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Standing balance : age-related differences in postural responses to continuous perturbations

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Standing balance : age-related differences in postural responses to continuous perturbations

A thesis submitted to Faculty of Graduated and Postdoctoral Studies,

in partial fulfillment of the requirements for the Degree of Doctor of Philosophy.

Department of Cellular and Molecular Medicine, Neuroscience Program,

Faculty of Medicine, University of Ottawa, Canada

Your file Votre référence
ISBN: 0-494-10992-0
Our file Notre référence
ISBN: 0-494-10992-0

To my grandmother

AUTHORISATION

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CONTRIBUTION OF EACH CO-AUTHOR IN THE PUBLICATIONS

All studies reported in this thesis were conducted under the supervision of Dr. Heidi Sveistrup. Unless otherwise specified all experimental work was carried out by Nicoleta Bugnariu. All manuscripts reproduced in this thesis (Chapters 2, 3, 4, and 5) were written by Nicoleta Bugnariu and revised by Dr. Heidi Sveistrup.

Chapter 2:

Title: Age related changes in postural responses to continuous perturbations

Journal: Paper submitted to Experimental Brain Research

Authors: Nicoleta Bugnariu and Heidi Sveistrup

Under the supervision of Nicoleta Bugnariu, two students, Kiera Kowen and Cristina Maris worked in the lab for the summer. They assisted with digitalization process and provided assistance to the subjects during experiments.

Chapter 3:

Title: Age-related changes in postural responses to externally- and self-triggered continuous perturbations

Journal: Paper to be submitted to Experimental Brain Research

Authors: Nicoleta Bugnariu and Heidi Sveistrup

Under the supervision of Nicoleta Bugnariu, a physiotherapy student, Sean Gallager assisted during experiments by spotting the subjects.

Chapter 4:

Title: Stimulation of cutaneous mechanoreceptors from foot plantar surface boundaries improves old adults' postural responses to continuous perturbations

Journal: Paper to be submitted to Journal of Neurophysiology

Authors: Nicoleta Bugnariu and Heidi Sveistrup

Under the supervision of Nicoleta Bugnariu, a physiotherapy student, Carolyn Bryanton assisted during experiments by spotting the subjects.

Chapter 5:

Title: Development of a model explaining age-related differences in postural responses to continuous perturbations

Journal: Paper to be submitted to Journal of Biomechanics

Authors: Nicoleta Bugnariu, Nicholas Bugnariu and Heidi Sveistrup.

Nicholas Bugnariu provided the expertise for implementation of the model and simulations in Simulink and Matlab.

ABSTRACT

This series of studies used an oscillating platform paradigm to investigate the effects of aging on anticipatory and reactive mechanisms of postural control. We hypothesized that young adults would use anticipatory mechanisms in response to predictable postural perturbations and that aging would be characterized by a decrease in anticipatory postural muscle activity resulting in less effective balance control.

Young and old healthy adults were asked to maintain standing balance on a force platform that oscillated continuously 20 cm peak-to-peak in the anterior/posterior (A/P) direction at successively increasing frequencies of 0.1, 0.25, 0.5 to 0.61 Hz. Subjects completed trials of externally- and self-triggered perturbations. The effect of mechanical stimulation of the foot plantar surface boundaries on postural responses of older adults was tested. Postural responses to perturbations were characterized using centre of pressure (COP), centre of mass (COM), muscle activity (EMG) and number of steps. A mathematical model representing the body motion in response to continuous sinusoidal platform perturbations was implemented.

Young adults used anticipatory adjustments regardless of the degree of predictability of postural challenges in externally- and self-triggered perturbations. Old adults responded to a predictable externally-triggered postural challenge using reactive postural adjustments independent of the frequency of platform oscillation, the direction of perturbation and without adapting over multiple trials. Old adults used anticipatory adjustments only in self-triggered perturbations or when additional sensory stimulation from foot plantar surface boundaries was available. The present series of experiments demonstrated for the first time that cutaneous stimulation of the foot plantar surface boundaries increases stability and facilitates the use of

anticipatory control strategies. These results support the importance of cutaneous mechanoreceptors at the boundaries of the foot plantar surface for the control of postural reactions evoked by continuous perturbations.

The results from these experiments clearly show that the ability to compensate for an impending and highly predictable perturbation decreases with aging. The age-related difference in the control of standing balance on a continuous oscillating platform recorded in experimental data was partially explained through increased levels of sensory noise and neural delays in the simulated data of old adults. Our results support the concept of a dynamic stability, according to which, in addition to the horizontal location of the COM with respect to the base of support, the magnitude and direction of its corresponding velocity provide critical information pertaining to one's ability to control balance. Based on model work, we demonstrated that the acceleration parameters of a perturbation must be taken into account when calculating stability limits. We derived for the first time the equations for calculating these stability limits related to continuous translations of the base of support.

TABLE OF CONTENTS

LIST OF TABLES

Page

CHAPTER 4

LIST OF FIGURES

CHAPTER 4

CHAPTER 5

LIST OF ABBREVIATIONS

A/P	anterior-posterior
BE	back extensors
BOS	base of support
CNS	central nervous system
COM	centre of mass
COP	centre of pressure
EMG	electromyographic activity
ETP	externally-triggered perturbation
G	gastrocnemius
H	hamstring
M/L	medial-lateral
NE	neck extensors
NF	neck flexors
NO STIM	no stimulation of cutaneous mechanoreceptors
Q	quadriceps
STIM	stimulation of cutaneous mechanoreceptors
STP	self-triggered perturbation
TA	tibialis anterior

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CHAPTER 1 GENERAL INTRODUCTION

1.1 NORMAL POSTURAL CONTROL

1.1.1 Defining postural control

There are two conceptual theories that describe the neural control of posture and balance: the reflex/hierarchical theory (Shumway-Cook 1989) and the systems theory (Woollacott and Shumway-Cook 1990). According to the reflex/hierarchical theory, posture and balance result from hierarchically organized reflex responses triggered by independent sensory systems. During development there is a progressive shift from the dominance of primitive spinal reflexes to higher levels of postural reactions, until mature cortical responses dominate. According to the systems theory, postural control emerges from an interaction of the individual with the task and the environment. The ability to control the body's position in space emerges from a complex interaction of musculoskeletal and neural systems, collectively referred to as the postural control system.

Postural control involves controlling the body's position in space for the dual purposes of orientation and stability. Postural orientation is defined as the ability to maintain an appropriate relationship between the body segments and between the body and the environment for a specific task (Horak and Macpherson 1996). Postural stability, or balance, is the ability to maintain the body in equilibrium, either when it is at rest (static equilibrium) or when it is in steady state motion (dynamic equilibrium). Traditionally, balance was defined as the ability to maintain the projected center of mass (COM) within the limits of the base of support (BOS), referred to as stability limits. During quiet stance, stability limits are defined as the area encompassed by the outer edges of the feet in contact with the ground. The COM is defined as a point at the center of the total body mass, determined by finding the weighted average of the center of mass of each body segment. Within the BOS, supporting ground reaction forces are generated. The center of pressure (COP) is the point within the BOS at which the sum of ground reaction forces can be considered to act.

Postural control can be defined as the process by which the central nervous system (CNS) generates the appropriate patterns of muscle activity required to regulate the relationship between the COM and the BOS (Maki and McIlroy 1996). Under static conditions, passive muscle stiffness could, in theory, maintain a stable upright posture. For activities of daily life, however, the maintenance of stability is a dynamic process, involving establishing equilibrium between destabilizing and stabilizing forces (McCollum and Leen 1989). Destabilizing forces arise because of movement of the body and interaction with the environment. In order to maintain stability, coordinated muscle activity is required to either relocate the COM through movement of the different body segments or adjust the BOS, for example by taking a step (Brauer 1998).

Recent research has expanded the traditional definition of balance and stability limits since this concept reflects primarily a static view of stability and, arguably, is suitable only when one's COM velocity is negligible. In daily living, the velocity of the COM is neither small nor negligible and stability limits are not fixed boundaries but change according to the task, the individual's functional and physiological capacities, as well as anatomical and environmental constraints (Pai 2003).

Combining empirical approaches with mathematical modeling, Pai and colleagues demonstrated that in fact the position of the COM can be outside the BOS if the COM velocity has the appropriate magnitude and direction. In fact, a dynamic model taking into accounts both COM location and velocity relative to the BOS, has better predictive capacity than a static model for estimating the initiation of stepping (Pai et al. 1997, 1998, 2000). These findings suggest that the central nervous system (CNS) controls not only the relative displacement between the COM and the BOS, but also relative velocity to maintain stability during movement.

Although COP excursions do not match COM excursions, the COP can be used as a biomechanical measure of stabilizing postural reactions since the COP is the variable used to control the COM (Winter et al. 1998, Rietdyk et al. 1999). Moreover, to maintain standing balance, the trajectory of the COM must remain within the extreme COP positions. Patton et al. (1999) demonstrated that when a subject maintains balance under normal conditions, the COP safety margin is a valid measure of relative stability because it directly measures how large a perturbation would be to initiate a fall. The COP safety margin is defined by the spatial safety margin, the minimum distance of the COP to the edges of the feet, and the temporal safety margins, the minimum extrapolated time for the COP to reach the edges of the feet. Time is a critical consideration because reflex loops and muscle activation patterns have appreciable delays. To prevent a fall, the COP must generate torques that accelerate the COM away from the stability limits. Hence, for tasks in which balance is recovered, the COP can be a sensitive indicator of relative stability. Reductions in COP excursions and localization of the COP in central regions of the BOS close to the ankle joint for increased percentages of time reflect increased stability.

