1,11) = 22.43; p = 0.0006).

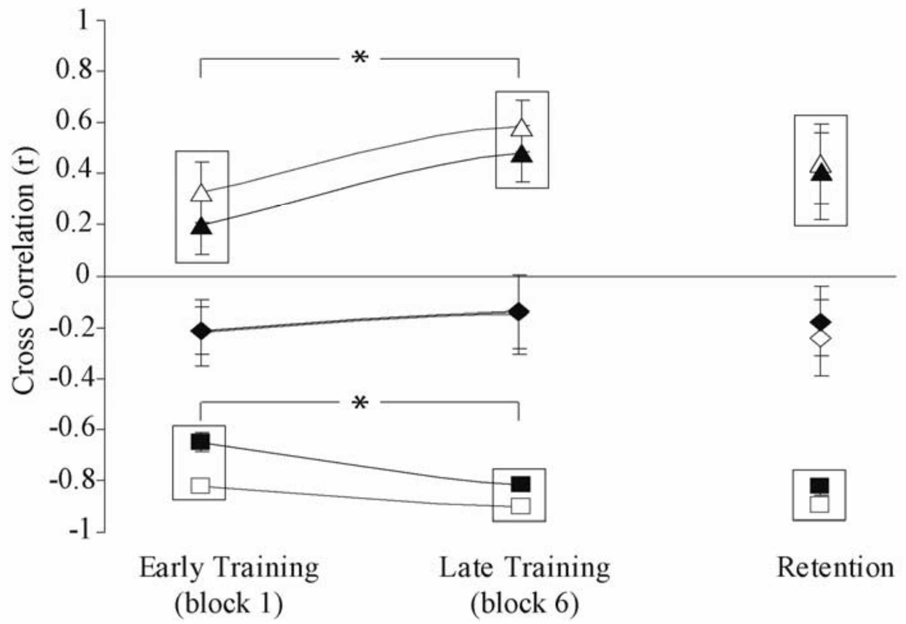

Fig. 3.4: Group correlations between joint angle and platform motion. Repeated segment performance is denoted by *white* markers. Random segment performance is denoted by *black* markers. Ankle joint correlations are represented by *squares*, knee joint correlations are represented by *diamonds*, and hip joint correlations are represented by *triangles*. Error

bars represent the standard error of the mean. Asterisks indicate significant differences between blocks while block outlines indicate significant differences between segment types ($p<0.05$).

Retention Performance

On day two, participants did not demonstrate significant losses in the performance gains achieved during training on day one. The maintenance of these improvements provides evidence for learning. Group COM gain scores remained near 0.53 and joint angle correlations with platform motion remained highly negative for the ankle and positive for the hip, suggesting that participants maintained a strategy which aimed to stabilize their COM in space rather than follow platform motion. Most participants also maintained their ability to predict the frequency of platform motion as demonstrated by COM relative phase scores that remained near zero.

Statistical analysis of COM gain indicated a main effect of block ($F(2,22) = 8.73$; $p = 0.0016$) and segment ($F(1,11) = 59.36$; $p <0.0001$) but post hoc analysis revealed that COM gain during retention testing was not significantly different from late training for random or repeated segments ($p = 0.21$) indicating that there was no differential loss of improvement between segment types during the retention interval (Fig. 3.2). There was also a main effect of block ($F(2,22) = 10.72$; $p = 0.0006$) and segment ($F(1,11) = 49.43$; $p < 0.0001$) for COM gain variability. Post hoc analysis revealed that COM gain was even less variable during retention testing on day two compared to late training on day one ($p = 0.0001$). Analysis of COM phase indicated a main effect of block ($F(2,22) = 31.83$; $p < 0.0001$) but again, post hoc analyses revealed that performance during the retention block on day two was not significantly different from late training (p = 0.059) and remained significantly different from behaviours adopted in early training (p < 0.0001) (Fig. 3.3). There was an interaction between block and segment for COM phase variability (F(2,22) = 5.69; p = 0.010) but post hoc analyses revealed that variability did not increase during the retention interval for either the random (p = 0.64) or repeated segment (p = 0.75) and there was no significant difference between segment types during retention testing (p = 0.38). In addition to maintenance of changes for COM measures, post hoc analyses of joint angle correlation with platform motions revealed no significant loss in the relationship between ankle joint and platform motion (p = 0.94) or hip joint and platform motion (p = 0.75) during the retention interval (F(2,22) = 10.85; p = 0.005) and ((F(2,22) = 6.36; p = 0.0066); Fig. 3.4) respectively. For both measures however, there was a main effect of segment type indicating that the repeated segment (F(1,11) = 76.59; p < 0.0001) was more highly correlated with platform motion than the random segment (F(1,11) = 30.28; p = 0.0002) in both late training and retention testing. Together, these results demonstrate that similar to COM outcomes, the differences between segment types did not increase during the retention interval and as such, the repeated segment was not learned more effectively than the random segments.

3.4.2 Protocol B: Matched Amplitudes and Mean Velocities

To ensure that the differences between segment types which emerged early in training were not driven by differences in the characteristics of platform motion (e.g. level of challenge) for repeated versus random segments (Vaquero et al. 2006; Chambaron et al. 2006), we examined RMS amplitude of the platform signal for individual trials in early training (block one) for Protocol A. Results revealed consistently lower RMS amplitude for the random versus repeated segments but comparable RMS amplitudes for the random segments across trials. Based on these findings, we could not rule out the possibility that differences in outcome measures between segment types were driven by a platform artefact.

Statistical analysis of the primary outcome measure (COM mean gain) for participants exposed to the modified protocol indicated a segment x trial interaction (F(6,50) = 3.05; p = 0.013) but post hoc analysis (Bonferroni correction) revealed no consistent difference between random and repeated segments (Fig. 3.5) suggesting that the differences observed between segment types in protocol A resulted from differences in platform characteristics.

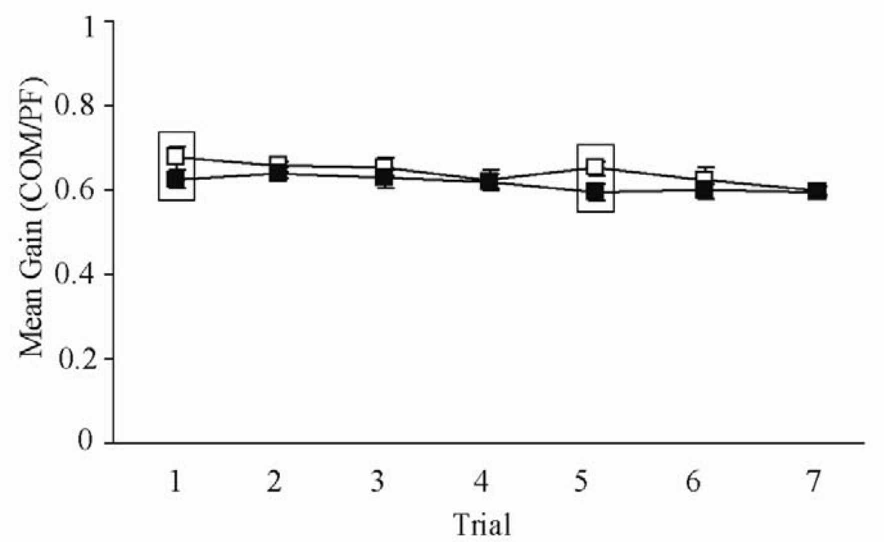

Fig. 3.5: Group averages of COM gain for each trial in block one (Protocol B). Repeated segment performance is denoted by *white* squares. Random segment performance is denoted by *black* squares. Error bars represent the standard error of the mean. Block

outlines indicate significant differences between segment types ($p<0.05$ with Bonferroni correction).

3.5 DISCUSSION

In the current study, participants demonstrated the ability to learn adaptive postural responses to continuous, variable amplitude platform motion as evidenced by the maintenance of postural control changes across days of testing. Unlike the results of Shea et. al. (2001) and those who have reported implicit motor sequence learning in upper limb tracking tasks (Pew 1974; Wulf and Schmidt 1997; Magill 1998), performance improvements in the current study could not be attributed to implicit learning of the temporal relationship between perturbation sequence elements. Early differences in behaviour did emerge between random and repeated segments in Protocol A but these differences did not increase with practice as would be expected if participants exploited their prior exposure to the repeated segment. Furthermore, the differences between the segment types no longer existed once the average amplitude and velocity of the perturbation sequences were matched in Protocol B. Thus, changes in balance performance with practice were driven by non-specific learning.

The goal of the current task was to avoid falling without taking a step. Theoretically, this goal could have been achieved in one of three ways: 1) by tracking the motion of the platform using a ’ride’ strategy which would have produced COM mean gain values close to 1.0, 2) by “anti-tracking” the motion of the platform such that when the platform moved forward, the COM moved backward and vice versa, or 3) by minimizing COM motion in space which could serve to stabilize gaze or minimize energy expenditure. In the current study, participants aimed to minimize their COM motion with practice. Although participants might have improved their COM control further by knowing the sequence of perturbations in the repeated segment, this information was not necessary to avoid falling (Cleeremans and McClelland 1991; Chambaron et al. 2006).

Based on the platform dynamics in the current study, participants could have exploited prior knowledge of up to three features of platform motion to improve postural stability: 1) the sequence of platform amplitudes and/or resulting changes in velocity, 2) the forward and backward turnaround times (frequency) since this feature was held constant, or 3) the boundaries of platform motion. Based on our results, participants did not learn the sequence of amplitudes. A COM shift from phase lag to phase lock however, provides evidence for a control strategy that utilized the frequency of platform motion. It appears however, that learning was not limited to the tuning of the turnaround time. Since the magnitude of COM displacement improved (became smaller) with training and COM phase/gain correlations were weak, we suggest that participants also gathered information about the boundaries of platform motion, allowing the CNS to establish an appropriate gain to withstand the largest perturbations. If the improvements in gain had been driven by predictions about the frequency of platform motion, we would have expected the correlation to be stronger. Instead, the results suggest that COM gain changes were independent of phase changes. Changes in gain control with practice are also observed when young, healthy participants receive a random mixture of discrete perturbations (Horak et al. 1989; Beckley et al. 1991).

We propose that the current study lends further support to Chambaron et al. (2006) who argue that evidence for sequence learning in continuous tracking tasks might be driven in part by peculiarities in the repeated segment and not implicit sequence learning per se. We propose therefore, that implicit sequence learning does not occur for compensatory posture control. From a functional view, it is reasonable to suggest that postural motor learning is non-specific. In an environment that contains an infinite number of challenges to stability, the posture control system must be flexible. Acquiring general knowledge about features in the environment serves better to achieve this flexibility than developing a series of motor responses that are limited to serving a specific sequence of stimuli.

Evidence for the extraction of general features in an unpredictable environment has been reported for both upper limb and discrete compensatory postural tasks. In these studies, postural motor responses tended toward a default value corresponding to either a medium sized perturbation in Horak et. al. (1989) or to the largest perturbation in Beckley et. al. (1991) depending on the degree of unpredictability and the risk. Ioffe et. al. (2004) also reported a general strategy of voluntary posture control in a random target task requiring corresponding movements of the centre of pressure. It should be noted that in the current study, sequence learning might have been masked by a transition period between relatively short segment intervals. While this possibility is conceivable, Perruchet et. al. (2003) have also reported that lengthy intervals can result in an overload of information that makes it difficult to learn the task; creating an equally disadvantaged training condition.

Changes in postural coordination patterns with practice

The second goal of the present study was to describe the postural patterns that emerged with practice and to determine whether experience should be considered an important factor influencing the postural coordination pattern used to maintain balance (Horak and Macpherson 1996; Horak et al. 1989). Since we were interested in observing the evolution of balance control with practice, we chose 0.5 Hz as the frequency of platform motion. This frequency is not associated with the emergence of a characteristic postural control pattern (Buchanan and Horak 2001) and therefore we reasoned that it would offer the greatest opportunity for change.

Early in training, participants adopted an ankle strategy to maintain equilibrium as evidenced by large negative correlations between ankle and platform motion. This finding is similar to that reported by Ko et. al. in 2001 for constant amplitude oscillations near 0.5 Hz. As participants became more familiar with the task however, hip-platform correlations increased suggesting the addition of compensatory motions at the hip to allow better stabilization of the COM in space. There was no change in knee-platform correlations indicating that the involvement of this joint in the evolution of a learned balance response was minimal. The joint motion of the lower limbs that accompanies this trunk-locked-in-space strategy serves to limit the transfer of reactive forces and decreases the energy requirements necessary to maintain whole-body stability (Sparrow and Newell 1994). In this way, participants learn to maintain balance with greater energy efficiency.

Environmental challenges are often unpredictable in magnitude and/or timing and our expertise in responding to these challenges is a reflection of learning, not short term adaptation. Most studies of posture control have focussed on the latter and are limited in their ability to provide insight into strategies resulting from long term improvements. Under the current conditions, any attempt to learn specific characteristics of the perturbation may overload the processing capacity of the CNS and its ability to respond quickly enough to maintain balance. The present results are important in describing the capability of the nervous system to engage in relatively permanent changes in compensatory posture control by extracting regularities from a variable environment and adopting a generalized control strategy to maintain balance.

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Chapter 4

PRACTICE-RELATED IMPROVEMENTS IN POSTURE CONTROL DIFFER BETWEEN YOUNG AND OLDER ADULTS EXPOSED TO CONTINUOUS, VARIABLE AMPLITUDE OSCILLATIONS OF THE SUPPORT SURFACE

4.1 OVERVIEW

Healthy older adults were repeatedly exposed to continuous, variable amplitude oscillations of the support surface to determine 1) whether age affects the capacity for postural motor learning under continuous perturbation conditions with limited predictability and 2) whether practice leads to modifications in the control strategy used to maintain balance in older adults. During training, a translating platform underwent 45-second trials of constant frequency (0.5 Hz) and seemingly random amplitude oscillations (range ± 2 to 15 cm). In the middle 15 seconds of each trial, the same sequence of oscillation amplitudes was presented to participants but they were not informed of this repetition. The repeated sequence was the same as the sequence used in Van Ooteghem et al. (2008) and was therefore used for analyses. To examine learning, participants performed a retention test following a 24-hour delay. Kinematic data were used to derive spatial and temporal measures of whole body centre of mass (COM), trunk, thigh, and shank segment orientation, and ankle and knee angle from performance during the repeated middle segment. Results showed that with training, older adults maintained the capacity to learn adaptive postural responses in the form of improved temporal control of the COM and minimization of trunk instability at a rate comparable to young adults. With practice however, older adults maintained a more rigid, ‘platform-fixed’ control strategy which differed from young adults who shifted toward a ‘gravity-fixed’ control strategy that minimized their COM motion in space. This study provides important insight into the ability of older adults to demonstrate preserved ability for longer-term improvements in postural regulation.

4.2 INTRODUCTION

It is well documented that the incidence of postural instability increases with advancing age (Horak et al. 1989; Tang and Woollacott 2004) but there is less consensus regarding age-related deficits in motor learning (Seidler 2006). Despite age-related impairment in controllability, balance loss could be reduced if training induced positive changes in the central nervous system's (CNS) ability to adapt to environmental disturbances. To date, little empirical research has examined the permanency of training-related changes in balance control in older adults, particularly under conditions that lack predictability. The goal of the current study was to determine whether older adults maintain the capacity to learn a novel balance task requiring continuous postural regulation.

Postural instability can result from both self-initiated and externally-imposed perturbations but the greater risk of balance loss exists when perturbations to stability are external and unpredictable (Horak et al. 1997). Young adults exposed to discrete postural disturbances with limited predictability such as a push or slip, generate motor responses that tend toward a default value corresponding to a medium-sized perturbation (Horak et al. 1989) or to a size appropriate to withstand the largest perturbation (Beckley et al. 1991). Responses depend on the degree of unpredictability and the risk associated with an inappropriate response (Pavol et al. 2002; Bhatt and Pai 2005). Studies exploring the effects of age on short-term adaptability of compensatory postural responses to discrete perturbations and to continuous, predictable perturbations (i.e constant amplitude and frequency) suggest that with age, the CNS maintains some ability to modify balance behaviour based on prior experience (Hocherman et al. 1988; Woollacott and Manchester 1993; Horak and Kuo 2000; Bhatt et al. 2006; Fujiwara et al. 2007). These adaptations have been attributed to temporary changes in sensory and motor processes (Bhatt et al. 2006).

Only recently, have studies examined age and adaptability in the context of longer-term changes in balance behaviour (Pavol et al. 2002; Pavol et al. 2004; Pai and Bhatt 2007). In these studies, older participants repeatedly exposed to discrete slip perturbations show decreases in fall occurrence at similar rates as young adults but they also remain more likely than young adults to fall during re-exposure. Such studies of longer-term retention are fundamental to our understanding of the extent to which older adults can reduce their likelihood of falling by learning to recover from a postural perturbation. To date, no study has examined learning capacity in older adults for continuous balance tasks with limited predictability despite the possibility that the responses required for stability under discrete versus continuous perturbation conditions require different adaptive capabilities (Grabiner et al. 2008) or rely on different control systems (Maki and Ostrovski 1993).

Pavol and Pai (2002) proposed that the long-term goal of the central nervous system in unpredictable circumstances is to acquire an optimal movement strategy that decreases the likelihood of losing balance and reduces dependence on reactive responses. Either by choice or by necessity (e.g. age-related functional decline, perception of stability limits), it is possible that older adults will optimize their control using a different movement strategy than young adults or that they will demonstrate a different degree of adaptation. The motor learning literature shows equal rates of performance improvements for young and older adults on some motor tasks but not others (Seidler 2006), so we were uncertain whether rates of improvement would be comparable across groups during the acquisition phase on day one but we hypothesized that default posture control strategies would differ between groups.

In a recent paper (Van Ooteghem et al. 2008), we described the behaviour changes of young participants who maintained balance in response to continuous, variable amplitude motion of a translating platform. With practice, participants improved their balance control by shifting from an ankle strategy toward a multi-segmental control strategy that allowed them to stabilize their centre of mass (COM) in space. Performance improvements were maintained after a 24-hour delay period providing evidence for learning. The purpose of the current study was to explore differences in behaviour between young and older adults on the variable amplitude platform task in an effort to characterize the adaptive capacity of older adults under these conditions.