1.1.2 Systems of postural control

In a systems approach, postural control requires a complex interaction of musculoskeletal and neural systems (Figure 1). Musculoskeletal components include joint range of motion, spinal flexibility, muscle properties, and biomechanical relationships among linked body segments. Neural components include motor processes, such as neuromuscular response synergies, sensory processes and higher-level integrative processes essential for mapping sensation to action and ensuring anticipatory and adaptive aspects of postural control. Other higher-level neural processes referred to as cognitive influences on postural control include processes such as attention, motivation, and intent.

1.1.2.1 Motor mechanisms for postural control

In quiet stance, stability is achieved through body alignment, which minimizes the effect of gravitational forces and muscle tone, keeping the body from collapsing in response to the pull of gravity. Three main factors contribute to muscle tone: (a) intrinsic stiffness of the muscles (Basmajian and De Luca 1985); (b) background muscle tone, which exists normally in all muscles because of neural contributions (Kendall and McCreary 1983); and (c) postural tone, the increased activation of antigravity muscles (Ghez 1991, Massion and Woollacott 1996).

The organization of movement strategies employed to recover stability when stance is perturbed has been studied by using, among other paradigms, a variety of moving platforms (Nashner 1976, Allum and Pfaltz 1985, Diener et al. 1982). Nashner and colleagues (Nashner 1977, Nashner et al. 1979, Horak and Nashner 1986) have described the characteristic patterns of muscle activity, called muscle synergies, underlying movement strategies used to recover balance in response to brief displacements of the supporting surface. These movement patterns, referred to as the ankle, hip and stepping strategies, are used in either a reactive or anticipatory manner to maintain equilibrium.

Ankle Strategy

The ankle strategy restores the COM to a position of stability through body movement centered primarily about the ankle joints. Figure 2 (A and B) shows the typical synergistic muscle activity and body movements associated with corrections for loss of balance in the forward and backward direction. For example, motion of the platform in the backward direction (Figure 2 A) causes the subject to sway forward. Reactive postural muscle activity begins at about 90 to 100 msec after perturbation onset in the gastrocnemius muscle, followed at 20 to 30 msec delays by activation of the hamstring and paraspinal muscles. In response to a backward body sway (Figure 2 B), muscle activity begins in the tibialis anterior, followed by activation of the quadriceps and abdominal muscles (Nashner 1977, Horak and Nashner 1986). Activation of the gastrocnemius muscles produces a plantarflexion torque that slows and then reverses the body's forward motion. In contrast, activation of the tibialis anterior produces a dorsiflexion torque that slows and then reverses the body's backward motion. Activation of the more proximal hamstring and paraspinal muscles or quadriceps and abdominal muscles maintains the hip and knees in an extended position. Without the synergistic activation of the hamstrings and paraspinal or the quadriceps and abdominal muscles, the indirect effect of the gastrocnemius or tibialis anterior ankle torque on proximal body segments would result in forward or backward motion of the trunk mass relative to the lower extremities. The ankle movement strategy described earlier appears to be used most commonly in situations in which the perturbation to equilibrium is small and the support surface is firm. Use of the ankle strategy requires an intact range of motion and adequate strength in the ankle muscles.

Hip Strategy

The strategy controlling motion of the COM by producing large and rapid motion at the hip joints with antiphase rotations of the ankles has been identified as the hip strategy (Horak and Nashner 1986). In response to a forward sway of the body, the typical synergistic muscle activity begins in the abdominal muscles about 90 to 100 msec after perturbation onset, followed by activation of the quadriceps muscles (Figure 2 C). In response to a backward sway of the body, the muscle activity begins in the paraspinal muscles about 90 to 100 msec after perturbation onset, followed by activation of the hamstring muscles (Figure 2 D). Horak and Nashner (1986) suggest that the hip strategy is used to restore equilibrium in response to larger, faster perturbations or when the support surface is compliant or smaller than the feet.

Stepping Strategy

When feet-in-place strategies are insufficient to recover balance, a stepping strategy is used to change the base of support to encompass the COM. The stepping strategy is used not only in response to perturbations that move the COM outside the BOS (Shumway-Cook and Horak 1989) but also when the COM is well within the BOS (Brown et al. 1999, McIlroy and Maki 1993). Most studies examining recovery of balance discourage stepping responses by giving instructions to subjects to refrain from stepping unless absolutely necessary (Maki 1993). McIlroy and Maki (1993) investigated the relationship between the prevalence of stepping responses and the instructions given to the subject and found that early automatic postural responses were recorded in ankle muscles in all trials, whether they resulted in stepping or not. Although the frequency of stepping tended to be higher when no specific instructions were given compared to when subjects were instructed to "keep feet in place", the differences were not significant (McIlroy and Maki 1993).

Upper Extremities Strategies

Part of the dynamic control of balance is achieved through compensatory arm movements such as grasping, counterbalancing and protective arm movements that absorb impact energy or shield the head during a fall. Maki and McIlroy (1997) reported that upper extremities strategies are prevalent reactions to instability and appear to play a more important functional role in maintaining upright stance than has generally been appreciated.

Mediolateral Stability

In the lower limb, very little mediolateral (ML) movement is possible at the ankle and knee joints; therefore, in contrast to anteroposterior (AP) postural control, mediolateral control of balance occurs primarily at the hip and trunk rather than at the ankle (Kapteyn 1973, Winter et al. 1993). Hip abductor and adductor muscle groups are activated in the control of the loading and unloading of the two legs with mediolateral sway (Maki et al. 1994b, Horak and Moore 1989). Mediolateral muscle patterns; in contrast to the distal-to-proximal AP muscle response patterns, are organized in a proximal-to-distal direction, with hip muscles being activated before ankle muscles (Horak and Moore 1989).

Adapting Motor Strategies to the Postural Task

While the ankle, hip, and stepping strategies and their associated muscular synergies are presented as discrete entities, most neurologically intact individuals use various combinations when controlling sway in the standing position (Horak and Nashner 1986). Studies in cats suggest that some muscles within the synergy may be tightly coupled but other muscle activity may be highly modifiable. The CNS thus does not simply control posture through controlling forces at individual joints but controls more general functions, such as antigravity support and horizontal stability (Jacobs and Macpherson 1996). The characteristics of postural responses are constantly modulated so they are appropriate to the task and refined to optimize response efficiency with repeated exposure to a given postural task (Woollacott et al. 1988, Pavol and Pai 2002).

Adults show stereotyped muscle response synergies when sway is forward or backward, but the responses are more variable in other directions (Moore et al. 1988, Henry et al. 1998). Moreover, people standing on a movable platform while performing different additional upper extremity tasks continued to use the ankle strategy but changed the coupling of the arm to the trunk to accommodate multiple task goals (Moore et al. 1992). Finally, as perturbation velocities gradually increase, subjects do not simply shift from using forces primarily at the ankles at the low velocities to forces primarily at the hip for higher velocities. Instead they continue to increase forces applied at the ankle and at a certain critical threshold point begin to add forces at the hip. This point varies from subject to subject, with some subjects using primarily forces at the ankle for most perturbation velocities (Jensen et al. 1996).

1.1.2.2 Sensory systems contributing to postural control

Effective postural control requires more than the ability to generate and apply forces for controlling the body's position in space. In order to know when and how to apply restoring forces, the CNS must have an accurate representation of where the body is in space and whether it is stationary or in motion. Peripheral inputs from visual, somatosensory (proprioceptive and cutaneous) and vestibular systems provide specific information about body's position and movement with respect to gravity and the environment within different frames of reference (Gurfinkel and Levick 1991).

Visual inputs give information about the position and motion of the head with respect to surrounding objects and provide a reference for verticality. Visual inputs include both peripheral visual information and foveal information though there is some evidence to suggest that the peripheral or a large visual field stimulus is more important for controlling posture (Paillard

1987). Visual inputs are an important source of information for postural control, although they are not absolutely necessary and may sometimes provide conflicting information because of the visual system's difficulty in distinguishing between object and self-motion.

The somatosensory system provides the CNS with position and motion information about the relationship of body segments to one another and about the body in reference to supporting surfaces. Somatosensory receptors include muscle spindles and Golgi tendon organs (sensitive to muscle length and tension), joint receptors (sensitive to joint movement and stress), and cutaneous mechanoreceptors, including Pacinian corpuscles (sensitive to vibration), Meissner's corpuscles (sensitive to light touch and vibration), Merkel's discs (sensitive to local pressure) and Ruffini endings (sensitive to skin stretch). Under normal circumstances, when standing on a firm, flat surface, somatosensory receptors provide information about the position and movement of the body with respect to a horizontal surface. Kavounoudias et al. (1998) showed that changes in skin pressure under the foot sole signal how far the body is leaning and the CNS uses this information to straighten the posture.

The vestibular system provides the CNS with information about the position and movement of the head with respect to gravity and inertial forces and is important in distinguishing between object and self- motion. The semicircular canals sense angular acceleration of the head and are particularly sensitive to fast head movements, such as those occurring during gait or imbalances such as slips, trips, and stumbles (Horak and Schupert 1994). The otoliths signal linear position and acceleration of the head with respect to gravity and respond mostly to slow head movements, such as those occurring during postural sway.

1.1.3 Two basic mechanisms used to regulate posture: reactive and anticipatory

The CNS routinely compensates for both predictable and unpredictable postural challenges, using either anticipatory or reactive mechanisms of control (Figure 3). Sensory-based reactive strategies consisting of automatic postural adjustments constitute the primary defence against unexpected, external perturbations, such as those experienced while standing on a platform that moves unexpectedly (Nashner 1976). Since reactive postural adjustments act quickly, they manage the regulation of posture on a crisis basis. The anticipatory mechanism involves anticipating the effect of a movement or external perturbation on posture and coordinating the activation of postural adjustments to minimize the postural disturbance. Anticipatory adjustments typically occur before or simultaneous with the onset of disturbance, whether self-generated or externally generated (Massion 1992, Lyon and Day 1997, Toussaint et al. 1997, Shiratori and Latash 2001).

Anticipatory aspects of postural control prepare sensory and motor systems for postural demands based on previous experience and learning. Adaptive postural control involves modifying sensory and motor systems in response to changing task and environmental demands. Postural responses are not shaped by stimulus characteristics alone, but also by adjustments in central set (Horak et al. 1989a, Hansen et Woollacott 1988). Central set allows individuals to modify their automatic responses to a postural stimulus by taking into account prior experience with perturbation characteristics and the effectiveness of their prior responses. This relationship between peripheral stimulus characteristics and postural responses affords efficient and effective responses when the stimulus is predictable but inappropriate responses when the stimulus characteristics change unexpectedly. The effectiveness of the anticipatory reactions is maximal under conditions of known type (Nashner 1976, Nashner and Berthoz 1978, Horak and Nashner 1986) and timing (Horak et al. 1989a) of a postural disturbance.

There is increasing evidence that, in general, the CNS also attempts to compensate for unpredictable perturbations through anticipatory adjustments. Evidence from discrete upper-limb tasks illustrates the CNS attempts to compensate for forthcoming perturbations of unpredictable magnitude or occurrence (Shiratori and Latash, 2001). A continuous dynamic process of adjustment in which anticipatory control of each task execution is adjusted based on the conditions and outcome of the previous execution takes place over two to three trials (Thoroughman and Shadmehr 2000, Scheidt et al. 2001). Based on responses of young healthy adults to perturbations of uncertain occurrence during a sit-to-stand task, Pavol and Pai (2002) suggested that the CNS adjusts anticipatory control even in the presence of perturbations that are unpredictable in magnitude or occurrence, and regardless of whether perturbations affect only single-limb (Pavol and Pai 2002) or whole-body postural tasks (Toussaint et al. 1997). In preparation for a potential perturbation, the CNS makes short-term anticipatory adjustments to reduce the likelihood of balance loss based on the conditions last experienced. Over a longer term, the CNS adapts to acquire an "optimal" movement strategy that decreases the overall probability of balance loss and reduces dependence on reactive responses (Pavol and Pai 2002).

The reactive and anticipatory mechanisms of postural control are not exclusive. Rather, Frank and Earl (1990) propose that they are accessed based on a time-derived continuum whereby the earliest postural adjustments relative to the perturbation would be an anticipatory mechanism. This strategy provides a degree of additional safety for postural control since, in the case of an inappropriate or ineffective anticipatory adjustment, a reactive postural adjustment can be used as a backup for additional control. Sensory information about the body orientation and motion is used to detect instability and to generate appropriate stabilizing responses by triggering reactive or anticipatory corrections and by updating adaptive reactions.

1.2 TESTING POSTURAL CONTROL

A stable system is one whose movement is not significantly altered from a desired trajectory even when it is perturbed (Brauer 1998). In general, two forms of external perturbations have been used to test the stability of postural control: informational and mechanical.

Informational perturbations change the nature of the information available from the environment either by removing or manipulating the sensory input (e.g., eyes closed, cooling of feet plantar skin) or by creating transient conflicts between different sources of information (e.g., moving visual fields, support surfaces that distort proprioceptive information from feet and ankles) (Maki and McIlroy 1996)

Mechanical perturbations involve destabilizing forces acting on the body, imposed by the environment or arising from volitional movements, and disturbing the relationship between the COM and the BOS.

Studies of the two basic mechanisms used to regulate posture, reactive and anticipatory postural adjustments, have focused primarily on either reactive mechanisms following discrete perturbations of the support area (for review see Massion 1998) or on anticipatory mechanisms (for review see Massion et al. 1999) associated with motor tasks such as raising the arm.

1.2.1 Transient perturbations or discrete perturbations are usually generated by a moving platform that can translate or rotate the BOS in different directions with different magnitudes of displacement, velocity and acceleration. The largest body of data on compensatory postural reactions comes from discrete perturbations experiments in which the movement of the feet was constrained, the "feet-in-place" reactions. The motor strategies used to recover balance have already been described. In contrast to muscle response latencies to visual cues signalling perturbations of balance, which are on the order of 200 msec, somatosensory responses are activated at 80 to 100 msec delays (Nashner et al. 1979). For comparable accelerations, muscle responses to vestibular signals are about one tenth of the magnitude of the somatosensory responses induced by the displacement of the feet. This suggests that vestibular inputs play only a minor role in recovery of postural control when the support surface is displaced horizontally (Dietz et al. 1991). The vestibular system however is important for balance control during visual and somatosensory system conflict (Black and Nashner 1985). Because somatosensory responses to support surface translations appear to be much faster than those triggered by vision and stronger than those triggered by vestibular inputs, it has been suggested that neurologically intact adults tend to rely on somatosensory inputs to trigger postural responses to transient horizontal perturbations to stance (Diener et al. 1986, Dietz et al. 1991).

1.2.2 Paradigms that facilitate simultaneous examination of both reactive and anticipatory mechanisms

The bimanual load-lifting task

In order to understand the relationship between reactive and anticipatory postural control mechanisms, the perturbations induced must be comparable. One experimental paradigm used to address this question is the bimanual load-lifting task (Hugon et al. 1982; Hay and Redon 1999). The task requires that seated subjects maintain a stable elbow position in the presence of unloading of the forearm. Unloading is accomplished either "passively" by the experimenter or "actively" by the subject's own contralateral arm. In the active and predictive situation, central programming incorporates both anticipatory postural adjustments and a voluntary load-lifting movement resulting in high postural stability. In the passive and unpredictable situation, reactive compensation is used to minimize the postural disturbance of the forearm. The goal of the anticipatory postural activity elicited during the load-lifting task is similar to that of the anticipatory postural activity recorded in standing subjects performing arm movements. In both tasks, the postural muscle activity serves to minimize the destabilizing effect of the movement on the body or limb. The functional significance of the anticipatory postural activity however is not the same. Postural reactions in the upper trunk preceding the movement of the arm are less relevant than whole body movements for the study of postural reactions implicated in the maintenance of standing balance.

Continuous platform perturbations

A continuously oscillating platform paradigm creates perturbations of similar magnitude that can be compensated for using either reactive or anticipatory postural adjustments. This permits investigation of the respective involvement of the two mechanisms of posture control in standing subjects. A person standing on a continuously oscillating platform will respond to the initial unpredictable movement of the platform with a reactive response. As the platform continues to oscillate at a fixed frequency, the perturbation induced becomes predictable and subjects are able to compensate for the postural challenge using an anticipatory mechanism (Corna 1999, Dietz et al. 1993). If one parameter of a continuous perturbation changes unexpectedly, for example the frequency of oscillation increases, the subject is again required to use a reactive mechanism of postural control. Once the platform stabilizes at a new frequency, the subject has the possibility to switch again from reactive to anticipatory control.

In young adults, two task-specific postural patterns produced as a function of the frequency of support surface translation during anterior-posterior (A/P) platform motion, have been described: i) the "ride" of the platform with a posture reminiscent of the upright stance at translation frequencies slower than 0.5 Hz and ii) the "head fixed" pattern where subjects actively fix the head in space, letting their legs and trunk move at oscillation frequencies greater than 0.5 Hz (Buchanan and Horak 1999). With increases in platform oscillation frequency, the gradual transition from the "ride" to the "head fixed" pattern is made through sequential recruitment of available degrees of freedom in the form of ankle, then knee, and then hip joint motion (Buchanan and Horak 2001).

1.3 AGING AND POSTURAL CONTROL

Since maintaining stability requires the CNS to generate appropriate, complex motor responses based on selective and rapid integration of sensory information from multiple sources, age-related changes in musculoskeletal, sensory systems, and neural processing and conduction of information could all potentially impact on postural control in older adults.

1.3.1 Age-related changes in musculoskeletal system

Several changes in the musculoskeletal system of older adults have been reported including: reduced muscle strength (Buchner and deLateur 1991, Whipple et al. 1987), decreased size and number of muscle fibers with a predilection for type II fast twitch, decreases in number of motoneurons and number of motor units (Aniansson et al. 1986), increases in intrinsic muscle stiffness (Blanpied and Smidt 1993), decreased range of motion and loss of spinal flexibility leading to a characteristic flexed or stooped posture (Studenski et al. 1991, Lewis and Bottomley 1990).