4.3 MATERIALS AND METHODS

4.3.1 Participants

Ten healthy, older adults (7 males, 3 females) ranging in age from 54-80 (mean 66 ± 7.8 years) and height from 157.5 to 183 cm (mean 171 ± 9.2 cm), volunteered to participate. Prior to inclusion in the study, a telephone questionnaire was administered to ensure that participants were free of severe deficits or disorders that could affect postural control. Upon clinical examination, six participants were unable to stand on foam with eyes closed for 30 seconds. One of these participants also exhibited somatosensory loss as determined by reduced Semmes-Weinstein monofilament threshold detection on the plantar surface of the foot and by an inability to detect 128 Hz vibration on the great toe. The methods used in the study were approved by the Oregon Health and Science University Institutional Review Board and by the Office of Research Ethics at the University of Waterloo (ORE #12479). All participants provided informed consent prior to data collection. For comparison, data from 12 young, healthy adults reported previously in Van Ooteghem et. al., (2008) was used. Young adults ranged in age from 19-29 (mean 24.3 ± 2.8 years) and in height from 160 to183 cm (mean 171 ± 7.4 cm).

4.3.2 Task and Procedures

Participants stood on a hydraulically driven, servo-controlled platform that could be translated horizontally forward and backward. To prevent falls without restricting motion, subjects wore an industrial safety harness tethered to a sliding hook on an overhead rail. They were instructed to maintain balance while standing with eyes focused on a poster approximately 2m straight ahead and arms crossed at the chest; aiming to avoid stepping if possible. The platform oscillated at a fixed frequency of 0.5 Hz and variable amplitude ranging from ± 2 cm to the largest amplitude that participants could withstand without taking a step (maximum ±15 cm). The maximum amplitude ranged from 80-100% of the 15 cm maximum delivered to young adults in a previous study (Van Ooteghem et al. 2008). Only two participants were unable to maintain balance with their feet in place at this magnitude. For these two participants, platform oscillations were scaled to their maximum (12 and 13 cm). To decrease the likelihood of a step or fall, the platform was offset forward by 6 cm at the start of each trial and the first movement of the platform was in the backward direction.

Trials were composed of three, 15-second segments containing seemingly random oscillations; however, the middle segment included a sequence of platform movements that occurred in every trial. Participants were not informed of this repetition. The repeated sequence of platform oscillations was embedded in the middle of each trial to conceal the repetition and improve the likelihood that participants would deem the perturbation environment unpredictable. The middle segment contained the same sequence of oscillations as the middle segment in Van Ooteghem et al.. (2008) and was therefore used for analyses. The first and third segments in the present study were matched for average velocity of translation by deriving the sequences from the pool of amplitudes that defined the middle segment. This method decreased the possibility that the segments would present different degrees of challenge to participants or that the repeated sequence of oscillations would be detected. Combined, the three segments produced a 45-second trial.

Data collection began with a 20-second trial of constant amplitude translation (8 cm), which served to familiarize participants with continuous platform motion. Testing consisted of six blocks of seven trials with a 2-minute rest period between blocks. To separate temporary performance effects from more permanent changes in behaviour that would reflect learning, participants returned for a seven-trial retention test approximately 24 hours following practice.

4.3.3 Data Recording

A Motion Analysis System (Santa Rosa, CA) with six cameras captured three-dimensional spatial coordinate information about body segment displacements and the movement of the platform. Reflective markers were placed bilaterally on the following anatomical landmarks: fifth metatarsophalangeal, lateral malleolus, lateral femoral condyle, greater trochanter, anterior superior iliac spine, iliac crest, styloid process, olecranon, acromion process, lateral mandibular joint and on the xyphoid process. A marker was also placed on the back of the platform. Data were sampled at 60 Hz and low pass filtered using a 2nd order, dual pass Butterworth filter with a cut-off frequency of 5 Hz. The position of the centre of mass (COM) of each body segment in the antero-posterior (AP) direction was calculated using the kinematic data and anthropometric data provided by Winter (1990). Whole body COM position (in space) in the AP direction was derived from the weighted sum of the individual segment COM locations using a custom-designed MATLAB program (Mathworks, Natick, MA). Right side marker data were also used to determine trunk, thigh, and shank segment orientation in the sagittal plane. The trunk segment was defined from the acromium process to the greater trochanter, the thigh segment from the lateral femoral condyle to the greater trochanter, and the shank segment from the lateral malleolus to the lateral femoral condyle. Ankle and knee angles were calculated from foot, thigh and shank segments.

4.3.4 Outcome Measures

Mean gain of the COM (COM peak displacement/platform peak displacement) and mean relative phase of the COM (COM time peak/platform time peak) were derived using the methods described in Van Ooteghem et al.. (2008). Together, gain and phase were quantified to examine spatial and temporal control of the COM. Theoretically, a COM gain value of 1.0 would occur if participants adopted a "platform-fixed" control strategy that allowed their COM to travel as far as the platform. Alternatively, a small COM gain would be achieved if participants stabilized their trunk in space (termed "gravity-fixed") and allowed their lower limbs to travel with the platform. Temporally, positive relative phase values would occur under conditions of COM phase lead relative to platform motion and would indicate predictive control of COM motion. In addition to COM measures, alignment of the trunk relative to gravitational vertical was calculated. The decision to use this measure was driven by the trunk's significant contribution to the COM and is supported by evidence that the ability to limit undesirable motion of the HAT segment (head, arms, and trunk) is the key factor distinguishing older adults who fall from those who don't (Grabiner et al. 2008). Tilt (in space) was determined for each time point and these values were averaged for each segment within a trial to determine mean tilt and mean tilt variability. Positive values indicated forward trunk tilt. We considered low variability to reflect more consistent, stable posture of the trunk segment. COM gain, COM phase, and trunk tilt variability were defined as primary outcome measures for balance control. To further describe the COM control strategy, secondary analyses of lower limb postures were conducted by examining time series for thigh and shank segments and by calculating mean ankle and knee joint angle position and variability. Negative thigh segment orientation, positive shank segment orientation, and smaller knee joint angle indicated a flexed-knee control strategy while lower ankle and knee joint variability reflected more rigid postures of the lower limbs.

4.3.5 Data Analyses

To evaluate the effects of age on skill acquisition, outcome measures for the middle (repeated) segment of each trial were compared to previously collected data for young adults (Van Ooteghem et al. 2008). Mixed model ANOVAs with 2 (group) x 6 (training block) were used to analyze performance improvements on day one. Levene's test for homogeneity of variance was conducted prior to the analysis of each variable. Linear regression was used to determine the slope of mean COM gain and phase (log transform) for individual participants during the six blocks of training on day one. This data was analyzed using one-sample t-tests (p=0.01). To examine retention in older adults, the block of retention trials completed on day two was compared to early (block one) and late (block six) training on day one using one-way repeated measures ANOVAs. Retention comparisons were restricted to primary outcome measures that showed substantial changes in older adults during training on day one (COM phase, trunk tilt and trunk tilt variability). *Post hoc* analyses were conducted using one-way repeated measures ANOVAs for significant interactions between group and training block, or Tukey's studentized range (HSD) tests.

An acceptable significance level was 0.05 unless otherwise noted and only those trials in which participants did not take a step were included. In total, 33/504 trials were omitted from training data in young adults and 31/490 trials were omitted from training and retention data for older adults due to stepping.

4.4 RESULTS

4.4.1 Acquisition Performance

Participants in the current study showed differences in both spatial and temporal control of their COM relative to young adults. Larger COM-to-surface displacement ratios (COM gains) in older adults indicated that they had poorer postural stability in space because they allowed their body COM to be displaced farther with surface displacements, particularly during forward translations (Fig. 4.1a and b). Statistically, COM gain differences were revealed by an interaction between group and training block ($F(2,39)=4.59$; $p=0.016$ (Greenhouse-Geisser); Fig. 4.1c) accompanied by a main effect of group ($F(1,20)=9.239$; $p=0.006$). Post hoc analysis indicated that young adults had significantly lower gains than older adults as early as block one ($p<0.0001$). Main effects analysis of training block for older adults revealed that they did decrease their gain significantly ($F(5,45)=6.23$; $p=0.0002$) with practice however, these reductions were modest relative to young adults (average 4.6 ± 4.7% versus 15.6 ± 10.4%). Examination of individual participants showed a significant change in gain for 7/12 young adults but only 1/10 older adults as measured by a slope that was significantly different from zero ($p<0.01$). It should be noted, that three of the young participants who did not show significant gain reductions with training were those who had the smallest gain in early training (range: 0.3645 to 0.5105) indicating a possible floor effect for these participants. Reanalyzing the COM gain data without these three participants further strengthened the interaction between group and training block ($F(2,32)=8.37$; $p=0.001$; Greenhouse Geisser). Further, post hoc tests showed that changes in gain for older adults occurred during early exposures to the task as evidenced by significant differences between block one and the remaining training blocks which did not differ from one another.

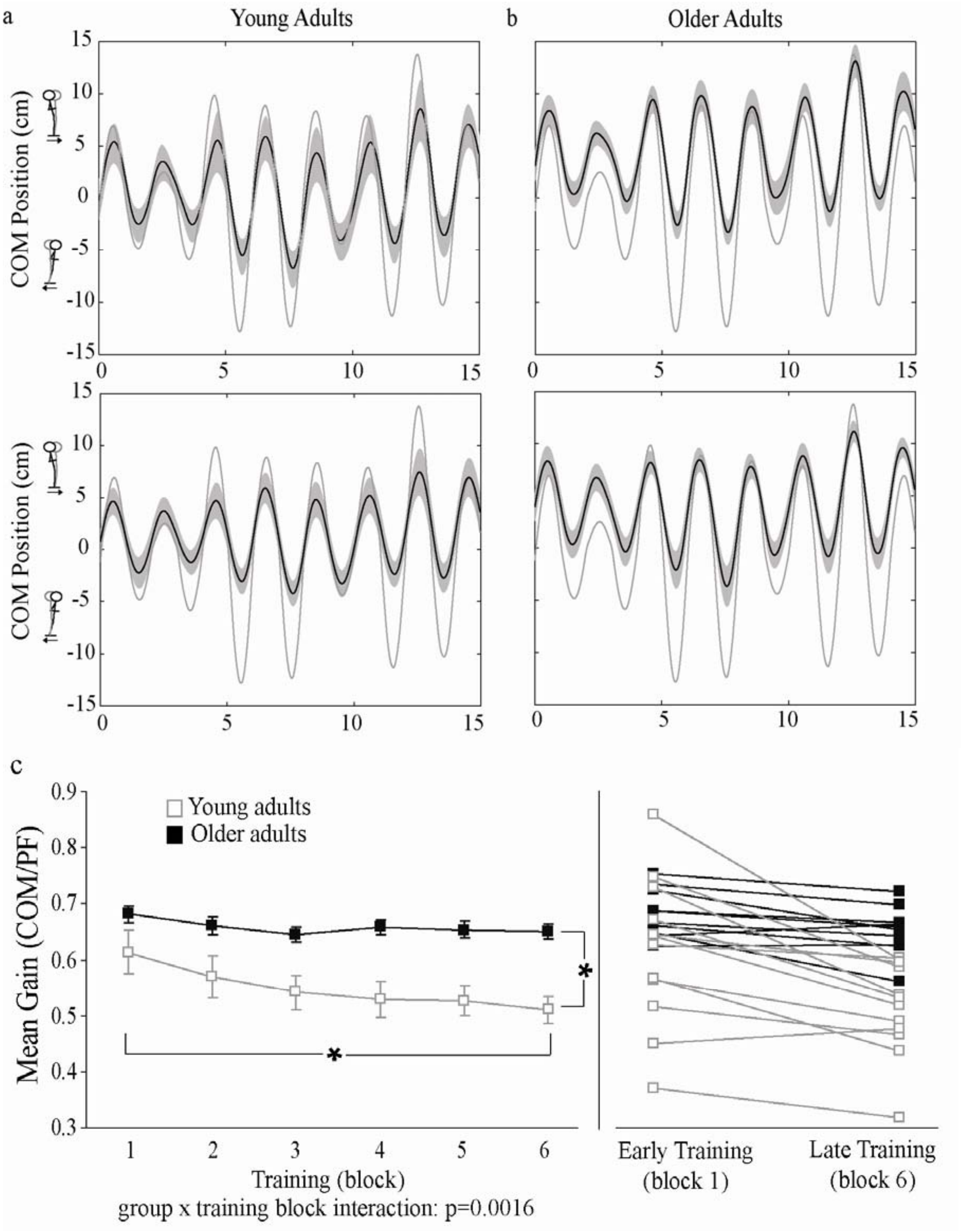

Fig. 4.1: Group average tracings of a) young adult COM motion in early (top) and late (bottom) training and b) older adult COM motion in early (top) and late (bottom) training. *Black* trace denotes COM motion. *Shaded* bands represent standard deviation of the mean. Grey trace denotes platform motion. c) Group (left) and individual (right) changes in COM gain with training. Error bars represent standard error of the mean. Young adult data taken from Van Ooteghem et al.. (2008)

The temporal control of the COM also differed between young and older adults. Analysis of mean relative phase between COM and platform displacements revealed a main effect of block (F(2, 36)=42.990; p<0.001(Greenhouse-Geisser) and group (F(1,20)=8.433; p=0.009; Fig. 4.2). Examination of individual participants showed a significant change in phase for all young adults and 8/10 older adults (p<0.01). Unlike young adults however, most older adults (7/10) did not achieve temporal phase lock (defined as less than two degrees phase lag) between COM and platform displacements.

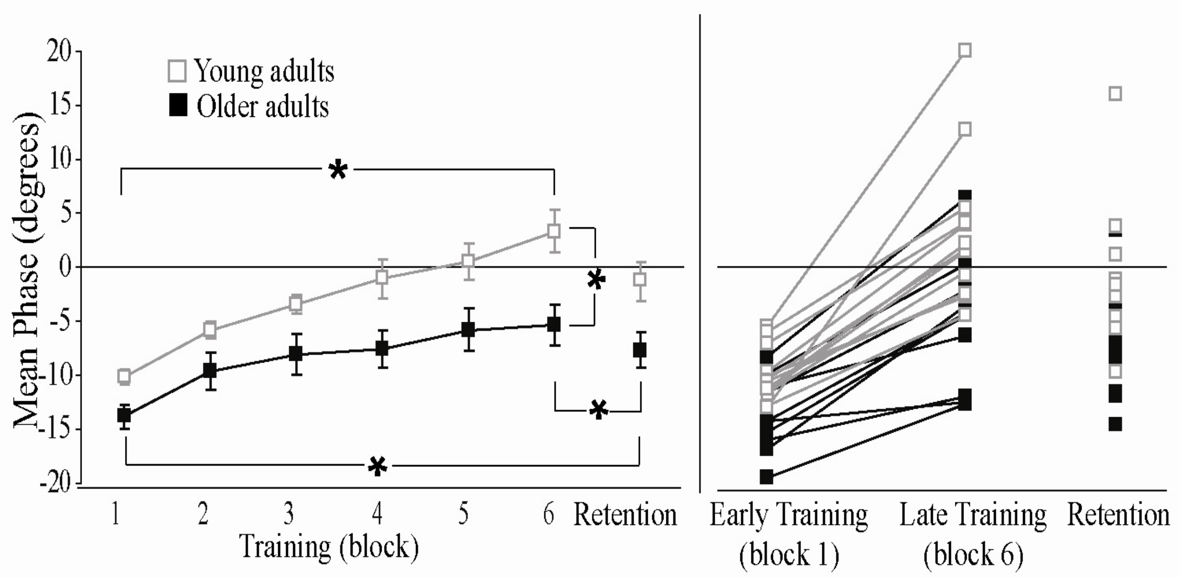

Fig. 4.2: Group (left) and individual (right) changes in COM phase during training and retention testing. Positive values represent COM phase lead relative to platform motion. Error bars represent standard error of the mean. Asterisks indicate main effects significant at $p<0.05$. Young adult data taken from Van Ooteghem et al.. (2008).

Changes in mean trunk tilt and trunk tilt variability with training were similar for young and older adults (Fig. 4.3) despite group differences in COM gain and phase. For both groups, mean trunk position shifted from a slightly flexed to upright posture (from 1.58° ± 6.73° to -0.58° ± 4.82° for young adults and 1.86° ± 5.57° to -1.60° ± 4.24° for older adults) as evidenced by a main effect of block (F(1,29)=9.73; p=0.002 (Greenhouse-Geisser); Fig. 4.3a). Young and older adults also showed comparable decreases in amount of trunk motion with training as indicated by a main effect of

block for trunk tilt variability (F(1, 27)=11.13; p=0.001 (Greenhouse-Geisser); Fig. 4.3b). These results suggest that the ability to improve trunk control was preserved with age regardless of the strategy used to maintain balance on the platform.