The association between strength and physical function is large; however, the amount of strength needed for physical function depends on the task. For compensatory postural responses neither maximal muscle forces nor maximal range of motion are required; therefore mild reductions in musculoskeletal capacity may not disturb the capacity of old adults to generate appropriate postural responses. In fact, studies of both feet-in-place and compensatory stepping reactions to anterior/posterior postural perturbation have demonstrated that healthy old adults have the muscle force, range of joint motion and speed of motion required to generate these reactions (Alexander et al. 1992, Luchies et al. 1994, McIlroy and Maki 1996). In addition, the maximum ankle muscle torque and rate of ankle muscle torque development have been shown to be similar between young and old adults in response to backward and forward platform translations (Hall et al. 1999).

1.3.2 Age-related changes in sensory systems

Age-related changes in the visual system include loss of ability to discriminate low spatial frequencies (Schultz et al. 1993), reduced acuity and contrast sensitivity (Sekuler and Hutman 1980), and reduced depth perception and dark adaptation (Wolfson 1992). The vestibular system shows a loss of labyrinthine hair and nerve cells (Rosenhall and Rubin 1975) and changes in the vestibulo-ocular reflex with age (Paige 1991). A less reliable vestibular function due to aging causes the nervous system to have difficulty in dealing with conflicting information coming from the visual and somatosensory systems. Reductions in proprioception (Skinner et al. 1984, Thelen 1998) and marked decreases in touch sensitivity, two-point discrimination (Bruce 1980) and vibration sense particularly in the lower limbs (Kenshalo 1986, Brocklehurst et al. 1982) have been reported in old adults. These reductions are associated with a loss in density and sensitivity of dermal receptors and innervating sensory fibers.

Deterioration of sensory inputs has been cited as an important factor influencing the postural control in older adults. Old adults depend more heavily on vision to substitute for other deteriorating sensory sources (Hytonen et al. 1993), in particular for controlling lateral stability (Maki 1993, 1995). Moreover, their visual acuity plays an important role especially when ankle and plantar sensation are disrupted (Lichtenstein et al. 1988, Lord et al. 1991, 1994). Age-related loss of cutaneous sensation is well documented in old adults (Kenshalo 1986) and appears to correlate with impaired control of postural sway (Lord et al. 1991, Brocklehurst et al. 1982) as well as with increased risk of falling (Lord et al. 1994, Anacker and DiFabio 1992). Furthermore, the mild to moderate peripheral neuropathy impairing foot and ankle sensory information (van den Bosch et al. 1995), that is often present in elderly substantially decreases unipedal balance control (Richardson et al. 1996b) and is thought to contribute to the six fold increase in injurious falls (Richardson et al. 1992, 1996a). In support of the importance of cutaneous sensation, manipulation of plantar sensation was reported to have an effect on afferent nerve activation and postural sway, feet in place stabilizing reaction, compensatory stepping reactions, as well as perceptual illusory responses of whole-body leaning in stabilized subjects (Okubo et al. 1980, Watanabe and Okubo 1981, Diener et al. 1984, Do et al. 1990, Magnusson et al. 1990a,b, Hamalainen et al. 1992, Fitzpatrick and McCloskey 1994, Wu and Chiang 1997, Maki et al. 1999, Perry et al. 2000, Kavounoudias et al. 1999, Roll et al. 2002).

1.3.3 Age-related changes in central and peripheral nervous system

It has been suggested that age-related changes in CNS integrative mechanisms may contribute to a larger degree to postural dysfunction than sensory deficits (Wolson et al. 1992, Teasdale et al. 1991, Horak et al. 1989). Progressive age-related loss of neurons, dendrite and reduced branching, altered transmitter metabolism (Kirshen et al. 1984) and a general slowing of information processing (Stelmach et al. 1985) in conjunction with decreased nerve conduction velocity, could detrimentally impact the generation of complex postural responses.

Postural control in older adults may place increased demand on high-level CNS resources such as attention (Stelmach et al. 1990). Decrements of performance on postural stability measures were reported with the addition of a cognitive task (dual task paradigm), with differences between healthy young and older adults becoming more evident as the task complexity was increased. This implies that the amount of attention required for posture is dependent on the degree of instability inherent in the task and that older adults require more attention to perform the postural task (Teasdale et al. 2001, Shumway-Cook et al. 1997). When exposed to unexpected platform perturbation while undertaking a secondary task, the attentional requirements for recovery of balance were higher for older than young adults (Brown et al. 1999), the postural muscle responses were too small for balance recovery and older subjects were required to step earlier (Rankin et al. 2000).

1.3.4 Age-related changes in anticipatory and reactive postural control mechanisms

A propensity to take a step or fall in novel situations may be the result of impaired anticipatory mechanisms. Anticipatory processes related to postural control enable the selection of appropriate sensory and motor strategies needed for a particular task or environment. Many older adults have problems making anticipatory postural adjustments quickly and efficiently (Inglin and Woollacott 1988, Frank et al. 1987). This inability to stabilize the body in association with voluntary movements may be a major contributor to falls in elderly people. Older adults are less likely to introduce anticipatory postural adjustments and shift the COM over the stance leg prior to unloading the foot when stepping to recover balance (McIlroy and Maki 1996). Age-related changes in the ability of older adults to activate postural muscle responses in an anticipatory manner were evident through significantly longer postural muscles onset latencies in old than young adults (Inglin and Woollacott 1988, Frank et al. 1987).

Older adults are less able to adapt to predictable task conditions. In response to repeated small perturbations, old subjects do not show the progressive reduction in sway observed in young adults (Stelmach et al. 1989c). Experimental evidence suggests that the time course of sensorimotor adaptation is moderately degraded with age (Bock and Schneider 2002). There is accumulating evidence of age-related declines in sensorimotor performance such as stimulus discrimination and the utilization of pre-cues (Cerella 1990, Hale et al. 1987). Slower adaptation of postural control responses to various transient perturbations and task conditions has been reported in old adults (Woollacott et al. 1986, Horak et al. 1989c, Peterka and Black 1990).

In old subjects, the distal-to-proximal sequence of muscle activation characteristic of the ankle strategy and normally evoked by anterior-posterior platform translations, is often distorted. Specifically, there may be greater co-contraction of antagonistic muscles and the onset of muscle activation and associated joint torque is delayed (Manchester et al. 1989, Shepard et al. 1993, Stelmach et al. 1989b, Wolfson et al. 1992, Woollacott et al. 1986). Old adults are more likely to take multiple steps in response to forward and backward perturbations (Luchies et al. 1994, McIlroy and Maki 1996) and show greater variability in controlling head motion. This may decrease the ability to acquire accurate visual and vestibular information for the control of postural responses (Keshner 2004).

Postural responses to continuous perturbations may provide complementary information about the integrity of anticipatory and reactive control mechanisms. Nardone et al. (2000) tested the postural coordination of elderly subjects standing on a periodically moving platform. At slow frequencies of platform movement (0.2 Hz), elderly subjects tended to stabilize the head more than the hip, with the legs compensating for most of the imposed platform displacement. The displayed pattern in older adults resembled the head fixed pattern that was observed in young adults at frequencies above 0.5 Hz (Buchanan and Horak 1999). The muscle activity patterns and COP-BOS relationship in response to continuous oscillations in old adults remain unknown.

1.4 MODELING POSTURAL CONTROL

Clinical assessments can routinely quantify regional limitations in a joint or body segment such as deficits in muscle strength or proprioceptive sensation. However, such quantification generally does not provide clinicians with a global evaluation of a patient's functional status because of its lack of connection to the patient's ability to perform daily tasks. Recent efforts have been directed toward deriving novel measures and modeling approaches that may provide more insight into the underlying mechanisms of postural control.

A simple inverted pendulum model of human stance and stability in the sagittal plane may include only two segments, one representing the symmetrical placement of the feet and the other segment for the rest of the body. Despite the limitations introduced by a simplified model of human body that makes the assumption that all corrective responses are located at the ankle joint and that the rest of the body behaves as a unit, the inverted pendulum model has been used extensively with appreciable results (Pai et Patton 1997, Pai et Iqbal 1999, Pai et al. 2000, Stirling and Zakynthinaki 2004). Although a multiple segment model of the human body may be more realistic, the equations of motion for multiple link models are complex, nonlinear and highly coupled and often do not have analytical solutions (Iqbal and Pai 2000).

In contrast to experimental settings, which are difficult to manipulate especially with human subjects, mathematical models provide a framework allowing systematic manipulation of parameters and can assist in characterizing experimental conditions and explaining experimental results. Moreover, when models achieve a good representation of experimental data, their predictive ability can be used to extend results to similar populations in different paradigms. Such predictions may provide guidance for developing intervention programs for improving stability when perturbed.

Mathematical modeling has been used to identify: i) a feasible stability region for safely terminating anterior movement of a simple pendulum connected to a stationary BOS, (Figure 4) based on the relationship between the horizontal COM velocity-position and the BOS (Pai and Patton 1997) and ii) thresholds for step initiation induced by support surface translations (Pai et al. 2000).

The connection between regional deficits and global functional impairment may be established based on the computational methods associated with the proposed conceptual framework. In fact, computational methods have been applied to estimate the impacts of reductions in ankle strength on functional BOS on balance and stability (Pai and Patton 1997). For example, a deficit in strength will have a negligible effect on the feasible stability region until it exceeds 51% from the normal value for the dorsiflexor muscles or 35% for the plantar flexors (Pai and Patton 1997). Computational methods can also be applied to the search for movement strategies that are optimal for the control of balance. For instance, the model predicts that if a person increases the COM velocity and/or shifts the COM anteriorly before the onset of a slip, the initiation of a backward fall can be avoided (Pai and Iqbal 1999).

To successfully maintain balance and counter the mechanical effects of a perturbation such as a moving platform, the central nervous system (CNS) makes adaptive adjustments to improve the stability of the body COM state, its velocity and position. Such control relies on accurate internal representations of body orientation and stability limits. The stability limits are a function of anatomical, physiological, and environmental constraints and therefore can be calculated based on physical laws of motion (Pai et al. 2003).

In human stance control, the CNS receives delayed information from a multisensory system and uses this information to estimate body orientation relative to the environment. Standing balance is not an easy and straightforward task for the nervous system since: i) exact estimation of body orientation is not possible because all sensory information is received with a certain time delay; ii) the sensory signals may not always be reliable as, for instance, in older adults with age-related loss of proprioception (Skinner et al. 1984, Speers et al. 2002); and iii) the estimation of body orientation involves an integration of different sensory systems each with its own coordinate frame (Mergner et al. 1997). Thus, the CNS can only provide a best possible estimate of body orientation and base the corrective response on this estimate. Optimal estimation theory has proven its power in modelling man-machine systems and human spatial orientation (Borah et al. 1988). A multisensory integration model of human stance control based on optimal estimation theory has showed that despite transient external perturbations, a controller was able to stabilize a model of an inherently unstable standing human with neural time delays of 100 ms (van der Kooij et al. 1999). A model to study and quantify the impact of noise and neural delay on standing balance in young and old adults perturbed by a constantly sinusoidal platform translation has not been developed.

1.5 RATIONALE FOR PROPOSED APPROACH

Age-related changes in both reactive and anticipatory postural adjustments elicited during standing have clearly been demonstrated. However, the experimental paradigms most often used to test these two mechanisms of postural response resulted in distinctly different perturbations to the body. Thus, the ability to determine relative integrity of the two mechanisms or ability to use the individual mechanisms as people age remains a challenge. For example, it is possible that an older adult demonstrates significant alterations in the postural muscle activation pattern following an unexpected posterior translation of the support surface suggesting a decrease in the reactive mechanism efficiency. The same person may show normal postural muscle activation patterns preceding the raising of an arm. It is difficult to establish how the two mechanisms change relative to one another within the same population when two distinct paradigms are used since components of the postural reactions, such as postural muscle activity and body kinematics, are dependent on the kind of perturbation.

To address this issue, the present series of experiments used a continuously moving platform to create perturbations of standing balance of similar magnitude that could be compensated for using either reactive or anticipatory postural adjustments. Moreover, these experiments address an issue that has received little attention: how are reactive and anticipatory strategies employed during continuous perturbations to standing posture? Most of the postural control literature has explored postural control under conditions of a single perturbation. Movements as common as walking introduce continuous perturbations that the CNS must both react to and anticipate in order to maintain upright stance. These experiments extended the work of Buchanan and Horak (1999, 2001), Dietz et al. (1993) and Nardone et al. (2000) with a focus on the analysis of muscles onset latencies and the age-related changes in the postural responses to predictable and unpredictable sinusoidal translations of the support surface.

The first study examined age-related differences in postural responses to externally-triggered continuous perturbations and the integrity of reactive and adaptive mechanisms of control. In the second study, the manipulation of experimenter-triggered versus participant-triggered transitions from one frequency to another frequency of perturbation was a novel approach to examine the subjects' ability to take advantage of known characteristics of perturbations and to determine whether older adults could adopt anticipatory postural control. Since age-related loss of lower-limb cutaneous sensation is well documented and has a strong correlation with impaired control of postural sway (Lord et al. 1994), the purpose of the third experiment was to determine if additional sensory information from the plantar surface enables older adults to use the anticipatory mechanism more consistently in the continuous oscillating platform paradigm. In order to gain insights about the impact of neural delay and sensory noise, and to calculate stability limits for the continuous translation perturbations, a dynamical model was developed and compared to experimental data in a fourth study.

The manner in which the CNS uses anticipatory adjustments to reduce the potential balance loss during postural tasks when perturbations are or are not predictable is of particular relevance for fall prevention in old adults. However, the age-related changes in the ability of the CNS to immediately or through a longer term adaptation process identify and use such anticipatory postural control strategies have not been determined. The continuous oscillating platform paradigm is well suited for exploration of mechanisms underlying postural control.

1.6. HYPOTHESES AND OBJECTIVES

1.6.1 Objectives

A. Characterize the age-related differences underlying the response to continuous postural perturbations in terms of:

- postural muscle onset latencies, probability of recruitment and complexity
- displacement of the COP and it's relationship to the safety boundaries
- displacement of the COM
- phase relationships between time series of platform, COP and COM movements
- number of steps taken in response to perturbations

B. Develop a mathematical model able to reproduce the experimental data in order to:

- gain insights about the contribution of noise and neural delay in the control of standing balance
- determine stability limits for a continuous anterior-posterior translation task

1.6.2 Hypotheses

Clinical and research evidence suggests that the mechanisms of postural control are affected by age.

Experiment 1

We hypothesized that the ability to use adaptive and anticipatory postural adjustments to compensate for an impending and highly predictable perturbation decreases with age. In addition, although both young and older adults would necessarily use a reactive mechanism to maintain their balance during unexpected transitions in oscillation frequency, we hypothesized that over a number of cycles at a constant movement frequency, young adults would shift from the reactive response used in transition period towards an anticipatory mechanism, but that a similar shift would be slower or not observed in older adults. It was hypothesized that compared to young adults, old adults would:

1) use the appropriate set of postural muscles but at onset latencies consistent with a reactive mechanism of control;
2) display increased number of steps and require increased external support to prevent falls; and
3) display a greater relative lag in the relationship between the COP with the platform and COM with the platform.

Experiment 2

It was hypothesised that if the old adults' anticipatory mechanism of postural control was available to them in response to continuous perturbations, a self-triggered perturbation would facilitate the use of this mechanism. It was further hypothesized that in the self- versus externally triggered perturbations, the capacity of subjects to take advantage of known timing and perturbation characteristics and use the anticipatory mechanism of control would be reflected in:

1) earlier postural muscle onset latencies;
2) shorter phase lags between platform and COP time series;
3) smaller amplitudes of COP displacement and decreases in the percentage of time the COP was located in extreme regions of the BOS; and
4) fewer steps.

Experiment 3

It was hypothesized that the stimulation of cutaneous sensation from the plantar foot boundaries would lead to increased stability and would enable old adults to use anticipatory mechanism in response to externally- and self-triggered perturbations. We predicted that in contrast to a no stimulation condition, the effect of stimulation would be manifested in:

1) reduced excursions of the COP toward the BOS boundaries;
2) decreased percentage of time the COP would be located in extreme regions of the BOS;
3) earlier postural muscle onset latencies;
4) shorter phase lags between the platform and COP movement; and
5) improved ability to resist stepping.

Experiment 4

A mathematical model that reproduced the experimental data was created. It was hypothesized that the age-related difference in the control of standing balance on a continuous oscillating platform would be partially explained through increased levels of noise and neural delays in old adults. It was also hypothesized that compared to younger adults, older adults would more often cross the safety boundaries of the stability limits predicted by a dynamic model.

Fig. 1 Conceptual representation of systems contributing to postural control.

(Reprinted with permission from: Shumway-Cook A, Woollacott MH (2001) Motor Control Theory and PracticalApplications, 2nd edition, Lippincott, Williams & Wilkins, p 165)