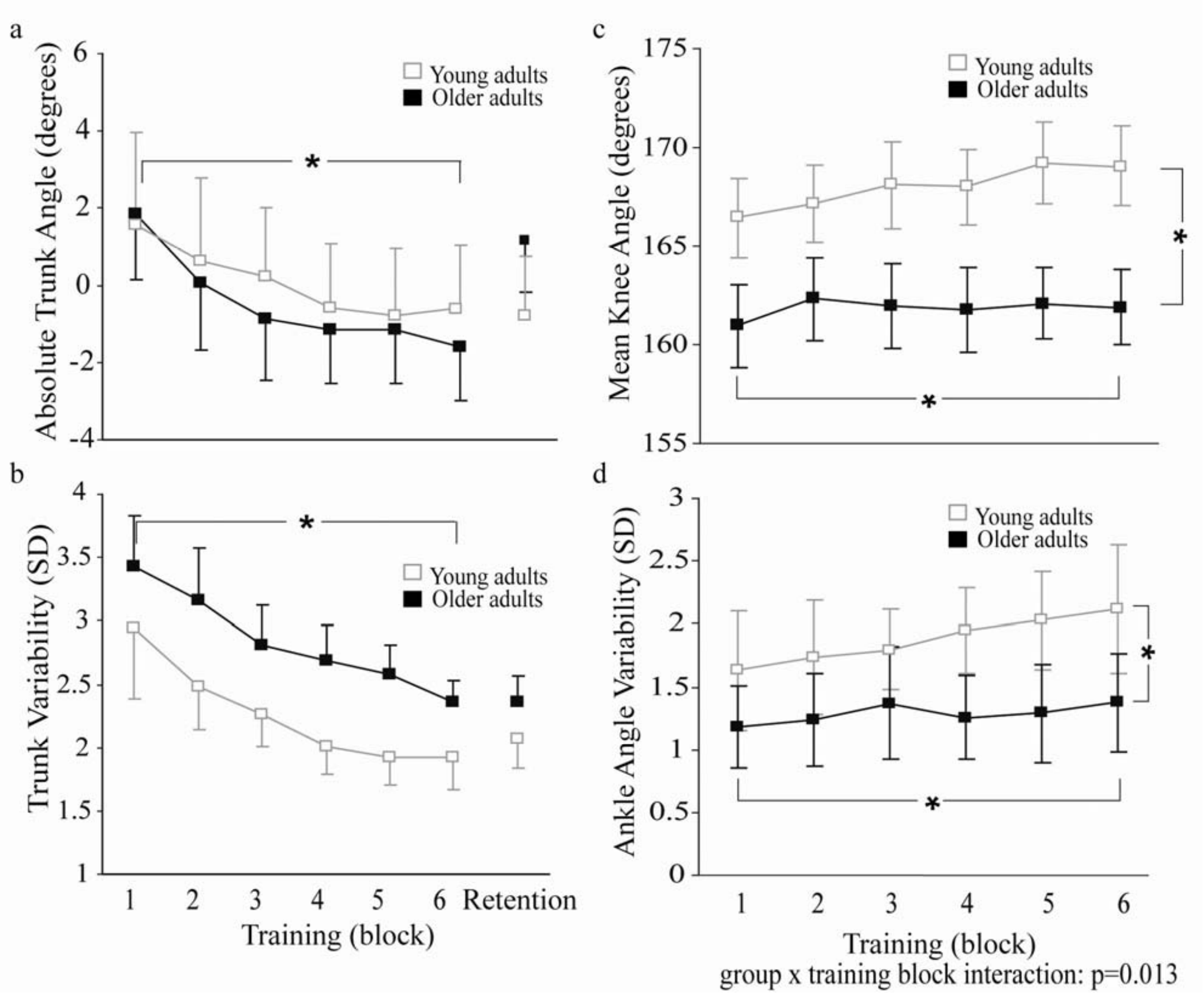

Fig. 4.3: Group changes in a) trunk tilt with respect to gravity during training and retention b) trunk tilt variability during training and retention, c) knee angle during training, and d) ankle angle variability during training. Error bars represent standard error of the mean. Asterisks indicate main effects significant at p<0.05. Young adult data taken from Van Ooteghem et al.. (2008)

Ankle and knee joint angle analyses indicated that young and older adults approached the task by adopting different behaviours in their lower limbs. A group effect for mean knee joint position revealed that older adults showed significantly greater knee flexion throughout the task (F(1,20)=5.11; p=0.035; Fig. 4.3c). A main effect of block however, indicated that both groups decreased knee flexion with training (F(2,45)=4.68; p=0.012 (Greenhouse-Geisser)). Both groups also showed comparable decreases in knee joint variability with training (F(3,53)=5.23; p=0.004; not shown). Although there was no main effect of group or training block for mean ankle joint position, an interaction between training group and block existed for ankle joint variability (F(2,47)=4.42; p = 0.013 (Greenhouse-Geisser); Fig. 4.3d). Post hoc analyses revealed that ankle angle variability was significantly less for older adults in both early (p<0.0001) and late training (p<0.0001) and that despite group differences, older adults did show modest increases in ankle angle variability (F(5,45)=5.25; p=0.001).

Despite significant group effects for knee joint position, examination of time series for trunk, thigh, and shank segment motion in individual participants revealed that after training, three older adults adopted lower limb motions comparable to young adults (Fig. 4.4a) while five others were characterized by adjustments in segment alignment with persistent negative tilt of the thigh segment (Fig. 4.4b). Another two participants showed negligible change in limb motion with training. The participant shown in Fig. 4.4b was also characterized by the smallest change in COM gain with training.

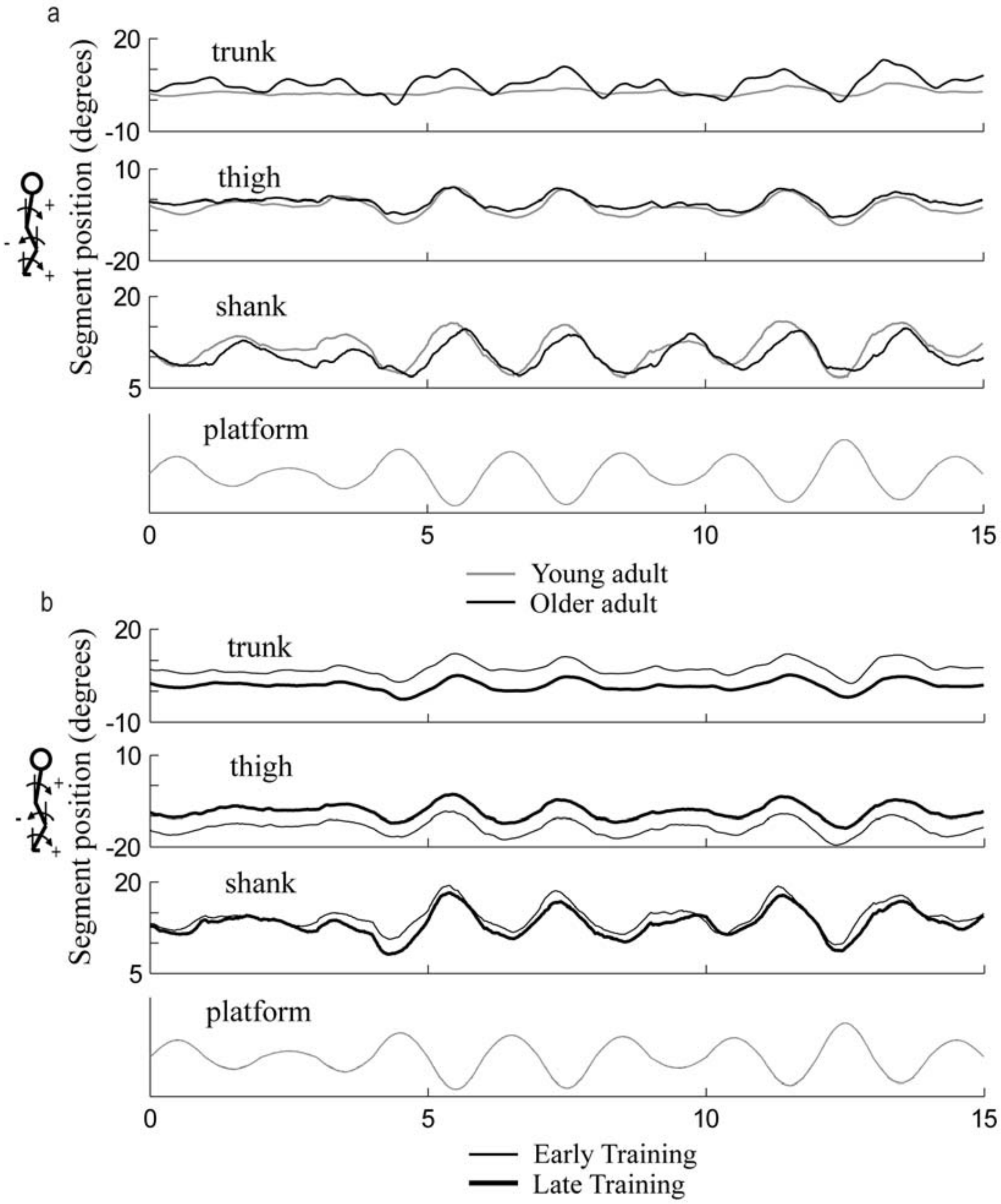

Fig. 4.4: Trunk, thigh, and shank segment time series for a) representative young and older adult showing similar lower limb motion during late training and b) representative older adult during early and late training characterized by persistent flexed postural alignment. *Grey* trace denotes platform motion. Young adult data taken from Van Ooteghem et al.. (2008)

4.4.2 Retention Performance

Retention performance was analyzed for the three variables (COM phase, trunk tilt and trunk tilt variability) that showed substantial changes with training on day one. For all measures, older adults demonstrated some maintenance of performance improvements providing evidence for learning. A main effect of test block (early training, late training, retention) revealed that older adults showed some loss of the temporal shifts in COM demonstrated during late training on day one (F(2,18)=36.19; p<0.0001; Fig. 4.2). Post hoc comparisons however, revealed that phase lag during retention testing remained significantly less than the lag observed in early training. Analysis of trunk tilt and trunk tilt variability also produced a main effects of test block (F(2,18)=6.472; p=0.008 and F(1,10)=18.87; p=001 (Greenhouse-Geisser) respectively) but post hoc comparisons revealed no significant loss in trunk control from late training on day one to retention testing on day two (Fig 4.3a and 4.3b).

4.5 DISCUSSION

The results presented here demonstrate that older adults possess an ability to learn adaptive postural responses to continuous, variable amplitude postural perturbations. Adaptations included improved temporal control of their COM in response to the constant frequency of platform motion and minimization of trunk instability at a rate comparable to young adults. Longer-term learning was demonstrated by improved retention test performances relative to early practice. The two groups however, differed in their approach to the task. In general, older adults adopted a more rigid, flexed knee posture throughout training. This strategy differed from young adults who gradually shifted toward a straight-legged, multi-segmental control strategy that enabled them to minimize their COM motion (Van Ooteghem et al. 2008). To our knowledge, this is the first study to describe the effects of age on the ability to learn a continuous balance task with perturbations that have limited predictability; in this case, with constant frequency but variable amplitude.

The main finding of the study is that age did not affect the ability of participants to show some improvement in compensatory posture control with practice under conditions requiring continuous postural regulation, or to show longer-term retention of these improvements. The predominant change in older adults occurred in their ability to control trunk motion. With training, both young and older adults aligned their trunk more vertically and reduced overall trunk motion. These changes occurred at similar rates for the two groups however; young adults exhibited an accompanying shift from an ankle strategy to a multi-segment, gravity-fixed control strategy (Van Ooteghem et al. 2008). In contrast, older adults showed a more platform-fixed strategy evidenced by greater COM gain most notably during forward translations (Fig. 4.1b), and less ankle angle variability. Large COM gains during forward translations suggest that the control strategies adopted by older adults were driven in part, by efforts to avoid backward balance loss.

Our results agree with previous studies showing that the general response of older adults to constant amplitude/frequency perturbations is to adopt a rigid movement strategy (Hocherman et al. 1988; Wu 1998). Of greater interest for describing practice-related changes in older adults, we show that this platform-fixed strategy persists with training. Unlike the results of Hocherman et al. (1988) however, most older adults (7/10) in the current study did not stand on the platform with fully extended knees. We propose that differences in knee position in the current study reflect the need to limit transfer of reactive forces in a variable amplitude perturbation environment, perhaps to compensate for a decreased ability to control trunk movement.

Evidence for similar rigid response strategies in both predictable and non-predictable perturbation conditions could support the theory that postural equilibrium under various conditions can be achieved by a limited repertoire of response strategies (Horak and Nashner 1986). We suggest however, that modest training-related changes in control strategy amongst older adults reflect loss of CNS flexibility with age. As a group, older adults also showed less between-subject variability in COM gain than young adults (Fig 4.1c). This finding differs from results of clinical balance tests which typically report increases in variability with age (Era et al. 2006). In the current task, age-related limitations in joint and sensory system function might have constrained the number of options available to older adults. Alternatively, young adults could have possessed a larger range of reference experiences to assist in task performance, enabling some participants to anticipate the consequences of their movements (e.g. the young participant who had the lowest COM gain in early training was a surfer).

Larger COM gains in early training for most older adults provided an opportunity for this group to demonstrate greater practice-related change. Only one older adult however, showed a significant reduction in COM gain in response to variable amplitude platform motion. In this study, the frequency of platform motion was constant which may have served as a regulatory feature of the task (Magill 1998). All subjects demonstrated significant improvement in temporal control of the COM with practice at a rate comparable to young adults suggesting that with age, the CNS maintains an ability to tune into temporal regularities in the perturbation environment. It is important to note that given the same amount of training only three older adults achieved COM phase lock similar to a majority of young adults. An inability to achieve predictive control of COM like young adults could have been caused by age-related functional impairment in response latencies and reflex loop time (Woollacott et al. 1986; Maurer et al. 2006). In early training, older adults also showed a significantly greater phase lag providing support for age-related response limitations.

Possible reasons for strategy differences between groups and limited practice-related changes in strategy amongst older adults

Older adults exposed to the variable amplitude balance task adopted a rigid, flexed knee posture with their trunk fixed to the surface rather than to gravity, even after practice. Age-related changes both in joint mobility (i.e. joint stiffness, decreased range of motion) and sensory system function (i.e. visual, vestibular, or proprioceptive decline) could have forced older adults to persist with a simplified, default control strategy by limiting the CNS's ability to develop a robust internal representation of postural control. The effect of these changes could have been exacerbated by threat of falling, prompting older adults to self-select a different goal in response to variable amplitude platform motion (Horak and Kuo 2000) or to refrain from exploring alternate control strategies.

Generally, both groups aimed to decrease trunk motion but as suggested in our previous paper, the multi-segmental control strategy adopted by young adults may reflect efforts to improve efficiency during training (Van Ooteghem et al. 2008). It is possible instead, that the primary goal for older adults was to maintain a safe margin of stability between their COM and base-of-support in an effort to avoid stepping. In both studies, participants were instructed to maintain balance by keeping their feet in place. Previous research shows that older adults prefer to use a stepping strategy, even when the COM is well within the boundaries of the base-of-support (Maki and McIlroy 2005). Adopting a gravity-fixed control strategy similar to young adults would have decreased their margin of stability, particularly at amplitude extremes. Further, separation of the upper and lower body as observed in the gravity-fixed control strategy adopted by young adults in late training requires good joint mobility, particularly at the hips and ankles, appropriate timing of muscle activation to control the trunk, and intact vestibular function to keep the trunk relatively stable with respect to gravity. All of these requirements can become limited with age (Buchanan and Horak 2002; Tang and Woollacott 2004).

Age-related declines in sensory system function could have negatively affected older adults' ability to gather information about the perturbation characteristics or their body orientation; restricting their ability to evolve their control strategy with practice. If older adults experienced loss in vestibular or proprioceptive sensitivity, they might have shifted sensory system weighting toward vision (Lord and Menz 2000, Speers et al. 2002). The platform-fixed control strategy adopted by older adults produced a stable head position with respect to the trunk and head displacement which might have generated rich, optic flow information. Since the frequency of platform motion was constant, temporal regularity in the approach and retreat of a stable reference point might have provided helpful cues regarding body motion. Studies of the influence of static and dynamic visual cues on posture control have shown that dynamic visual cues contribute to fast stabilization of the whole body (Amblard et al. 1985).

Learning in a variable amplitude environment

For both COM phase and trunk tilt variability, retention test outcomes were better than pre-practice performance demonstrating older adults' capacity for postural motor learning in a variable amplitude environment. Some loss in the ability to exploit the temporal regularity in platform motion from late training to retention testing on day two did occur but this was also observed in young adults (Van Ooteghem et al. 2008). The decline in performance could be attributed in part, to a warm up decrement but this possibility needs to be explored further. The ability to control trunk motion however, was maintained across days of testing. Evidence for longer-term retention of these performance improvements in older adults provides important insight into the potential for sustainable changes in continuous postural regulation, despite kinematic strategies that were different from younger adults. More work must be done however, to examine older adults' persistence with a simplified control strategy that could offer less stability and be more energy demanding.

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Chapter 5

HEALTHY OLDER ADULTS DEMONSTRATE GENERALIZED POSTURAL MOTOR LEARNING IN RESPONSE TO CONTINUOUS, VARIABLE AMPLITUDE OSCILLATIONS OF THE SUPPORT SURFACE

5.1 OVERVIEW

Postural motor learning for dynamic balance tasks has been shown to occur in healthy older adults (Van Ooteghem et al. 2009; in press). The purpose of this study was to investigate the specificity of the knowledge obtained with balance training in this age group. Furthermore, this study was designed to examine whether embedding perturbation regularities within a trial masked demonstration of specific learning. Two groups of older adults were asked to maintain balance on a translating platform that oscillated back and forth with constant frequency (0.5 Hz) and variable amplitude motion (range ± 2 to 15 cm). One group of participants was trained using an embedded sequence protocol which contained the same series of variable amplitude oscillations in the middle 15-seconds of each trial, buried amongst random platform motion. A second group of participants was trained using a looped sequence protocol which consisted of a single 15-second training sequence repeated three times for each trial. All trials were 45-seconds in duration and participants were not informed of any repetition. To examine learning, participants from both groups performed a retention test following a 24-hour delay. Participants in the looped sequence protocol also received a transfer task which immediately followed retention testing. Specificity of learning was examined by comparing postural performance for repeated versus random sequences in the embedded sequence protocol and by comparing training versus transfer sequences in the looped sequence protocol. Using kinematic data, postural performance was measured by deriving spatial and temporal measures of whole body centre of mass (COM) and trunk orientation. Performance in both groups of older adults improved with practice; this improvement was characterized by general rather than specific postural motor learning. These findings are similar to previous work in young adults and suggest that age does not influence the type of learning which occurs for balance control. Evidence for generalized postural motor learning provides important insight into the potential for positive transfer of balance skill to other balance tasks.