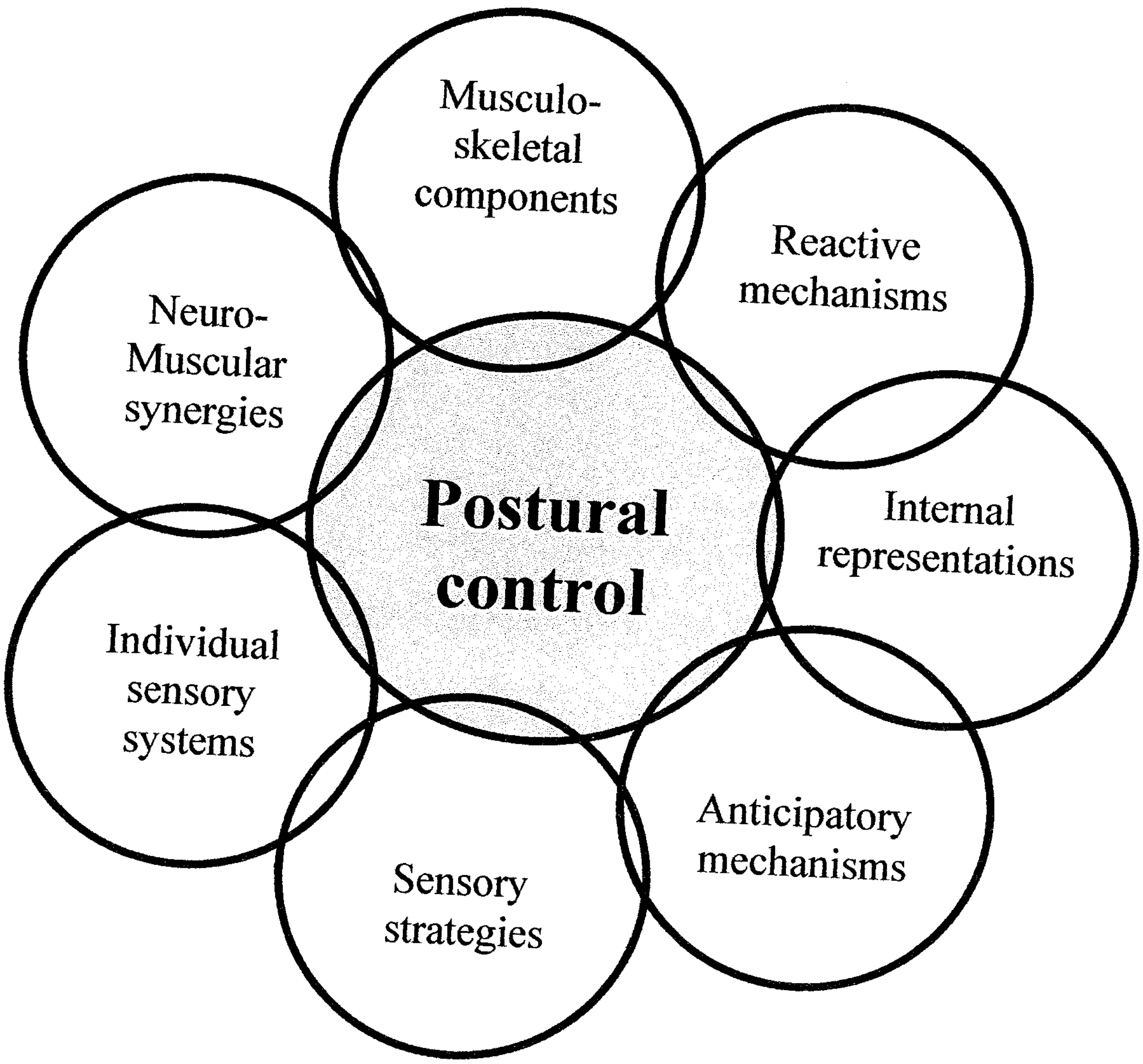
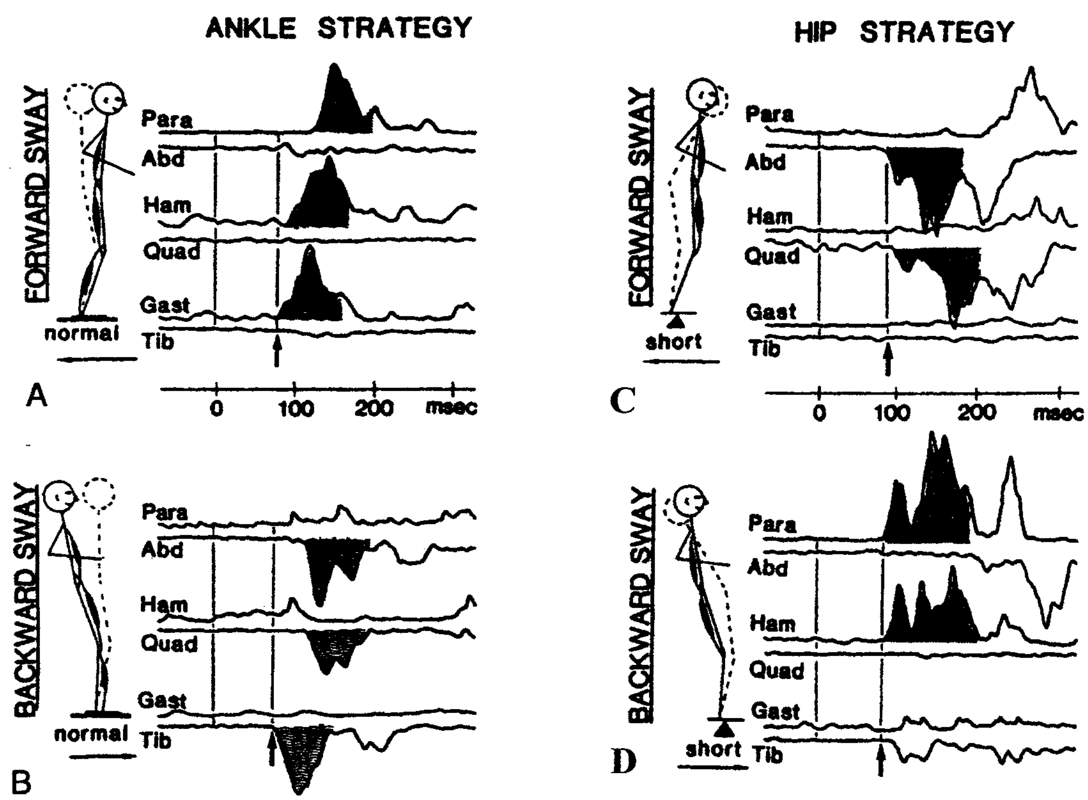

Musculo-
skeletal
components
Reactive
mechanisms
Neuro-
Muscular
synergies
Postural
control
Internal
representations
Individual
sensory
systems
Anticipatory
mechanisms
Sensory
strategies

Figure 1

Fig. 2 Left: Muscle synergies and body motions associated with ankle strategies for controlling forward (A) and backward (B) sway.

Right: Muscle synergies and body motions associated with hip strategies for controlling forward (C) and backward (D) sway.

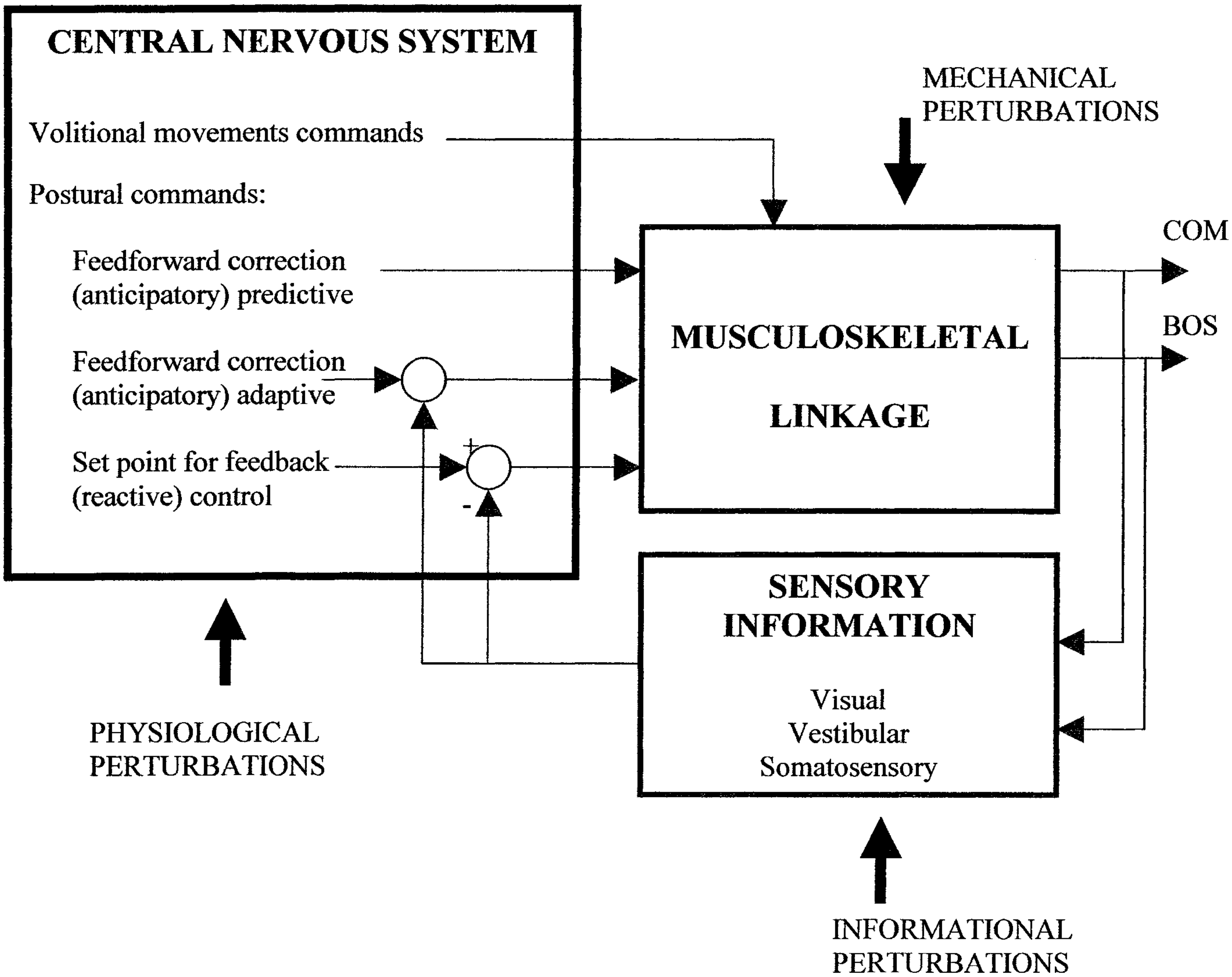
(Reprinted with permission from: Horak F, Nashner L (1986) Central programming of postural movements: adaptation to altered support surface configurations. J Neurophysiology, 55:1372)