5.2 INTRODUCTION

With practice, learners can acquire procedural knowledge about how to perform a motor skill, often unintentionally and without awareness of what was learned (Frensch 1998). Recently, such *implicit learning* has been reported for a dynamic balance task in young participants who were asked to track a visual signal with corresponding movements on a stabilometer (Shea et al. 2001). The Shea et al. study reported that participants engaged in sequence-specific learning; showing better retention of performance improvements for a repeated versus random sequence of stimuli without awareness of the repetition. While movement sequencing may facilitate learning for some motor tasks (e.g. dance, gymnastics), we recently argued that such sequence-specific learning could actually serve to constrain rather than enhance postural motor learning, particularly for a balance task requiring compensatory posture control (Van Ooteghem et al. 2008). In that study, we adapted the embedded-sequence methodology designed to explore implicit sequence learning and examined whether compensatory postural motor learning in young adults was general or specific. Rather than generate postural adjustments as had been done in Shea et al. (2001), participants were exposed to continuous, variable-amplitude oscillations of a translating platform and in each trial, a repeated sequence of translation amplitudes was embedded among random platform motion. Performance did improve with practice but learning was no better for the repeated sequence providing evidence for generalized rather than sequence-specific postural motor learning.

In the present study, we examined the nature of postural motor learning in older adults. Given the incidence of postural instability in this population, we reasoned that understanding the effects of age on learning could have tremendous impact on training efforts in this group. To begin exploring the capacity for older adults to learn a balance task, we exposed them to constant frequency, variable-amplitude oscillations of the support surface and examined practice-related improvements in performance (Van Ooteghem et al. 2009; in press). Results revealed preserved postural motor learning as measured by similar rates of improvement in performance between young and older adults and maintenance of behaviours that were better than those observed in early practice. Despite comparable rates of improvement, age-related differences in the control strategies used to maintain balance were observed. A majority of older adults persisted with a rigid, 'platform-fixed' control strategy while young adults shifted toward multi-segmental control that included increased motion about the hip joint. The simplified control strategy exhibited by older adults is compatible with other reports of age-related postural dyscontrol which shows preference for a rigid control strategy in situations that are likely to lead to loss of stability (e.g. large or fast perturbations) (Horak et al. 1989; Tang and Woollacott 2004).

Since young and older adults in Van Ooteghem et al. (2009; in press) adopted different control strategies with practice, it is also possible that they engaged in different forms of postural motor learning (i.e. specific versus general). The 'platform-fixed' strategy used by older adults suggests that this group was tracking platform motion, thus that they would extract sequence information to improve performance if exposed to the implicit sequence learning paradigm used in Van Ooteghem et al. (2008). This sequence information would be reflected in differential performance improvements for a repeated versus random sequence of platform perturbations. Acquiring knowledge about the sequence of perturbations would optimize the CNS's ability to engage in feed-forward control mechanisms that could improve pre-perturbation stability and decrease perturbation intensity (Bhatt et al. 2006). Prediction could be particularly advantageous for older adults because a) balance tasks present a greater challenge to stability due to age-related declines in sensorimotor function and b) the threat of an inappropriate response (i.e. a fall) is greater for this group. As a result, the CNS might sacrifice response flexibility (obtained via generalized-postural motor learning) for stability.

When the embedded-sequence protocol used in Van Ooteghem et al. (2008) and other studies of implicit sequence learning (Pew 1974; Wulf and Schmidt 1997; Magill 1998; Shea et al. 2001) is applied to continuous motor tasks such as balancing on a continuously moving platform, it is possible that sequence-specific learning is masked by 1) participants' inability to switch motor behaviour between random and repeated sequence types or 2) participants' assessment that it is not advantageous for them to do so (i.e. it is too difficult or inefficient for them to transition between a generalized control strategy and one that exploits the repeated sequence). Indeed, previous continuous perturbation studies with stepwise increases in translation frequency report gradual transitions between characteristic postural coordination patterns (Buchanan and Horak 2001) that occur over the course of three to five cycles (Dietz et al. 1993; Corna et al. 1999; Bugnariu and Sveistrup 2006). In Van Ooteghem et al. (2008), sequences were composed of 7.5 cycles and as such, it is possible that postural transitions did not occur in this time. It is also possible that participants did not receive enough practice to learn the sequence.

To rule out the possibility that our previous ‘embedded sequence’ protocol masked sequence-learning, we exposed two groups of older adults to one of two sequence-learning protocols. The first protocol - embedded sequence - was similar to that reported previously (Van Ooteghem et al. 2008). In the second protocol, participants were trained using a single training sequence of platform perturbations and then exposed to a “transfer” task. Using this “training and transfer” methodology, sequence-specific learning is characterized by a significant disruption to performance for transfer trials relative to late training. This methodology has also been used to examine sequence learning in serial reaction time tasks by training participants to respond to a repeating sequence of stimuli with corresponding key presses and then observing their reaction time in a transfer task which requires key press responses to stimuli presented in a random order (e.g., Nissen and Bullemer 1987). Together, results from the two protocols served to a) determine if older adults engage in general or specific postural motor learning and b) to validate a method of examining specific postural motor learning using the ‘embedded sequence’ of platform perturbations. We also examined the capacity for older adults to eventually achieve performances comparable to the young adults reported in Van Ooteghem et al. (2008) by exposing older adults to an extended practice period (50% more exposure to platform motion and 4 times more exposure to a repeated sequence than young adults). We hypothesized that older adults would demonstrate generalized postural motor learning in both experimental protocols and that performance discrepancies would persist between young and older adults despite additional training for the older adult group.

5.3 MATERIALS AND METHODS

5.3.1 Participants

Eleven healthy, older adults (3 males, 8 females) ranging in age from 60-79 (mean 68 ± 6.4 years) and height from 152.4 to 177.8 cm (mean 166 ± 8.9 cm), volunteered to participate. Prior to inclusion in the study, a telephone questionnaire was administered to ensure that participants were free of disorders that could affect postural control. Clinical examination revealed that one participant was at risk for loss of somatosensory function on the plantar surface of the foot as determined by the Semmes-Weinstein monofilament detection test and three participants exhibited reduced ability to detect 128 Hz vibration on the great toe and the ankle on one foot. The methods used in the study were approved by the Oregon Health and Science University Institutional Review Board and by the Office of Research Ethics at the University of Waterloo (ORE #12479). All participants provided informed consent prior to data collection. In addition, data from 12 young, healthy adults reported previously in Van Ooteghem et. al. (2008) and from 10 healthy older adults reported previously in Van Ooteghem et. al. (2009; in press) were compared with results of older adults in this study. Young adults ranged in age from 19-29 (mean 24.3 ± 2.8 years) and in height from 160 to183 cm (mean 171 ± 7.4 cm). The comparison group of older adults ranged in age from 54-80 (mean 66 ± 7.8 years) and in height from 157.5 to 183 cm (mean 171 ± 9.2 cm).

5.3.2 Task and Procedures

Two types of platform sequences were used in two protocols with two groups of older adults in this study. The first protocol consisted of a repeated sequence of platform oscillations embedded amongst two random sequences of perturbations. The second protocol consisted of a single training sequence coupled with a post-training transfer task which included random sequences of perturbations. In both protocols, a retention test was used to investigate learning.

The balance task required participants to stand on a hydraulically driven, servo-controlled platform that could be translated horizontally forward and backward. To prevent falls without restricting motion, subjects wore an industrial safety harness tethered to a sliding hook on an overhead rail. They were instructed to maintain balance while standing with eyes focused on a poster approximately 2m straight ahead and arms crossed at the chest, aiming to avoid stepping, if possible. The platform oscillated at a fixed frequency of 0.5 Hz and variable amplitudes ranging from ± 0.5 cm to the largest amplitude which participants could withstand without taking a step (maximum ±15 cm). To decrease the likelihood of a step or fall, the platform was offset forward by 6 cm at the start of each trial and the first movement of the platform was in the backward direction.

5.3.2.1 Embedded Sequence

In this protocol, trials were composed of three, 15-second segments containing seemingly random oscillations; however, the middle segment was a repeated sequence of platform movements that occurred in every trial (Fig. 5.1a). Participants were not informed of this repetition. The middle segment contained the same sequence of oscillations as the middle segment in Van Ooteghem et al. (2008). Unlike our previous study, the first and third oscillation segments were matched for average velocity of translation by deriving the sequences from the pool of amplitudes that defined the middle segment (termed the standard pool). This method decreased the likelihood that the segments would present different degrees of challenge to participants. Combined, the three segments produced a 45-second trial. Two participants who were trained using this protocol were unable to maintain balance with their feet in place at the maximum amplitude. For these two participants, platform oscillations were scaled to their maximum (12 and 13 cm).

Data collection began with a 20-second practice trial of constant amplitude translation (8 cm), which served to familiarize participants with continuous platform motion. Testing consisted of six blocks of seven trials, with a 2-minute rest period between blocks. To separate temporary performance effects from more permanent changes in behaviour that would reflect learning (Schmidt and Lee 2005), participants returned for a seven-trial, retention test approximately 24 hours following practice.

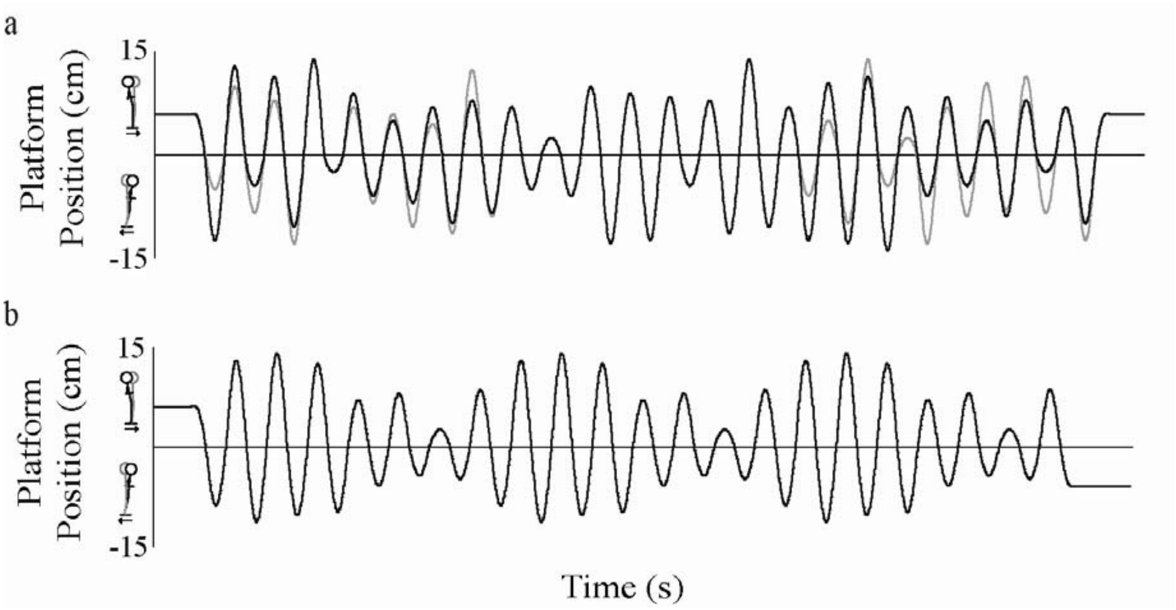

Fig. 5.1: a) An overlay of two trials from the embedded sequence protocol (max. range ± 15 cm) illustrating the repeated middle segment between two random segments. b) An example of platform motion for the looped sequence protocol (max. range ± 15 cm). Each trial consisted of three presentations of the same sequence.

5.3.2.2 Looped Sequence

In this protocol, participants received a 14-second, variable amplitude sequence which looped to create a three-segment trial (Fig. 5.1b). Each participant had a unique training sequence generated randomly from the standard pool used in the *embedded sequence* protocol to ensure that the average velocity of translation was consistent amongst participants and between protocols. All participants trained using this protocol were able to withstand the maximum platform displacement of ± 15cm.

Further precautions were taken to ensure consistent levels of difficulty across participants by establishing a criterion to account for large velocity changes at platform zero-crossings that presented as discontinuities (described by participants as ‘jerks’) in platform motion. Under conditions of constant frequency and variable amplitude platform motion, the magnitude of velocity change at the zero-crossing is dependent upon the current (N) and previous (N-1) amplitude in the sequence. Using the formula ((N-(N-1)/N)*100), we examined the velocity change at each zero-crossing in the repeated sequence of the *embedded sequence* protocol and found that it contained three decelerations (large amplitude N-1 to small amplitude N) and one acceleration (small N-1 to large N) that were driven by successive amplitudes which were ≥50% different (Fig. 5.2). In order to match the frequency of discontinuities in the current protocol, any randomly generated training sequence which had more than three decelerations or more than one acceleration violating this criterion difference was excluded.

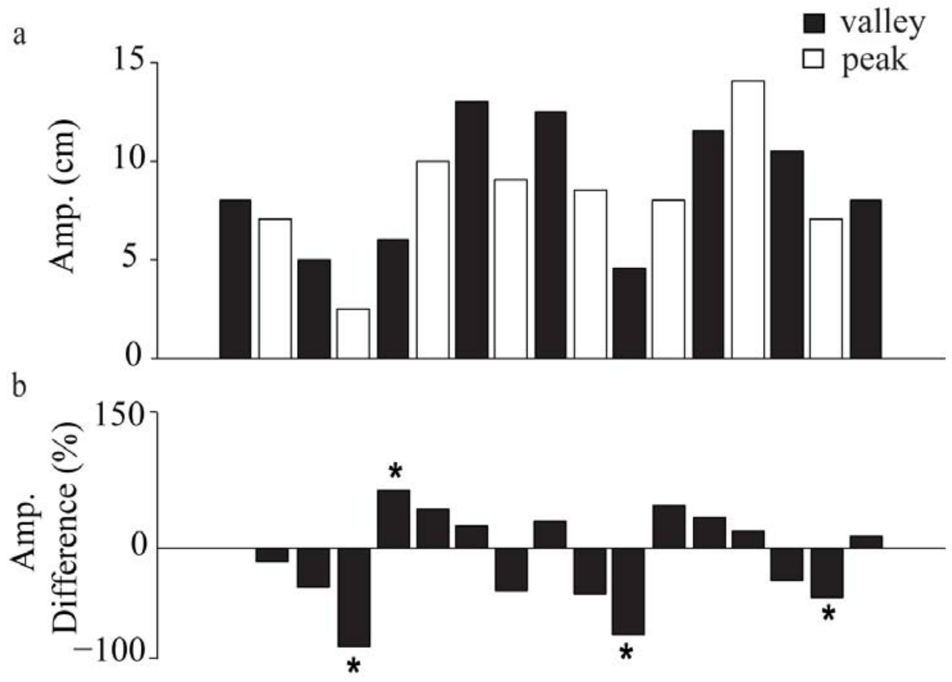

Fig. 5.2: a) Amplitude of each anterior (peak) and posterior (valley) displacement of the platform for the repeated middle segment of the embedded sequence protocol. Anterior displacement is denoted by the *white* bars. Posterior displacement is denoted by the *black* bars. b) Amplitude difference for successive peaks and valleys. Asterisks denote amplitude differences that are ≥ to the 50% criterion value.

Data collection began with a 20-second practice trial of constant amplitude translation (8 cm), which served to familiarize participants with continuous platform motion. Testing consisted of nine blocks of seven trials (50% increase from the *embedded sequence* protocol), with a 2-minute rest period between blocks. To separate temporary performance effects from more permanent changes in behaviour, participants returned for a three-block retention test approximately 24 hours following practice. In the *embedded sequence* protocol, the retention test contained a single block of trials. A longer retention test in this protocol was intended to examine retention and possible relearning (Schmidt and Lee 2005). Immediately following the retention test, participants underwent a transfer test to examine whether performance improvements were dominated by general or sequence-specific learning. The transfer test consisted of one block of random trials. Each of these trials was composed of three segments of random amplitude sequences drawn from the standard pool which met the criteria for number of 'jerks'. The same block of transfer trials was given to all participants.

5.3.3 Data Recording

A Motion Analysis System (Santa Rosa, CA) with six cameras captured three-dimensional spatial coordinate information about body segment displacements and the movement of the platform. Reflective markers were placed bilaterally on the following anatomical landmarks: fifth metatarsophalangeal, lateral malleolus, lateral femoral condyle, greater trochanter, anterior superior iliac spine, iliac crest, styloid process, olecranon, acromion process, lateral mandibular joint and on the xyphoid process. A marker was also placed on the back of the platform. Data were sampled at 60 Hz and low pass filtered using a 2nd order, dual pass Butterworth filter with a cut-off frequency of 5 Hz. The position of the centre of mass (COM) of each body segment in the antero-posterior (AP) direction was calculated using the kinematic data and anthropometric data provided by Winter (1990). Whole body COM position (in space) in the AP direction was derived from the weighted sum of the individual segment COM locations using a custom-designed MATLAB program (Mathworks, Natick, MA). Right side marker data were also used to determine trunk segment orientation in the sagittal plane. The trunk segment was defined from the acromium process to the greater trochanter.

5.3.4 Outcome Measures

Mean gain of the COM (COM peak displacement/platform peak displacement) and mean relative phase of the COM (COM time peak/platform time peak) were derived using the methods described in Van Ooteghem et al. (2008) to examine spatial and temporal control of the COM. In addition to COM measures, variability in the alignment of the trunk relative to gravitational vertical (termed trunk tilt variability) was calculated as described in Van Ooteghem et al. (2009; in press). COM phase and gain were chosen for consistency with primary outcome measures identified in previous studies (Van Ooteghem et al. 2008; Van Ooteghem et al. 2009; in press). Trunk tilt variability was included because it previously showed substantial training-related changes in older adults (Van Ooteghem et al. 2009; in press). To compare performances across different sequences of platform motion, trunk tilt variability was normalized to the mean platform velocity change for each segment (embedded sequence protocol) and each training sequence (looped sequence protocol).

5.3.5 Data Analyses

To evaluate whether participants improved performance with practice and if they engaged in general or sequence-specific learning, primary outcome measures (COM gain, COM phase, TTV) were analyzed separately for both the *embedded* (*ES)* and *looped (LS) sequence* protocols.