ANKLE STRATEGY
HIP STRATEGY
FORWARD SWAY
BACKWARD SWAY
Para
Abd
Ham
Quad
Gast
Tib
normal
short
A
B
C
D
0
100
200
msec

Figure 2

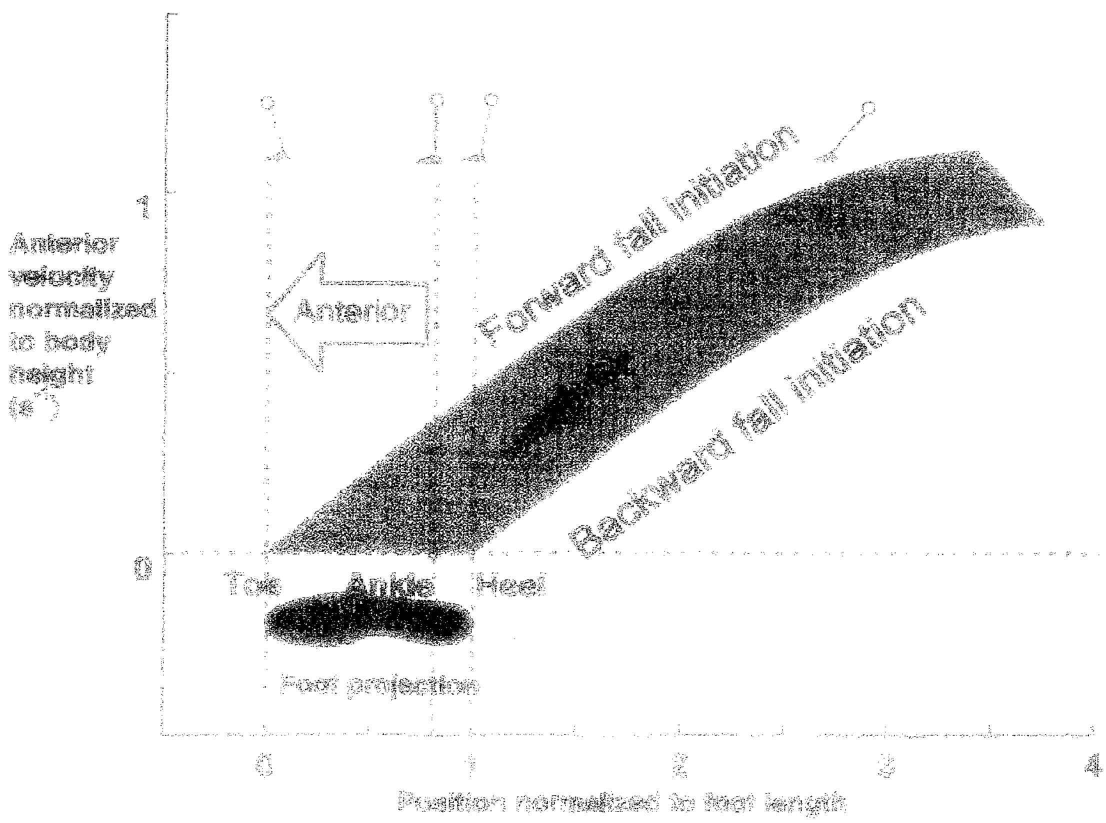
Fig. 3 Conceptual model of the posture control system. In reactive control, sensory information is used to continuously update corrective changes to the COM or the BOS. In anticipatory control, pre-programmed stabilizing reactions are released either predictively (anticipatory postural adjustments) or in reaction to sensory information pertaining to the state of instability (adaptive anticipatory reactions). Mechanical perturbations involve change in the forces acting on the body (due to movement of the body and/or interaction with the environment). Informational perturbations pertain to transient change in the nature of the information available from the environment. Physiological perturbations refer to transient internal events that disrupt the operation of the neural control system *(Reprinted from: Maki BE and McIlroy WE (1996) Postural control in the older adult, Clinics in geriatric medicine, vol. 12(4), p 637, with permission from Elsevier).*



CENTRAL NERVOUS SYSTEM
Volitional movements commands
Postural commands:
Feedforward correction
(anticipatory) predictive
Feedforward correction
(anticipatory) adaptive
Set point for feedback
(reactive) control
+
-
MECHANICAL
PERTURBATIONS
MUSCULOSKELETAL
LINKAGE
COM
BOS
SENSORY
INFORMATION
Visual
Vestibular
Somatosensory
PHYSIOLOGICAL
PERTURBATIONS
INFORMATIONAL
PERTURBATIONS

Figure 3

Fig. 4 Feasible horizontal center of mass velocity-position region (shaded diagonal band) for terminating anterior movement of a simple pendulum connected to a stationary base of support. Forward falls would be initiated if states exceed the upper boundaries, while backward falls would be initiated if states dropped below the lower boundaries. The initiation of a fall is also defined as any dynamic condition that causes the feet to move. The bold arrow indicates the direction that a trajectory would travel in terminating movement. Velocities and positions are normalized by body height and foot length, respectively. *(Reprinted from: Pai YC and Patton J, (1997), Center of mass velocity-position predictions for balance control, J Biomechanics, vol. 30 No 4, p 350, with permission from Elsevier)*



Anterior velocity normalized to body height (s^{-1})
1
0
Anterior
Forward fall initiation
Backward fall initiation
Toe
Ankle
Heel
Foot projection
0
1
2
3
4
Position normalized to foot length

Figure 4

Chapters 2, 3, 4 and 5 are four manuscripts submitted to different journals in the format of the journals.

CHAPTER 2

Age related changes in postural responses to continuous perturbations

ABSTRACT

An oscillating platform paradigm was used to investigate the effects of aging on anticipatory and reactive mechanisms of postural control under a single paradigm. We hypothesized that young adults would use anticipatory mechanisms in response to predictable postural perturbations and that aging would be reflected by a decrease in anticipatory postural muscle activity resulting in less effective balance control. Young adults (22.3 ± 2.1 years old, n=8) and Old adults (70 ± 4.2 years old, n=8) were asked to maintain their balance while standing on a platform that oscillated sinusoidally 20 cm peak-to-peak in the anterior/posterior (A/P) direction. Platform oscillation started at a frequency of 0.1 Hz and after intervals of 80-100 seconds the frequency was suddenly and without warning increased successively to 0.25 Hz, 0.5 Hz and 0.61 Hz. The first three cycles at 0.1 Hz and the first five cycles at higher frequencies were considered transition periods and were analyzed separately. The remaining cycles at each frequency of platform translation constituted the steady state periods during which the platform motion was constant and predictable. Postural responses to perturbations were characterized using centre of pressure (COP), centre of mass (COM), and muscle activity (EMG) data.

The old adults responded to a predictable postural challenge using reactive postural adjustments independent of the frequency of platform oscillation, the direction of perturbation and without adapting over multiple trials. Old subjects displayed greater displacement of the COP than young adults and no significant scaling of COM displacements was evident with increases in platform frequency. Increased phase lags between platform-COP and platform-COM signals in the old adults illustrate a behaviour driven mainly by platform movement, suggesting the use of reactive postural mechanism. Compared to young adults, postural muscles were activated consistently later in the oscillation cycle in both transition and steady state periods by the old adults for both directions of platform movement. In young adults, earlier postural muscle activity was recorded in the transition period and values remained stable during the steady state period at every frequency. No shift in postural muscle onset latency was noted during the transition period in the old adults. Moreover, old adults did not reach the same values of anticipatory or early postural muscles onset latencies as the young adults even after 10, 30 or 40 cycles in the steady state periods at 0.25, 0.5 and 0.61 Hz respectively. The results from these experiments clearly show that the ability to compensate for an impending and highly predictable perturbation decreases with aging.

Keywords: Aging, Postural Control, Platform Perturbation, Electromyogram, Stance, Balance

INTRODUCTION

Regulation of postural stability and orientation are fundamental requirements of most motor tasks. Studies of the basic mechanisms used to regulate posture have focused primarily on either reactive or anticipatory postural adjustments. Sensory-based reactive strategies are the primary defence against unexpected, external perturbations, such as those experienced while standing on a platform that moves without warning (Nashner 1976, for review see Massion 1998 but c.f. Henry et al. 1998). The anticipatory mechanism (Cordo and Nashner, 1982) involves anticipating the effect of a movement or external perturbation on posture and coordinating the activation of postural adjustments to minimize the postural disturbance such as when raising the arm or leg (Bouisset 1991, Massion 1992 but c.f. Vernazza et al. 1999a, b, Massion et al. 1999, Teyssedre et al. 2000).