For the ES protocol, two-way (segment type x training block) repeated measures ANOVAs were used for all statistical comparisons. Outcome measures were compared between segment two (repeated) and segment three (random) similar to a previous study using this protocol (Van Ooteghem et al. 2008). To examine whether performance differed between sequence types during the acquisition phase, data were analyzed by comparing across blocks of trials on day one in a 2 (segment) x 6 (block) RMANOVA. Retention performance was analyzed using a 2 (segment) x 3 (block) RMANOVA which included early (block 1) and late (block 6) training on day one and the retention test block on day two. Post hoc analyses were conducted using one-way repeated measure ANOVAs for significant interactions between segment type and training block, or Tukey's studentized range (HSD) tests.

For the LS protocol, data from the middle segment of the looped sequence trials were analyzed using one-way repeated measure ANOVAs unless otherwise noted. Restricting the analyses to the middle segment of each trial ensured that any within-trial adaptation that might have occurred did not interfere with our investigation of longer-term learning. Acquisition performance was analyzed by examining data across the nine training blocks on day one. To determine if participants maintained performance improvements following a delay period, paired t-tests (Bonferroni corrections) were used for planned comparisons between a) the first retention block on day two and the last block of training on day one, b) the first retention block on day two and the first block of training on day one, and c) the last retention block on day two and the last block of training on day one. Sequence-specific learning was also explored using paired t-tests between the first retention block and the transfer block.

To determine whether additional exposure to the moving platform was beneficial to older adults, mixed model ANOVAs were used first to compare the middle segment in six blocks of training for older adults in the ES versus LS protocols to ensure that the two groups of older adults performed similarly despite the change in protocol. For variables that were not significantly different, a mixed model ANOVA between young adults (data from Van Ooteghem et al. 2008) and older adults in the LS protocol for the first six blocks of training was used to explore an age effect. Finally, post hoc analyses using Tukey's studentized range (HSD) tests to compare block six (equivalent to 'late' training in the ES protocol) and block nine for the LS group were conducted on the one-way ANOVA that examined acquisition. This analysis was conducted to determine whether additional practice lead to further improvements in performance.

An acceptable significance level for all statistical tests was 0.05 unless otherwise noted and only those trials in which participants avoided taking a step were included. In total, 31/490 trials were omitted from the ES protocol and 21/1001 trials were omitted from the LS protocol.

5.4 RESULTS

5.4.1 Embedded Sequence (ES) Protocol

Although significant improvement in postural stability was observed with practice, older adults did not take advantage of the repeated sequence of perturbations to improve balance control. A main effect of block was observed for trunk tilt variability during the acquisition phase on day one (F(1.3,12.1)=10.474; p=0.004 (Greenhouse-Geisser); Fig 5.3a) but there were no differences between segment types (F(1,9)=0.923; p=0.362). COM phase during acquisition also showed a main effect of block (F(5,45)=37.99; p<0.001; Fig 5.3b) and no differences between segment types (F(1,9)=0.93; p=0.36). Finally, there were main effects of training block (F(5,45)=4.37; p=0.002) and segment type (F(1,9)=12.95; p=0.006) for COM gain however, the reductions in COM gain were minimal with a mean decrease of 4.6% (0.68 ± 0.04 to 0.65 ± 0.04) for the repeated segment and 3.6% (0.66 ± 0.05 to 0.64 ± 0.05) for the random segment (Fig. 5.3c).

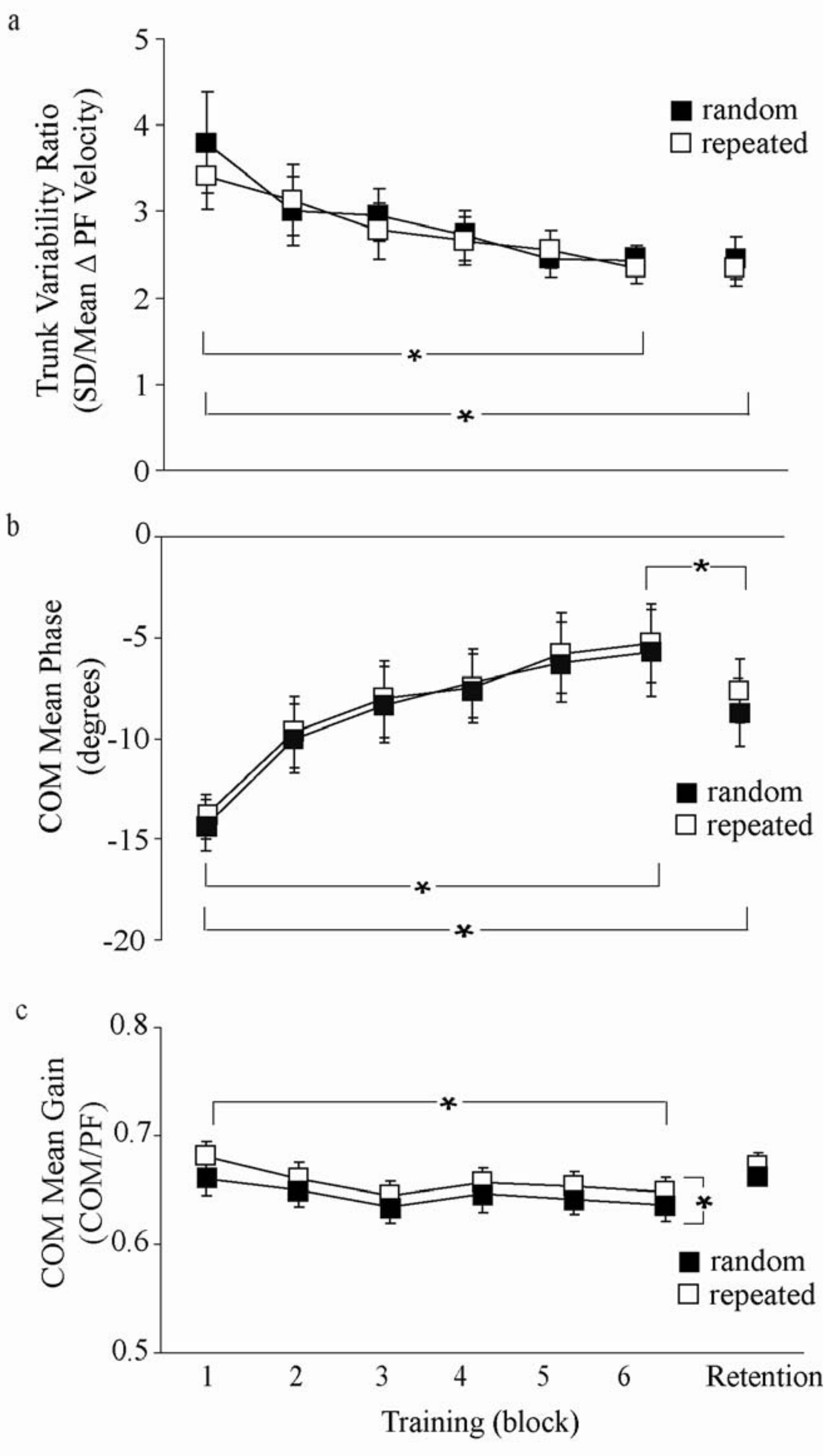
a
Trunk Variability Ratio (SD/Mean Δ PF Velocity)
5
4
3
2
1
0
■ random
□ repeated
*
*
b
COM Mean Phase (degrees)
0
-5
-10
-15
-20
*
■ random
□ repeated
*
*
c
COM Mean Gain (COM/PF)
0.8
0.7
0.6
0.5
*
*
■ random
□ repeated
1
2
3
4
5
6
Retention
Training (block)

Fig. 5.3: Group changes in a) trunk variability, b) COM phase, and c) COM gain for training and retention phases of the embedded sequence protocol. Repeated segment performance is denoted by *white* squares. Random segment performance is denoted by *black* squares. Error bars represent standard error of the mean. Asterisks indicate significance at $p<0.05$.

On day two, participants demonstrated some maintenance of the improvements achieved during the acquisition period on day one, providing evidence for longer-term learning. Trunk tilt variability showed a main effect of block ($F(1.1,10.3)=13.13$; $p=0.004$ (Greenhouse-Geisser)) but no effect of segment type ($F(1,9)=4.81$; $p=0.06$). Post hoc analysis indicated that the block effect was driven by a significant difference between the retention block (average 2.4 ± 0.71) and early training on day one (average 3.6 ± 1.54) and not between late training (average 2.4 ± 0.56) and the retention block. COM phase control also showed a main effect of block ($F(2,18)=39.05$; $p<0.001$) but no effect of segment type ($F(1,9)=3.52$; $p=0.093$) and similar to trunk tilt variability, post hoc analyses indicated that performance during the retention test (average -8.27 ± 4.91°) remained significantly different from behaviours during early training (average -14.09 ± 3.71°). Participants lost an average of 2.74 ± 3.37° phase between the last training block and the retention block, which represented 32% of the gains achieved during training on day one. Finally, participants demonstrated longer-term retention of the small COM gain improvements achieved during the acquisition period. Although COM gain showed a main effect of block ($F(2,18)=4.98$; $p=0.02$) and segment ($F(1,9)=12.21$; $p=0.01$), post hoc analyses revealed that COM gain during retention testing was not significantly different from late training for repeated ($p=0.10$) or random ($p=0.06$) segments.

5.4.2 Looped Sequence (LS) Protocol

Despite the change in protocol, participants trained with a single sequence in the LS protocol also engaged in non-specific learning as evidenced by retention or rapid re-acquisition of improvements observed during acquisition and by transfer task performances which did not differ significantly from retention block one. During acquisition, trunk tilt variability showed a main effect of block ($F(2,21)=8.76$; $p=0.002$ (Greenhouse-Geisser); Fig 5.4a). Post hoc analysis indicated however, that appreciable decreases did not occur continuously throughout training. Rather, participants showed significant improvements in trunk control from block one to block two ($p<0.05$) and no difference in the remaining blocks. Significant shifts in COM phase (Fig. 5.4b) and significant reductions in COM gain (Fig. 5.4c) were also observed during acquisition ($F(2.6,26.5)=20.13$; $p<0.0001$; Greenhouse-Geisser and $F(2.3,22.6)=7.23$; $p=0.003$; Greenhouse-Geisser respectively). For COM phase, group performance improved from a mean of -8.22 ± 2.47° in early training (block one) to -0.2 ± 3.68° in late training (block nine) while a mean decrease of 7.76% occurred for COM gain (from 0.70 ± 0.04 in early training to 0.65 ± 0.05 in late training).

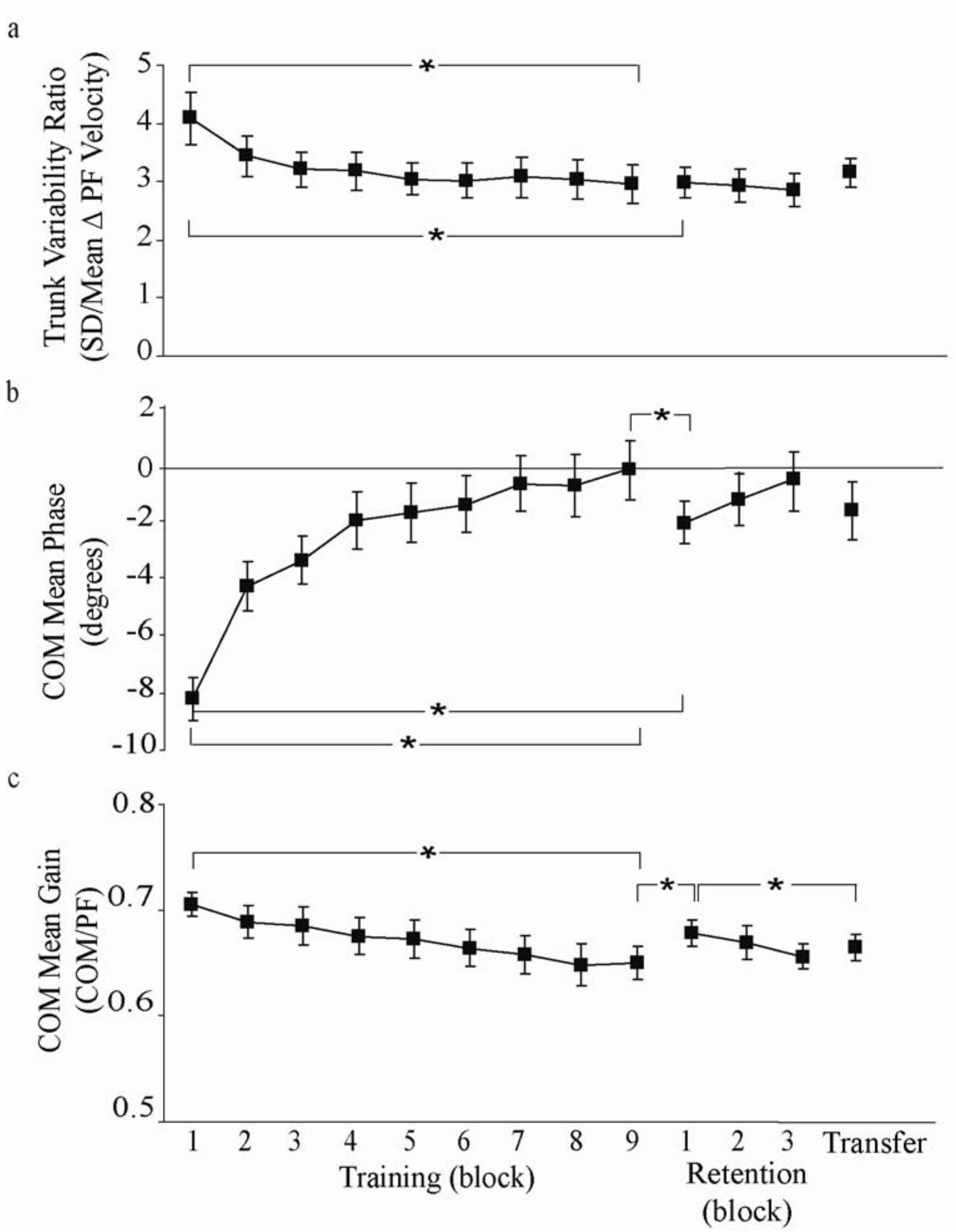

Fig. 5.4: Group changes in a) trunk variability, b) COM phase, and c) COM gain for training, retention, and transfer phases of the looped sequence protocol. Error bars represent standard error of the mean. Asterisks indicate significance at $p<0.05$.

Similar to results from the ES protocol, participants maintained improvements in trunk stability as evidenced by comparisons between the final block of practice on day one and the first retention block on day two (t(10)=-0.119; p=0.91). Significant losses in COM phase control (t(10)= 2.835; p=0.018) and COM gain control (t(10)=-4.571; p=0.001) did occur during the retention interval but performances remained significantly different from those observed during early training (t(10)=-6.13; p<0.0001 and t(10)=3.23; p=0.004 respectively). Further examination also indicated that later retention performances (block three) for both COM phase and COM gain were not significantly different from the final block of practice on day one ((t(10)=0.624; p=0.547) and (t(10)=-1.038; p=0.324)) indicating rapid relearning of COM gain and phase control upon re-exposure on day two.

To examine the specificity of learning, a comparison was made between the first retention block and the transfer block to determine whether participants exhibited poorer performance for the transfer block (i.e. lack of transfer). For all measures, performance was not disrupted by the presentation of a new perturbation sequence. Neither trunk tilt variability nor COM phase differed significantly from retention to transfer (t(10)=-1.55; p=0.16 and t(10)=-0.82; p=0.43 respectively). A significant difference was observed for COM gain but the change was in favour of a smaller gain during the transfer task (t(10)=3.31; p=0.008). Together, these findings demonstrate that performance improvements were not driven by sequence-specific learning.

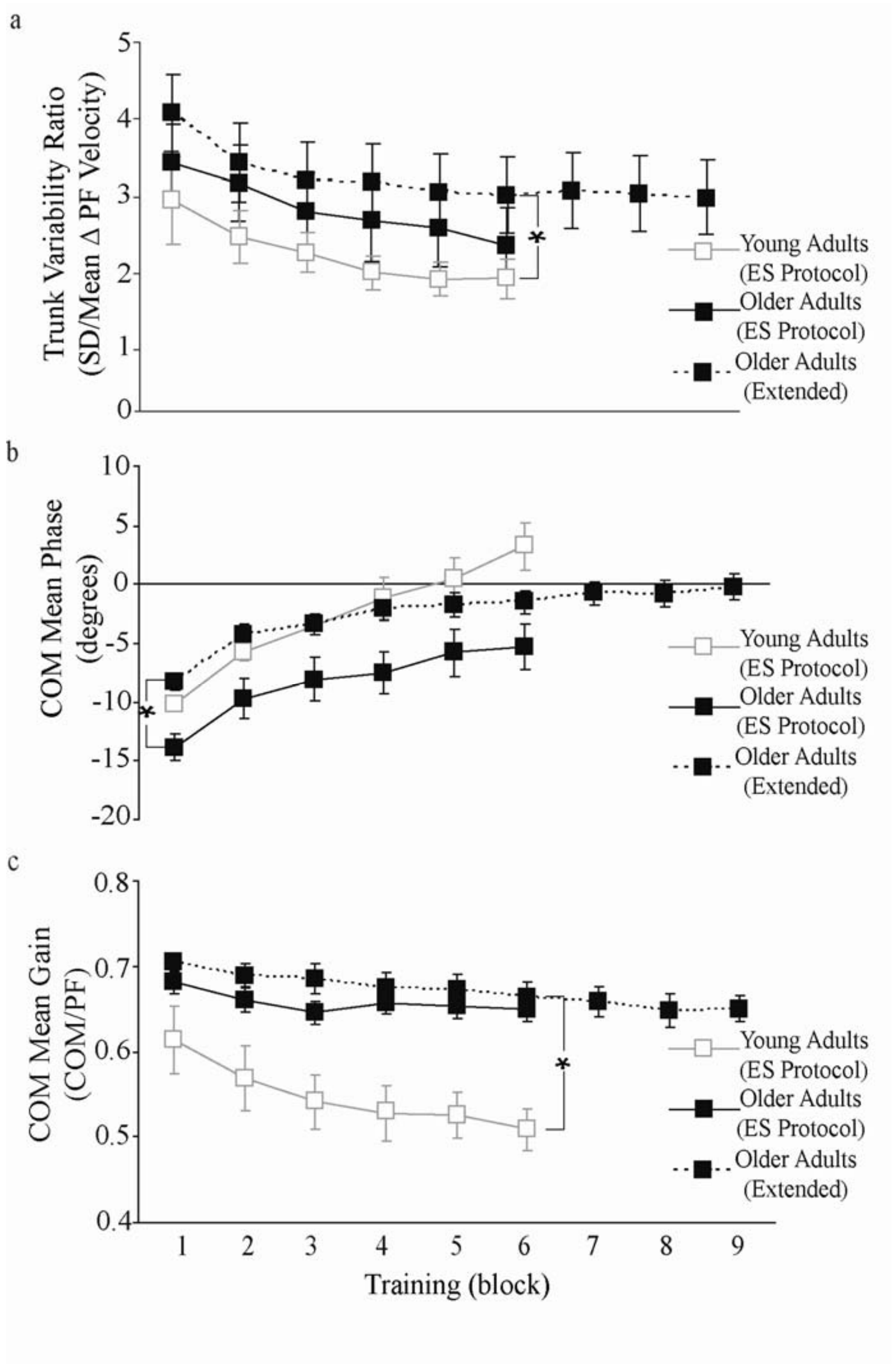

Fig. 5.5: Group changes in a) trunk variability, b) COM phase, and c) COM gain for the repeated segment of the embedded sequence protocol and the training sequence of the (extended) looped sequence protocol. Young adult performance in the embedded sequence protocol is denoted by the *grey* trace, older adult performance in the embedded

sequence protocol is denoted by the *black* trace and older adult performance in the looped sequence protocol is denoted by the *dashed* trace. Error bars represent standard error of the mean. Asterisks indicate significance at p<0.05. Young adult data taken from Van Ooteghem et. al. (2008)

Older adults given 50% more exposure to platform motion and four times more training with a repeated sequence in the LS protocol did not perform like young adults in the ES protocol (Fig. 5.5). Between-group comparisons for six blocks of training demonstrated that the ES and LS practice groups of older adults did not differ on measures of trunk tilt variability (F(1,19)=1.228; p=0.282) or COM gain (F(1,19); p=0.257) suggesting that the change in protocol did not affect these outcomes. COM phase lag however, was significantly less for older adults trained using the LS versus ES protocol (F(1,19)=7.326; p=0.014) and therefore, we did not analyze the effects of additional training for this variable. An age-comparison between young adults and older adults in the LS protocol revealed greater trunk tilt variability and COM gain for older adults following six blocks of training. Although a main effect of group existed for trunk tilt variability (F(1,21)=6.227; p=0.021), a main effect of training block also existed (F(1,1)=11.658; p=0.001; Greenhouse-Geisser), revealing that older adults improved trunk stability at a similar rate to young adults over six blocks of training. A comparison between block six and block nine of the LS protocol however, revealed that older adults did not demonstrate additional improvements in trunk tilt variability with added practice (p>0.05). For COM gain, an interaction between age and training block revealed that reductions in COM gain occurred at a slower rate for older adults (F(2,42)=3.544; p=0.04; Greenhouse-Geisser). Again, post hoc analyses revealed that additional training did not lead to further reductions in COM gain for this group ($p > 0.05$).

5.5 DISCUSSION

In both protocols examined here, older adults demonstrated the ability to learn adaptive postural responses to continuous, variable amplitude platform motion and, similar to the young adults in Van Ooteghem et al. (2008), performance improvements were not specific to the temporal relationship between perturbation amplitudes. Learning was demonstrated by maintenance of postural improvements across days of testing or in cases where performance declines occurred during the retention interval, by the ability to regain the previously acquired levels of proficiency with less exposure. Such rapid improvements during retention testing have been attributed to CNS priming for updates to the internal representation of stability (Pavol et al. 2002). Evidence for generalized postural motor learning suggests that training-related improvements in balance control could transfer to similar balance tasks.

In the ES protocol, trunk tilt variability was reduced similarly with practice for a repeated sequence versus randomly presented sequence of surface oscillations. There were also no differences in performance between repeated and random segments during retention testing, as would be seen if more effective learning had occurred for the repeated segment. In the LS protocol, non-specific learning was demonstrated by an ability to maintain retention test performance levels when presented with a new perturbation sequence in the transfer task. The lack of sequence-specific learning demonstrates that practice-related improvements in posture control were not due to a CNS ability to predict with cognitive anticipation, what event would occur next, despite the benefits to stability that could have arisen from exploiting perturbation amplitude regularities embedded in the trials.

Previously, we proposed that young participants could achieve the task goal of maintaining balance by developing an internal plan using other regulatory features or rules of the task, including the constant frequency or amplitude boundaries of platform motion (Van Ooteghem et al. 2008). This internal plan hypothesis could suggest that the nervous system is storing newly acquired knowledge about how to control balance under the current conditions and that retention demonstrates retrieval of this knowledge. The suggestion that upright stance is regulated by a limited repertoire of responses however, (Horak and Nashner 1986) might suggest that postural motor learning of a novel balance task defines the CNS process of determining which responses apply in the current situation and then refining those responses. A key element of this hypothesis is the concept of adaptive central set used to describe central predictive mechanisms based on expectation or experience with a postural task which has typically been illustrated using discrete perturbations (Horak et al. 1989; Horak et al. 1994). Here, postural motor learning would reflect longer-term retention of central set which, under the current continuous perturbation conditions, might be superimposed on feedback mechanisms. Regardless of the mechanism, evidence for general postural motor learning in healthy older adults demonstrates that the nature of learning does not change with age despite age-related differences in control strategy and the possibility of additional challenge or threat to stability due to sensorimotor decline.

Previous studies exploring the capacity of older adults to learn sequences have predominantly used upper limb tasks such as the serial reaction time (SRT) task, and have reported mixed findings regarding a preserved ability for older adults to engage in sequence learning (e.g. Howard and Howard 1997; Daselaar et al. 2003; Smith et al. 2005). Unlike the current study, these experiments did not include an element of personal risk which might make it disadvantageous to engage in sequence-specific learning, or use externally-evoked or paced stimuli that could make it impossible to do so. In Van Ooteghem et al. (2008), we proposed that specific postural motor learning could overload the processing capacity of the CNS and impair its ability to respond quickly enough to maintain balance. Learned responses with high specificity could also create added risk if they are inappropriate for transfer to a new perturbation environment. Both of these proposals suggest that sequence-specific learning could represent a less desirable type of learning for balance control. It should be noted that our ability to draw definitive conclusions about non-specific postural motor learning remains limited by the fact that we have not tested young adults using the LS protocol. Thus, it remains possible that an age effect contributed to the lack of sequence-specific learning observed in this protocol.

Although our results demonstrate that non-specific learning occurred in older adults, it remains possible that participants learned stimuli of particular relevance interspersed throughout the sequence (e.g. approximate number and/or general location of large excursions). Indeed, some participants developed declarative knowledge of some elements in the training sequence describing for example, that they “knew where the short jerks were and anticipated them”, or that they “felt a short oscillation before large, then short again”. Consistent with this possibility, a sequence-learning study with an arm reaching task demonstrated that response time decreases with training were attributable to general decreases in movement time with anticipatory shifts in onset times for only a few of the targets (less than 5%) in the sequence (Moisello et al. 2009). Developing responses based on a partial set of relevant stimuli (e.g. boundaries or large velocity changes) would enable participants to establish an appropriate gain to withstand the most disruptive perturbations while achieving some cost minimization with training (i.e. information processing, energy expenditure).

A secondary, clinically-relevant goal of this study was to examine whether additional practice for older adults would enable them to perform like young adults. In Van Ooteghem et al. (2009; in press), older adults showed significant improvements in postural stability with training but their performance remained significantly different from young adults. Since significant differences occurred in early training but did not increase with practice (i.e. there was no age x practice interaction), the differences could not be attributed to deficits in learning. As such, we were interested to know whether older adults could achieve performances comparable to young adults with additional practice. In the current study, participants in the LS protocol not only received 50% greater exposure to variable amplitude platform motion than both young adults (Van Ooteghem et al. 2008) and older adults in the ES protocol, their exposure was also restricted to a single training sequence. Under these conditions, performance improvements did not differ between the two groups of older adults for trunk tilt variability or COM gain. The COM phase lock achieved by older adults in the LS group differed from older adults trained using the ES protocol. Since these group differences existed as early as block one, it is possible that the two groups of older adults were inherently different or that the singular training sequence used in the LS protocol provided older participants with a performance advantage (e.g. less contextual interference) that enabled them to achieve greater temporal shifts in COM control. Comparisons between young adults and older adults trained using the LS protocol for six blocks of training showed significantly less trunk tilt variability and COM gain for young adults. These findings were not unexpected given that older adults started training with a performance disadvantage. The older adults however, showed no further improvements with additional practice and as a result, their performances remained significantly different from the young adults who underwent six blocks of training. Two possibilities could explain the lack of significant improvement with additional practice including a) that the rate of improvement was slowing or b) that participants were limited by transient performance effects such as fatigue, lack of motivation or difficulty maintaining focus on the task.

In summary, older adults trained using both the ES and LS protocols demonstrated generalized postural motor learning. To eliminate the possibility that an age effect limited sequence-learning under conditions of a single training sequence, we must test young adults using the LS protocol. Regardless of learning type, an important next step is to identify which cues are deemed critical for postural motor learning. Given this information, we can aim to improve balance performance by facilitating the search for these critical features.

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Chapter 6

GENERAL DISCUSSION

6.1 SIGNIFICANCE OF RESEARCH FINDINGS

In this thesis, we aimed to examine postural motor learning and the nature of improvements in compensatory posture control among healthy young and older adults repeatedly exposed to continuous surface motion via a translating platform. Borrowing from implicit sequence learning paradigms, we developed two experimental protocols using constant frequency and variable amplitude platform motion. By varying the perturbation amplitude during continuous platform motion, we sought to extend previous research findings by 1) examining capacity for adaptive postural *regulation* rather than transient postural *recovery* and 2) exposing participants to less predictable perturbations than had been studied to date.

Previous research examining compensatory posture control has predominantly explored CNS mechanisms for transient postural recovery which differs from the postural regulation necessary to combat continuous disruptions to stability (Diener et al. 1988; Maki and Ostrovski 1993; Nardone et al. 2000). In the former circumstance, balance is maintained by counteracting the effects of the perturbation. Under the latter circumstances, the continuous nature of the perturbation can be exploited. Studies using a periodically translating platform with constant amplitude-frequency motion have illustrated that healthy young participants exploit the inertia of the trunk and head while letting the legs go in a strategy described as a non-rigid, non-inverted pendulum (Corna et al. 1999). Continuous perturbation studies have provided insight into the capability of the posture control system to use both feedforward and feedback mechanisms for continuous postural regulation (Dietz et al. 1993). It is limited however, in drawing conclusions about postural regulation under conditions with limited predictability.

Although we know from observation of everyday tasks, that it is possible to produce relatively permanent changes in compensatory balance control with practice, empirical evidence has predominantly focused on short-term adaptations rather than the longer-term improvements necessary to demonstrate learning. The potential for longer-term changes in postural regulation is great given the results of motor learning research which show proficiency for retention in continuous tasks (Schmidt and Lee 2005, p.439). The perturbations used in this thesis were designed to mimic less predictable, continuous environmental challenges that occur in daily life such as walking; a cyclical task in which imposing perturbations are often of unknown magnitude and tasks such as standing on a boat or riding the subway which can be unpredictable in both magnitude and timing. The challenge imposed on the CNS when perturbation events lack predictability is that it has limited opportunity to utilize anticipatory control. As a result, it must rely on integrating sensory information about the disturbance in a timely manner to generate an appropriate postural response.

With practice in an unpredictable environment, adaptive postural recovery has been characterized by a tendency to develop a default neuromuscular response that differs based on the degree of unpredictability and the risk to stability (Horak et al. 1989; Beckley et al. 1991). Prior to this thesis, no studies had described adaptive postural regulation in response to continuous perturbations with limited predictability or investigated the nature of learning for compensatory posture control. These gaps in the literature together with varied support for adaptive balance control in older adults (Woollacott et al. 1986; Hocherman et al. 1988; Stelmach et al. 1989; Bugnariu and Sveistrup 2006) provided our rationale for exploring the effects of age on adaptive postural regulation. We also reasoned that understanding the potential for longer-term changes in balance behaviour in this population was particularly important given the incidence of postural instability in older adults and the associated need to train balance control. Applying key principles of motor learning to our experimental design including retention intervals (all studies) and a transfer task (study three) enabled us to draw conclusions about the permanency and the generalizability of the observed changes.

The main objectives of this thesis were to advance our understanding of compensatory posture control and postural motor learning. More specifically, we aimed to understand 1) what changes in the motor organization of compensatory posture control occur as a performer becomes more familiar with a novel balance task requiring continuous postural regulation, 2) whether these changes reflect learning, 3) whether learning is general or specific, and 4) if aging affects postural motor learning or the strategy used to maintain balance in this environment. We also aimed to validate our embedded sequence protocol by comparing outcomes to a second, modified protocol in older adults. From a theoretical perspective, we've gained important insight into practice-related changes in postural regulation in response to a continuous perturbation with limited predictability in both young and older adults and have identified age-related differences in the adaptive response.

Of clinical importance, we have demonstrated retention of practice-related improvements in postural regulation and developed new understanding about the nature of learning which governs these improvements. Moving forward, these outcomes will provide the basis for innovative and valuable research related to postural motor learning, some of which will be considered in greater detail later in this discussion.

6.2 LIMITATIONS

Prior to discussing the outcomes of the studies in this thesis, it is important to note that the results have been described in the context of the following assumptions and limitations. To begin, we assumed that variable-amplitude platform motion served as a novel balance task, reducing the contributions of previous postural motor learning to the acquisition of skill in the current task. It remains however, that balance control is a highly learned skill and that we cannot discount the contributions of previous postural motor learning to the acquisition of skill in the current task. Further, we are limited in our ability to characterize the expertise that participants might have possessed prior to their participation in our studies or to understand the influence of this experience on their performance. We did however, gather information regarding their involvement in physical activities and referred to this data in our interpretation of individual results, particularly if a participant’s performance deviated significantly from the group average.

From a methodological perspective, it is necessary to acknowledge several decisions which were made in establishing the protocols that could have bearing on our interpretation of the results. First, this thesis describes postural motor learning in a constant frequency environment. In our effort to extend previous work on adaptive postural regulation which has predominantly held both amplitude and frequency constant, we reasoned that a necessary next step was to investigate variability in one of these domains. We chose to vary amplitude based on evidence from discrete perturbation studies which demonstrates that variable amplitude perturbations engage predictive control based on prior experience (Horak et al. 1989) thus creating an environment which might benefit from learning the sequence of perturbations. We do recognize that coupling variable amplitude with constant frequency also created a variable velocity environment which could have benefitted from CNS's ability to encode stimulus velocity via peripheral feedback from velocity-sensitive muscles spindles (Horak et al. 1989).

Our decision to vary amplitude but not frequency together with mechanical constraints in platform motion (i.e. each excursion passed through a predictable mid-travel point) created some environmental regularity and therefore, impacts the ecological validity of our findings. While we must be cautious in drawing conclusions about postural motor learning in real-world activities which are even less predictable, exposing participants to practice in a semi-predictable perturbation environment afforded us an opportunity to examine whether the CNS developed learned responses based on specific perturbation characteristics (i.e. sequence) or broader regulatory features in the environment (e.g. constant frequency).

The second point worth noting is that all studies in this thesis utilized a platform frequency of 0.5 Hz. Our rationale for choosing this frequency was based on previous work examining the effect of platform dynamics on postural coordination. These studies demonstrated that a 0.5 Hz translation frequency is not associated with a fixed, characteristic postural coordination pattern (Buchanan and Horak 2001; Ko et al. 2001; Schieppati et al. 2002). It was reasoned therefore, that this frequency would provide the greatest opportunity for the evolution of balance control with extended practice. The results of study one support that a shift in the complexity of the postural strategy does occur with extended practice at this frequency in young, healthy adults. However, since the rigid control strategy that was adopted by older participants is typically observed in response to smaller amplitude and/or lower frequency perturbations, it is possible that the 0.5 Hz perturbation presented a particularly difficult challenge for older adults either because it is not associated with a characteristic postural coordination pattern or because the frequency was too great. Exposure to constant amplitude-frequency platform oscillations at 0.6 Hz did not lead to differences in behaviour between young and older adults (Nardone et. al., 2000) however; the platform dynamics in the current experimental task are presumably even more challenging.

Thirdly, participants in the current studies were asked to maintain balance with their arms crossed and feet in place if possible. Although these instructions placed limitations on the contributions of the arms to the balance response and could have forced some participants to use a non-preferred control strategy (i.e. feet-in-place rather than change-in-support), we reasoned that crossed arms would increase task challenge for young adults and that feet-in-place responses would eliminate the risk associated with trying to re-establish foot placement on the continuously moving platform. To adjust for the added challenge in older adults, the range of platform displacement was reduced from ± 15 cm to the largest amplitude that the participant could withstand without taking a step. Scaling was only necessary for two older adults.

Finally, it is important to consider that our examination of aging was restricted to healthy older adults, free of disorders that could affect postural control. Based on clinical assessment, 81% of the participants showed normal somatosensory function and 71% were able to maintain balance with unreliable surface information in the absence of vision (i.e. standing on foam with eyes closed) further demonstrating sensory system integrity. In addition, of the 16 participants who completed the Physical Activity Scale for the Elderly (PASE) (Washburn et al. 1993), 75% reported above average activity levels for their age and gender (Appendix B).

6.3 SUMMARY OF PRACTICE-RELATED CHANGES IN POSTURE CONTROL: YOUNG ADULTS

With repeated exposure to the variable-amplitude balance task, 58% of young adults showed significant improvements in the spatial control of their whole body COM as measured by COM gain, while 100% improved their temporal control (COM phase). COM gain values less than 1.0 indicated that participants did not aim to follow platform motion to maintain balance. It should be noted that three of the participants who did not show significant decreases in gain (i.e. zero slope) also had the smallest gain in early training indicating a possible performance floor effect for these participants. Combined with joint angle-platform correlations which revealed negative ankle correlations that became stronger and hip correlations that became positive with practice, we determined that participants tended toward stabilizing their COM in space by increasing lower limb joint motion. This "gravity-fixed" behaviour was further characterized by the results of study two which revealed improved trunk stability with practice as measured by decreases in the mean and standard deviation of participants' trunk angle relative to gravitational vertical (termed trunk tilt and tilt variability). COM-platform phase lock (or lead) in late training for a majority of participants (75%) demonstrated an ability to achieve predictive control of their COM motion. All of the observed changes in young adults were maintained across days of testing providing evidence for longer-term changes in balance behaviour.

6.4 SUMMARY OF PRACTICE-RELATED CHANGES IN POSTURE CONTROL: OLDER ADULTS

Older adults exposed to the variable-amplitude perturbation exhibited larger COM gains than younger participants, particularly for forward platform displacements. Despite the resulting potential for this group to show greater practice-related improvements, only one older adult showed appreciable decreases in COM gain. All participants improved temporal control of their COM but unlike young adults, a majority (70%) did not achieve predictive control when exposed to equal amounts of training. Since comparable rates of improvement in COM phase were observed for young versus older adults in study two however, the group differences observed in late training were not attributed to impaired learning. Rather, we concluded that COM phase lock could not be achieved by the older adults who started training with a significantly larger COM phase lag. This explanation was further supported by the results of study three which showed that with additional practice, older adults did eventually achieve predictive COM control. Based on COM gain results and lower limb data which showed less ankle angle variability and greater knee flexion throughout training, we determined that older adults used a rigid, flexed knee posture to stabilize their COM with respect to the platform; a behaviour we identified as "platform-fixed". A stable trunk with respect to the platform has also been used to describe healthy older adults responding to predictable surface oscillations (10 cm peak-to-peak at 0.2 Hz) with eyes closed, differing from the trunk locked in space strategy they used when vision was available (De Nunzio et al. 2007).

Further investigation of individual participants in the older adult group in study two revealed that three participants did adopt lower limb motions comparable to young adults however, the remaining participants either showed no change in lower limb motion (two participants) or changes limited to adjustments in segment alignment (five participants). The tendency for older adults to persist with platform-fixed behaviour did not restrict older adults in study two or study three from achieving comparable improvements in trunk control as defined by trunk tilt variability. Finally, unlike young adults who demonstrated maintenance of all observed improvements during the retention interval, older participants maintained improvements in trunk control but exhibited significant losses in COM phase control (average loss of 2.74 ± 3.37°). This loss however, was coupled with a rapid re-acquisition for participants in study three suggesting some priming effects in the CNS. Given that participants retained a more consistent, stable posture of the trunk segment and that losses in COM phase shift were modest and rapidly re-acquired following the retention interval, we conclude that healthy older adults maintain capacity for longer-term adaptive postural regulation.

6.5 GENERALIZABILITY OF POSTURAL MOTOR LEARNING

In the studies of this thesis, we adapted two methodologies designed to explore implicit sequence learning with the purpose of examining whether postural motor learning under continuous perturbation conditions, is general or specific. Similar improvements for a repeated pattern of perturbations versus random platform motion suggest that the CNS develops generalized responses to improve balance control. Further support for generalized learning was obtained by varying the sequence-learning protocol and exposing older adults to a looped training sequence followed by a transfer task. In study one, we hypothesized that sequence-specific learning would not occur for compensatory balance control. We argued that for some motor tasks, movement sequencing is vital to task success but that CNS flexibility (supported by generalized postural motor learning) is needed to respond to the infinite number of challenges to our stability, and better represents the highly practiced skill of balance control. This argument suggests that the capability to sequence learn could rest on the nature of the motor task and whether or not, it is best to do so. Indeed, other studies have also reported generalized learning in their investigations of sequence learning (Marsolek and Field 1999; van der Graaf et al. 2004). This task-dependent nature of sequence-learning could explain the difference in outcome between our study one which showed generalized learning and Shea et al. (2001) who showed sequence learning. It should also be noted however, that it remains possible sequence-specific learning would not have been reported in the Shea et al. study if outcome measures had focused on COM or joint coordination measures rather than a gestalt measure of performance like RMS error. In study three, we determined that older adults trained using either the embedded sequence (ES) or looped sequence (LS) protocol showed generalized improvements in stability with practice and thus, that the embedded sequence protocol did not mask sequence learning. Given that we did not test young adults using the LS protocol, it remains possible that young participants would demonstrate sequence-specific learning. We hypothesize however, that age does not influence the nature of postural motor learning for continuous balance tasks and that generalized learning would still occur in this group.

Although we are currently limited in fully describing what features of the task were learned, the predictive COM control observed in young (ES) and older (LS) adults suggests that one learned element was the constant frequency of platform motion. In this thesis, two possible mechanisms for such generalized learning were discussed. The first possibility was that the CNS developed new knowledge about how to control balance under these novel task conditions such that participants learned to cognitively anticipate perturbations to stability (e.g. by mapping frequency cues to motor commands). In this case, early learning might rely more heavily on peripheral feedback control while later learning would shift toward a combination of feedback control plus an internal plan (Philip et al. 2008). The development of such predictive mechanisms would be particularly well-suited to voluntary postural tasks such as the stabilometer task used by Shea et al. (2001) in which the CNS could use the knowledge to compare predicted versus actual movement outcomes. Recent reviews however, have also provided support for cortical contributions to externally-evoked postural responses (Maki and McIlroy, 2007; Jacobs and Horak 2007). Therefore it is possible that cognitive anticipation of perturbation events might occur with the variable-amplitude balance task.

A second possibility was that learning reflected a CNS process of selecting and refining appropriate postural responses from a pre-existing repertoire of postural movement patterns (Horak and Nashner 1986). This possibility is strongly influenced by the concept of central set, used to describe a CNS process of preparing sensory and motor systems for anticipated perturbations (Diener et al. 1988; Horak et al. 1989). Differentiation of these two possibilities has also been identified in developmental models of posture control in which the first step of development involves building a repertoire of postural strategies while later in development, children learn to select the most appropriate strategy (Adolph 2002; Assaiante et al. 2005).

For discrete perturbations, the central set effect is most prominent in the early component of the postural response, before the influence of peripheral sensory information. In the continuous perturbation conditions of this thesis, it is possible that a postural set effect is used in combination with feedback mechanisms which provide information about the velocity, amplitude, and direction of the perturbations. Horak et. al. (1989) showed directionally-specific set effects in response to unexpected amplitude such that when the amplitude was larger than expected, the response was underestimated and vice versa. Similar effects were not observed for unexpected velocity (which could be detected by peripheral feedback from muscle spindles or perhaps explained by a lower-level process of habituation). The abovementioned studies manipulated amplitude and velocity separately to examine central set and differed from the perturbation conditions of this thesis in which both amplitude and velocity were varied. Given the amplitude/velocity results of Horak et. al. (1989) and the continuous nature of the perturbations in the studies of this thesis, we argue for the contributions of both central and peripheral mechanisms, weighted differently throughout training. If practice leads to a shift in control from afferent mechanisms to central set, we might expect to see a breakdown in the relationship between the perturbation stimulus and neuromuscular responses (e.g. EMG activity will shift away from being scaled to perturbation amplitude). It is also possible that we would observe changes in muscle activation patterns (either gradual or discrete) associated with a practice-related change in control strategy. Possible insights into the neural organization of postural motor learning via EMG analyses will be discussed in greater detail in the Future Directions section of this Discussion.

6.6 AGE AND LONGER-TERM CHANGES IN POSTURAL REGULATION

Studies examining postural motor learning in healthy older adults exposed to repeated slip perturbations report an age-independent rate of decline in fall incidence and success upon re-exposure as measured by fewer falls and more rapid reacquisition of balance behaviour (Pai et al. 2003; Pavol et al. 2004; Bhatt and Pai 2005). In the studies of this thesis, we argue that the capacity for longer-term changes in postural *regulation* among healthy older adults compares to reports of practice-related improvements in postural recovery via slip training. Our results reveal comparable rates of improvement in trunk control between young adults and older adults exposed to the embedded sequence (ES) and looped sequence (LS) protocols as well as comparable rates of improvement in temporal control of COM between young adults and older adults exposed to the ES protocol (it should be noted that COM gain improvements were minimal for older adults). Further, upon re-exposure, young and older adults exhibited similar success for maintenance of improvements in trunk control. Although older adults did not maintain performance levels for COM phase, it does appear that the CNS was primed to more rapidly relearn COM control as evidenced in study three, by a re-acquisition of late-training performance levels within three retention blocks.

Similar *rates* of improvement in trunk control between young and older adults despite differences in postural behaviours might have been due in part, to the changes in lower limb kinematics and their contributions to improvements in temporal control of COM motion such that a decrease in COM phase lag reduced the need for corrective movements of the trunk. This explanation alone however, cannot fully account for the changes in trunk control since greater COM phase lag during retention testing did not translate into significant increases in trunk tilt variability. Another possibility which was not examined in this thesis is that practice-related changes in lower limb and trunk muscle activity lead to more coordinative muscle control defined by decreased co-activation and improvements in functionally relevant patterns of muscle activation (Grabiner and Enoka 1995, p 70). Given that overall whole-body postures differed between young and older adults, it is probable that different patterns of muscle activation were refined to achieve comparable rates of improvement in trunk stability. The link between whole-body posture and muscle activation was also addressed by Hocherman et al. (1988), who postulated that the dominant use of a rigid movement strategy in older adults on a continuously moving platform results from a need for a strategy that does not depend on accurate timing of muscle activation to stabilize the trunk.

Age-related differences in COM gain and COM phase control might be explained in part, by the persistence of a rigid, flexed knee posture in older adults and could reflect older adults' attempts to refine a preferred postural behaviour rather than undergo a shift in behaviour as was observed in young adults. Earlier discussion of age-effects which might contribute to the observed differences in postural behaviours between young and older adults included limitations in joint mobility or sensory system function, breakdown in timing of muscle activation, threat of falling, and preference for safe margin of stability rather than improved efficiency or optimization (Van Ooteghem et al. 2009, in press). These limitations could lead to a loss of ability to re-organize a strategy for control. Because older participants persisted with a platform-fixed behaviour, we suggest that aging results in some loss of the CNS's ability to develop an optimal plan-for–action which would exploit the reciprocal motion of the platform. Comparable conclusions have been drawn by Vernazza-Martin et al. (2008) who suggest that the effect of age on the execution of voluntary movements is expressed as changes in the kinematic strategy which reflect "over-control" rather than deterioration of the coordination between posture and movement. In their study, young and older participants showed similar outcomes in global COM control but different control strategies in response to a forward bend at the trunk.

The work on repeated slip exposures suggests that feedforward control serves to improve stability by counteracting the expected destabilizing effect of the perturbation and minimizing reliance on reactive responses (Pavol and Pai 2002). Improvements in temporal control of the COM were observed for both young and older adults in the current studies however, predictive control (defined as less than 2 degrees phase lag) was not achieved by all participants (75% and 43% for the repeated segment in young and older adults respectively). Feedforward control relies on the ability of the CNS to gather information about perturbation characteristics and body orientation. If age-related anatomical and physiological constraints diminish the quality of this information and subsequently the higher-level plan for action, the CNS might rely on feedback mechanisms instead.

Given that continuous tasks are rich in movement-produced feedback, participants who relied on sensory-driven control could be successful in maintaining balance even without feedforward control. The ability for many older adults (64%) in the LS protocol to achieve predictive control of COM in six blocks of training differed from the small percentage of participants in the ES protocol (20%) and raises the possibility that an environment with less "noise" enabled older adults to gather more robust information about the temporal regularity in the environment. This benefit however, may be limited by the possibility that training in an environment with restricted variability (LS vs ES protocols) could lead to a response strategy that is too highly specialized (Gentile 1972).

6.7 HOW DO FINDINGS INFORM BALANCE TRAINING FOR OLDER ADULTS?

The results of the studies in this thesis expand our understanding of the nature of postural motor learning, providing basic learning principles for balance training in older adults. In our studies, older adults demonstrated training-related improvements in balance control and some degree of maintenance following the retention interval. These findings provide promising results for the positive effects of balance training in this population. For a majority of participants, performance improvements reflected refinement of a preferred posture control strategy rather than a shift from one control strategy to another. This difference in control strategy between young and older adults did not disadvantage older adults when performance was measured via improvements in trunk control. Given these outcomes, it remains possible that training older adults to use a different ('non-preferred') control strategy based on predicted improvement in margin of stability, efficiency, etc. could actually lead to deterioration in performance (at least in the short-term) and increased risk of instability. Further, since it remains possible that the difference in control strategy reflects functional compensation for age-related decline in sensory and motor function rather than an inability to develop a plan for action, it would also be worthwhile to explore the benefit of sensorimotor rehabilitation on postural motor learning.

6.8 FUTURE DIRECTIONS

The results of this thesis form the basis for several research projects and ideas which could further enhance our present knowledge of postural motor learning. In the context of the methodologies used in this thesis, future research will be necessary to answer the following questions: 1) did the 0.5 Hz frequency limit practice-related changes in control strategy in older adults? 2) would young adults demonstrate sequence learning if exposed to the looped sequence protocol? 3) would sequence learning occur for a repeated sequence of discrete perturbations? 4) are the observed behaviours attributable to perturbation regularities (e.g. constant frequency)? 5) how would participants respond to a single, unexpected amplitude injected into a continuous perturbation? 6) how generalized is learning? (current protocols use random sequences that are highly similar to the training sequence so limited response generalization could lead to successful performance). The outcomes of these investigations would serve to rule out methodological explanations for the findings in this thesis and deepen our understanding of the nature of postural motor learning. Most importantly, questions 4 through 6 would advance our efforts to mimic perturbations in the environment by creating uncertainty in the magnitude *and* timing of perturbations to stability.

In the immediate future, we are interested in characterizing longer-term changes in trunk and lower limb muscle activity with training in older adults in an effort to better understand the neural mechanisms of adaptive postural regulation. Currently, it remains possible that training-related changes in muscle activation patterns existed in this group despite limited changes in lower limb kinematics. Such evidence would provide a more complete picture of CNS flexibility in healthy, older adults; providing insight into the extent to which muscle responses are pre-planned and to what extent they are tuned by sensory feedback.

Preliminary analyses of tibialis anterior (TA) and medial gastrocnemius (mGAS) muscle activity (as described in Appendix C) suggest that the efficiency of dorsiflexor and plantarflexor responses improved with practice as defined by decreases in iEMG for both forward and backward half-cycles of platform motion (Fig. 6.1 and Appendix D). A majority of participants maintained reduced levels of muscle activity following the retention interval (Appendix D).

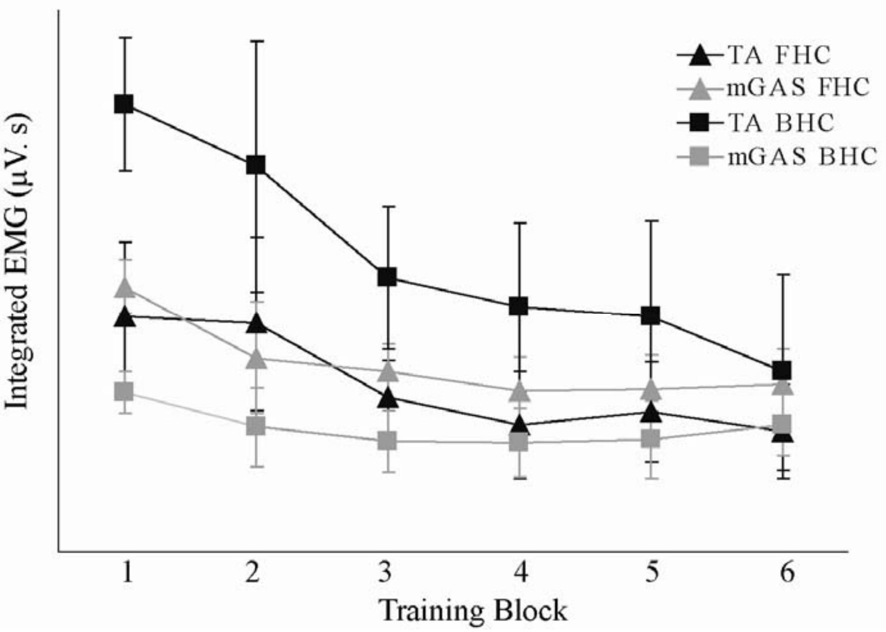

Fig. 6.1: Representative trace of magnitude of iEMG for TA (*black* trace) and mGAS (*grey* trace) during forward half-cycle (FHC) and backward half-cycle (BHC) of platform motion across 6 training blocks.

A representative trace of TA and mGAS illustrates that the change in muscle activity with training does not appear to include a shift in onset latency of EMG bursts (Fig. 6.2). Evidence for reduced amplitudes with consistent latencies is similar to that reported for repeated exposure to discrete perturbations by Horak et al. (1989). Inspection of TA and mGAS burst activity also reveals that burst activity cannot be attributed solely to stretch reflex responses as it also occurs during muscle shortening (for e.g. in mGAS when the platform is moving forward). That said, examination of response scaling to perturbation magnitude reveals that for some participants, increases in mGAS response magnitude were positively correlated to increases in perturbation amplitude during backward platform motion suggesting a functional requirement of this muscle rather than a pre-programmed response (Appendix E). For TA and mGAS (forward platform motion), participants exhibited poor correlation with platform amplitude which could suggest non-linear scaling of muscle responses (Maki and Ostrovski 1993), amplitude-dependent changes in postural strategy within the trial, or perhaps CNS development of a centrally-programmed, default postural response to unpredictable perturbation conditions (Horak et al. 1989). The latter possibility might best be demonstrated by three participants who showed a training-related decrease in correlation between mGAS iEMG and amplitude of backward platform motion.

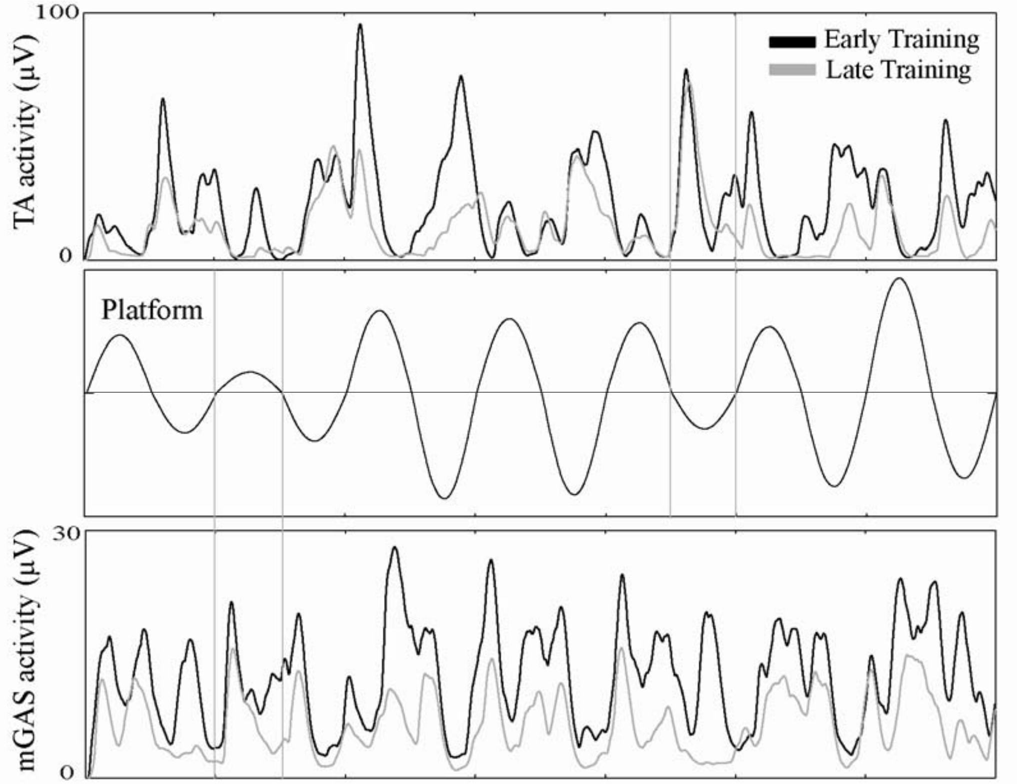

Fig. 6.2: Representative traces for TA (top) and mGAS (bottom) activity during early (block 1: *black* trace) and late (block 6: *grey* trace) training in an older adult participant. Middle plot illustrates platform motion (range: ± 15 cm).

Future analysis will need to confirm whether participants adopted a forward lean with repeated exposure to variable amplitude platform motion similar to reports for participants exposed to constant amplitude and velocity oscillations of the support surface (Hocherman et al. 1988; Dietz et al. 1993; Maki and Ostrovski 1993). Such training-related changes reflect pre-programmed positioning of the COM. Finally, we must investigate muscle responses occurring at other joints to more fully understand the control mechanisms underlying the observed responses.

Finally, in the longer term we are also interested in examining the capacity for training-related improvements in postural regulation among populations who are most vulnerable to balance loss (e.g. patients with Parkinson's disease (PD)). Our decision to examine postural motor learning in this group is further strengthened by the body of evidence which supports the role of the basal ganglia in motor learning (Doyon et al. 2009; Solivieri et al. 1997). The questions of interest are 1) whether learning in this group is general or specific and 2) whether learning is impaired as measured by rate and maintenance of performance improvements on the variable-amplitude balance task, relative to healthy, age-matched controls. Examining whether PD impairs the ability to learn the variable amplitude balance task would enable us to gain further insight into the neural mechanisms of postural motor learning. In the studies of this thesis, both young and healthy older adults engaged in non-specific learning of the postural task. It remains possible however, that the nature of learning would differ in patients with Parkinson's disease (PD). Previous research has shown varied support for preserved procedural learning in patients with PD including those studies which have explored implicit sequence learning in this population (Pascual-Leone et al. 1993; Krebs et al. 2001; Sarazin et al. 2002; Siegart et al. 2006). As hypothesized previously in this discussion, implicit sequence learning may be task specific and perhaps a less desirable type of learning for balance control. As such, it is presently unknown how previously reported deficits in implicit sequence learning in PD can inform our understanding of postural motor learning in these patients.

Previous research examining the effects of PD on postural set has shown that patients with PD develop postural set but have difficulty switching this set to accommodate changes in perturbation environment (Schieppati and Nardone 1991; Horak et al. 1992; De Nunzio et al. 2007). Chong et al. (1999) however, demonstrated that repeating discrete postural tasks (as might occur with balance training), did result in a gradual change in muscle pattern. In addition to understanding the capacity for and nature of learning in patients with PD exposed to a postural task with limited predictability, future work could serve to determine what conditions best support postural motor learning (e.g. random or predictable, implicit or explicit) and also whether training under these conditions can lead to improvements in the ability to quickly change set as would be required with sudden changes in environmental conditions.

6.9 CONCLUSIONS

The results of the studies in this thesis demonstrate that healthy older adults are capable of improving postural regulation with repeated exposure and that these improvements are either maintained during a retention interval or rapidly re-acquired. Evidence for longer-term retention has relevance for the positive effects of balance training although the meaningfulness of rapid re-acquisition for fall prevention remains to be explored. Significant positive training effects in both the embedded sequence and looped sequence protocols provide support for generalized postural motor learning in this population. It appears however, that training in an environment with less contextual interference (i.e. LS protocol) may have provided some benefit to older adults; enabling a greater number of participants to achieve predictive control of COM similar to young adults.

Despite comparable improvements in trunk control between young and older adults, a majority of older adults persisted with a postural behaviour that is potentially less efficient and less tolerable to unexpected postural perturbations. Given that older adults were effective in maintaining balance on the continuously moving platform as instructed, it appears that healthy aging may have most greatly affected optimization of postural responses. Limitations in the ability to optimize the postural response could be related to a breakdown in any of several sensory or motor components of the balance control system often observed with aging and their subsequent effect on the formation and modification of higher-level plans for action. The ability to functionally compensate for these losses in order to achieve the task goal however, demonstrates general plasticity of the CNS and integrity of the intact sensory and motor components. Whether less efficient posture control contributes to increased incidence of falling among older adults during activities of daily living is an important question for future research.

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APPENDIX B: PARTICIPANT CHARACTERISTICS

Table 1: Young Adult Participant Characteristics (ES Protocol)

	PLATFORM DISP. RANGE (± cm)	AGE (SEX)	HEIGHT (cm)
1	15	(M)	183
2	15	(M)	175
3	15	(M)	165
4	15	(M)	168
5	15	(M)	183
6	15	(F)	170
7	15	(M)	173
8	15	(F)	165
9	15	(M)	175
10	15	(F)	162
11	15	(F)	168
12	15	(F)	160

Table 2: Older Adult Participant Characteristics (ES Protocol)

	PLATFORM DISP. RANGE (± cm)	AGE (SEX)	HEIGHT (cm)	PASE (TOTAL SCORE)	SEMMES-WEINSTEIN			VIBRATION		ONE-LEG STANCE (FOAM + EC) (s)	ABC # items ≤ 70%
					Great Toe	5th Met. Head	Med. Midfoot	Great Toe	Ankle		
1	15	54 (M)	178	N/A	4.08	3.84	3.84	N	N	30	1
2	15	56 (F)	157	N/A	4.08	4.17	3.61	N	N	30	1
3	15	63 (M)	178	N/A	4.08	4.08	4.17	N	N	17	0
4	15	64 (M)	165	N/A	3.84	4.17	3.84	N	N	13.3	1
5	15	66 (F)	162	NON	3.61	4.08	3.84	N	N	6.4	0
6	15	67 (M)	183	115*	3.84	3.84	3.84	N	N	5.6	0
7	15	67 (F)	160	192	3.84	3.84	4.08	N	N	30	4
8	15	68 (M)	180	249	4.31	4.56	4.31	N	N	30	1
9	12	76 (M)	178	196	5.07	5.18	4.74	A	N	3.1	1
10	13	80 (M)	173	190	4.17	4.74	4.31	R	R	13.8	0

N/A = PASE scores were not calculated for participants < 65 years
NON = Participant did not complete and return the PASE questionnaire
* = below average activity level score for age and gender (note: all other participants scored above average for age and gender)
Semmes-Weinstein score ≥ 5.07 = at risk for somatosensory loss
N = normal vibration sense
R = reduced vibration sense
A = absent vibration sense

Table 3: Older Adult Participant Characteristics (LS Protocol)

	PLATFORM DISP. RANGE (± cm)	AGE (SEX)	HEIGHT (cm)	PASE (TOTAL SCORE)	SEMMES-WEINSTEIN			VIBRATION		ONE-LEG STANCE (FOAM + EC) (s)	ABC
					Great Toe	5th Met. Head	Med. Midfoot	Great Toe	Ankle		# items ≤ 70%
1	15	60 (F)	157	183	3.22	3.84	3.22	N	N	30	0
2	15	62 (M)	175	101*	4.08	4.56	3.61	N	N	11.4	0
3	15	63 (F)	152	173	3.61	4.08	2.83	N	N	30	0
4	15	64 (F)	155	180	3.84	4.08	3.89	N	N	30	1
5	15	65 (F)	165	207	3.84	3.84	3.61	N	N	30	0
6	15	65 (F)	168	77*	3.61	3.61	3.61	N	N	6.5	4
7	15	66 (F)	162	239	3.22	3.22	2.83	N	N	30	0
8	15	71 (F)	162	71*	3.22	3.61	4.31	R	R	17.1	2
9	15	74 (M)	178	282	4.31	3.84	3.84	N	N	30	0
10	15	77 (F)	170	76	4.08	4.08	3.84	N	R	30	0
11	15	79 (M)	178	130	3.84	4.74	3.84	R	R	4.8	0

* = below average activity level score for age and gender (note: all other participants scored above average for age and gender)

Semmes-Weinstein score ≥ 5.07 = at risk for somatosensory loss
N = normal vibration sense
R = reduced vibration sense
A = absent vibration sense

APPENDIX C: EMG METHODOLOGY

Data Collection

EMG activity was recorded using a custom made system and 2.5 cm, bipolar Ag-AgCl electrodes spaced 2 cm apart. Data was collected at 480 Hz from six muscles on the right side of the body: tibialis anterior (TA), medial gastrocnemius (mGAS), soleus (SOL), rectus femoris (RF), biceps femoris (BF), and lower erector spinae (LES). The same preamplifier/amplifier was paired with the same muscle across days of testing. Signals were amplified (x5000-20,000), band-pass filtered (15-2500 Hz), and stored for off-line analysis.

Data Analysis

EMG analyses were conducted on the middle segment of trials in the embedded sequence protocol. Restricting the EMG analyses to the repeated middle segment allowed for calculation of ensemble averages which addressed the issue of random error inherent in the EMG signal. Muscle responses were processed by 1) removing biases from the raw data, 2) full-wave rectifying the data and 3) applying a second-order, low pass filter with a cut-off frequency of 3 Hz (EMG profiles) or 100 Hz (integrated EMG). Ensemble averages of seven trials for each participant were calculated for each block. EMG activity was integrated over each half-cycle of platform motion. To compare integrated EMG activity within participants across days, mean muscle activity calculated over 5 seconds of a quiet stance trial was subtracted from the experimental trials. Normalized activity was only calculated for participants with no significant difference in quiet stance activity between days of testing (n=8). Since postural behaviours and EMG activities differ at anterior and posterior positions of platform motion (Dietz et al. 1993), EMG analyses were separated into forward and backward half cycles (FHC and BHC respectively) similar to that reported by Hocherman et. al. (1988). The peak positions in each half cycle were identified as the anterior and posterior turning points (ATP and PTP respectively)

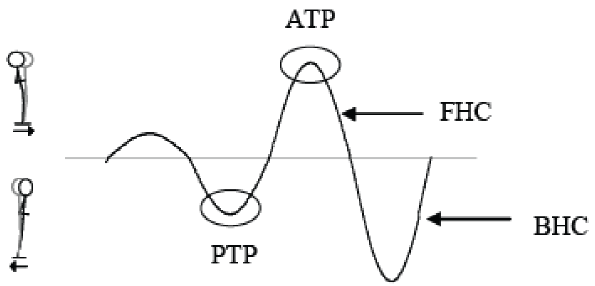

Fig. 1: Notation for platform motion and subsequent division of EMG data

The main points of interest for preliminary data analyses were 1) the change in the amount of EMG activity (iEMG) with training 2) the presence of EMG response scaling to the magnitude of the perturbation, and 3) the change in EMG timing with practice. To explore whether participants scaled their responses to perturbation amplitude, we correlated the magnitude of postural response (iEMG) for each half-cycle of platform motion to the peak platform amplitude (ATP or PTP) for that half-cycle. To examine whether the shifts in the temporal control of COM motion were driven by changes in the timing of muscle activation, we examined EMG profiles for evidence of leftward shifts in burst activity which would reflect predictive control.

APPENDIX D: NORMALIZED INTEGRATED EMG

Table 1: Average integrated EMG (iEMG) during forward (top) and backward (bottom) half-cycles of platform motion in right tibialis anterior (TA) for each participant. Data represents percentage of average iEMG during training block 1.

	BLOCK						
	1	2	3	4	5	6	RET
1	100	96.0	72.5	43.6	50.1	40.4	70.9
	100	84.8	65.9	50.0	47.6	33.9	58.0
2	100	79.1	81.5	65.9	60.8	53.9	112.6
	100	54.8	56.2	42.7	42.3	37.3	111.9
3	100	65.7	56.8	48.0	53.9	49.3	71.8
	100	80.6	72.7	57.1	61.3	54.4	78.7
4	100	49.3	39.0	52.9	38.3	27.8	42.2
	100	47.0	39.8	43.0	36.0	23.9	36.4
5	100	64.2	50.9	59.5	57.9	76.4	71.8
	100	67.0	64.5	71.6	61.8	78.0	75.2
6	100	63.2	64.5	51.4	47.3	28.2	121.1
	100	65.1	62.3	53.6	50.1	30.1	135.0
7	100	78.3	65.0	46.9	39.4	43.2	65.9
	100	70.5	58.5	44.4	37.5	36.4	63.3
8	100	109.1	75.9	63.1	54.4	58.1	75.5
	100	85.4	77.5	70.1	64.0	58.7	62.8
MEAN		75.7	63.3	53.9	50.2	47.2	79.0
		69.4	62.2	54.0	50.1	44.1	77.7
SD		19.4	14.0	8.1	8.2	16.1	25.6
		13.9	11.4	11.6	11.2	18.0	31.6

RET = Retention

Table 2: Average integrated EMG (iEMG) during forward (top) and backward (bottom) half-cycles of platform motion in right medial gastrocnemius (mGAS) for each participant. Data represents percentage of average iEMG during training block 1.

	BLOCK						
	1	2	3	4	5	6	RET
1	100	66.1	65.6	50.6	51.5	53.7	65.2
	100	67.1	63.5	51.6	55.0	68.8	98.2
2	100	63.6	57.5	63.7	69.9	58.8	68.0
	100	74.4	78.9	86.2	113.4	91.2	52.7
3	100	43.9	27.7	51.0	41.3	34.1	38.0
	100	60.3	40.1	60.0	59.0	39.1	24.6
4	100	77.4	80.5	63.8	64.7	60.1	59.7
	100	85.0	80.6	68.1	72.7	69.4	66.2
5	100	65.4	51.1	60.5	60.0	63.7	59.6
	100	66.9	50.1	59.3	74.4	81.2	70.4
6	100	87.0	85.4	83.5	65.9	55.9	79.9
	100	81.5	80.9	91.6	91.4	100.3	85.1
7	100	81.7	78.9	70.0	66.0	57.5	77.1
	100	80.2	72.8	65.9	70.1	61.7	75.7
8	100	59.3	35.7	40.3	32.1	23.3	62.8
	100	44.2	19.4	22.7	15.6	18.2	38.8
MEAN		68.0	60.3	60.4	56.4	50.9	63.8
		70.0	60.8	63.2	69.0	66.2	64.0
SD		13.7	21.3	13.3	13.6	14.3	12.9
		13.4	22.4	21.3	28.5	26.9	24.2

RET = Retention

APPENDIX E: IEMG CORRELATION WITH PLATFORM AMPLITUDE

Table 1: Correlation between tibialis anterior (TA) muscle activity (iEMG) and peak platform displacement during anterior turning points (left) and posterior turning points (right) in early and late training for each participant. Data represents Pearson correlation coefficients.

	EARLY TRAINING		LATE TRAINING	
	ATP	PTP	ATP	PTP
1	0.22	-0.06	0.29	-0.002
2	0.21	-0.47	-0.05	-0.42
3	-0.19	0.46	-0.15	-0.05
4	0.37	0.01	-0.59	-0.61
5	0.06	0.21	-0.15	-0.44
6	-0.05	0.11	0.12	-0.66
7	0.23	0.71	-0.12	-0.29
8	0.30	0.41	-0.08	-0.69
MEAN	0.14	0.17	-0.09	-0.40
SD	0.19	0.36	0.25	0.26

Table 2: Correlation between medial gastrocnemius muscle activity (iEMG) and peak platform displacement during anterior turning points (ATP-left) and posterior turning points (PTP-right) in early and late training for each participant. Data represents Pearson correlation coefficients.

	EARLY TRAINING		LATE TRAINING	
	ATP	PTP	ATP	PTP
1	0.35	0.64	-0.04	0.67
2	-0.34	-0.78	0.16	**0.94**
3	-0.08	0.76	-0.22	**0.76**
4	0.13	**0.84**	-0.24	0.57
5	0.19	**0.71**	0.32	0.20
6	-0.16	0.42	0.25	0.68
7	0.04	**0.94**	-0.17	0.67
8	-0.10	0.45	-0.14	**0.70**
MEAN	0.00	0.50	-0.01	0.65
SD	0.22	0.55	0.22	0.21

APPENDIX F: INDIVIDUAL CHANGES IN COM GAIN AND COM PHASE FOR OLDER ADULTS TRAINED USING THE *LOOPED SEQUENCE* PROTOCOL