These two mechanisms of postural control are not exclusive. Rather, Frank and Earl (1990) proposed that they are accessed on a time-based continuum. In addition, age-related changes in both reactive (Nardone et al. 1995) and anticipatory (Woollacott et al. 1986) postural adjustments elicited during standing on a moving platform have clearly been demonstrated. However, the experimental paradigms most often used to test these two mechanisms of postural response result in distinctly different perturbations to the body. The respective contribution of reactive and anticipatory adjustments can vary considerably according to the particular experimental condition.

Studies using a continuously moving platform permit us to investigate the respective contribution of the two mechanisms to posture control in standing subjects. A person standing on a continuously oscillating platform will respond to the initial movement of the platform with a reactive response. As the platform continues to oscillate at the same frequency, the perturbation induced becomes predictable and young subjects are able to compensate for the postural challenge by using an anticipatory mechanism (Corna et al. 1999, Dietz et al. 1993). If one parameter of a continuous perturbation changes unexpectedly, for example the frequency of the translation increases, the subject is again required to use a reactive mechanism of postural control. Once the platform stabilizes at the new frequency, the subject has the possibility to switch again from reactive to anticipatory control. When platform displacement conditions such as magnitude and direction are known, anticipatory reactions are used more consistently (Nashner et al. 1976, Horak et al. 1989).

In young adults, two task-specific postural patterns produced as a function of the frequency of support surface translation during anterior-posterior (A/P) platform motion, have been described: i) the "ride" of the platform with a posture reminiscent of the upright stance at translation frequencies slower than 0.5 Hz and ii) the "head fixed" pattern where subjects actively fix the head in space, letting their legs and trunk move at oscillation frequencies greater than 0.5 Hz (Buchanan and Horak 1999). With increases in platform oscillation frequency, the gradual transition from the "ride" to the "head fixed" pattern is made through sequential recruitment of available degrees of freedom in the form of ankle, then knee, and then hip joint motion (Buchanan and Horak 2001).

Postural coordination in elderly subjects standing on a periodically moving platform was reported by Nardone et al. (2000). At slow frequencies of platform movement (0.2 Hz), elderly subjects tended to stabilize the head more than the hip, with the legs taking up most of the imposed displacement. The pattern displayed by old adults resembled the head fixed pattern observed at higher frequencies in the young adults by Buchanan and Horak (1999).

In the present paper, we extend the work of Horak, Buchanan, Dietz and Nardone focusing on analysis of the age-related changes in the postural muscle responses to continuous sinusoidal translations of the support surface. The purpose of this study was to determine whether ageing is characterised by an inability to use anticipatory postural adjustments in response to externally- triggered predictable perturbations. We used an oscillating platform paradigm to create perturbations of similar magnitude that could be compensated for using either reactive or anticipatory postural adjustments. Although both young and old adults would necessarily use a reactive mechanism to maintain their balance in response to increases in platform oscillation frequency made without warning, we predicted that over a number of cycles at a constant platform frequency, young adults would shift from the reactive response towards an anticipatory mechanism but that a similar transition would not be observed in old adults.

METHODS

Subjects

Sixteen adults gave their informed consent to participate in this study. The experimental procedures were approved and performed in accordance with the Tri-Council Policy Statement on Ethical Conduct for Research Involving Humans (Canada). All participants were healthy volunteers with no history of falls, musculoskeletal or neurological problems. Eight young adults and eight old adults participated and an equal number of men and women were included in each group. Mean (± SD) age, height, weight, and foot length were: 22.3 ± 2.1 years, 170.9 ± 5.5 cm, 71.4 ± 10.8 Kg and 27.9 ± 2.2 cm for the young adults and 70 ± 4.2 years, 165.1 ±13.8 cm, 70.2 ± 14.7 Kg, and 27.4 ± 2.5 cm for the old adults respectively.

Task and procedures

Participants were asked to stand erect, eyes open, barefoot with feet shoulder width apart on a movable platform that was driven by an electric motor. They were asked to maintain their balance and to avoid taking steps unless absolutely necessary. If a step was taken, they were instructed to bring their feet back to the initial position. In order to prevent falls, subjects wore a loose harness attached to the ceiling while an assistant provided them with additional support if they were unable to maintain their balance. The platform oscillated sinusoidally 20 cm peak-to-peak in the anterior/posterior (A/P) direction. Platform oscillation started at a frequency of 0.1 Hz and after intervals of 80-100 seconds the frequency was suddenly and unexpectedly increased successively to 0.25 Hz, 0.5 Hz and 0.61 Hz. Trials consisted of 10 cycles at 0.1 Hz, 20 cycles at 0.25 Hz, 40 cycles at 0.5 Hz and 50 cycles at 0.61 Hz. Each subject completed two five-minute trials.

A Kistler force plate (Type 9286, Kistler Instrument Corp) was placed in the center of the moving platform and the subjects started all trials standing centered on the force plate. The ground reaction force and platform position signals were sampled at 600 Hz.

Reflective markers were placed on the left side of the body over the following landmarks: cathi of left eye, lateral mandibular joint, seventh cervical vertebra, acromion, greater trocanter, lateral femoral condyle, lateral malleolus, heel, and fifth metatarsophalangeal. One high resolution video camera, sampling at 60 Hz, recorded the position of the left side of the body in a sagittal view. A motion analysis system (APAS, Ariel Performance Analysis System) provided position information for calculation of total body center of mass (COM) kinematics.

Surface electrodes were used to record activity of the tibialis anterior (TA), gastrocnemius (G), quadriceps (Q), hamstrings (H), back extensor (BE), neck flexor (NF) and neck extensor (NE) muscles of the left side of the body. A ground electrode was placed on the left iliac crest. Raw EMG signals were preamplified, sampled at 600 Hz and full-wave rectified.

Data reduction

Since there was no training effect present between the two trials completed by each subject, the data were averaged across the two trials.

Kinetics and kinematics

The vertical component of ground reaction force (F_Z) was derived from summing the forces from the four piezoelectric crystals mounted in the corners of the force plate. The center of pressure (COP) displacements in both A/P and medial/lateral (M/L) directions were calculated using standard methods (Henry et al. 1998). The two-dimensional co-ordinates of body markers were filtered at 6Hz. A bilaterally symmetrical six-link body segment model composed of the feet, shanks, thighs, trunk, arms and head was used to estimate the total body center of mass (COM) position in the anterior-posterior direction (Vaughan et al. 1991).

Postural muscle activity

Postural muscle activity was identified as the first burst of activity that was greater than two standard deviations above the base line and that lasted more than 50 ms. Phasic activity in all postural muscles associated with postural responses to a perturbation of the support surface were coded relative to the beginning of each backward and forward platform translations. For each muscle, the probability of phasic activity associated with backward or forward perturbations was calculated for each frequency of platform oscillation. The presence of muscle co-contraction was also recorded. In order to be considered a dynamic postural response triggered by the surface perturbations and to be included in calculations of group postural muscle onset latencies, a muscle had to be active in at least 50 % of the directionally specific perturbations of each frequency. The only exception was made when calculating group values of onset latencies for the TA and G muscles in young adults who, at 0.1 Hz, recruited these muscles during 30 % and 20% of the perturbations, respectively.

Postural muscle onset latencies were coded initially in milliseconds relative to the point of change in direction of the platform which corresponds to the extremes in platform position (see Figure 1). Since the absolute duration of a cycle varied as a function of cycle frequency, relative muscle onset latencies were determined as a percentage of half-cycle time. A half-cycle was considered to be the movement of the platform from one extreme position to the other extreme position. For each postural muscle, onset latencies were coded positive if the burst occurred after time zero and negative if the bursts occurred before time zero.

Place Figure 1 near here

In previous reports of responses to oscillating platform movement (Buchanan and Horak 1999, 2001, Nardone et al. 2000), data from the first one-half to three cycles of platform movement or the first 10 sec after frequency change were discarded and analyses of the remaining cycles assumed to reflect steady-state behaviour. However, Dietz et al. (1993) reported that adaptation to an increase in oscillation frequency may take up to 4 cycles. Our interest was in exploring the relationship between reactive to anticipatory mechanisms of control. Since these mechanisms are not exclusive (Frank and Earl 1990) and it is likely that movements in one cycle influence the next one, data from the initial three cycles at 0.1 Hz and the first five cycles at 0.25 Hz, 0.5 Hz and 0.61 Hz were considered transition periods and were analyzed separately. The remaining cycles at each frequency of platform translation constituted the steady state periods during which the platform motion was constant and predictable.

Data analysis

Three way (Group (young, old) x Frequency (0.1, 0.25, 0.51, and 0.61 Hz) x Period (transition, steady state)) repeated measures analyses of variance (ANOVAs) were used to test for significant differences in the probability of postural muscle activation, postural muscle onset latencies as well as COP and COM displacements. When analyzing the probability of postural muscle activation, separate analyses were performed for muscles associated with a forward perturbation (TA, Q, and NF) and for muscle associated with a backward perturbation (G, H, BE and NE). Separate analyses of muscle onset latencies were performed for each muscle. P-values for post-hoc analyses were corrected according to the number of post-hoc comparisons made (p=.05 / number of comparisons).

Cross-correlation coefficients were calculated to describe the relationships between COP A/P and platform movement, COM A/P and platform movement, and COP A/P and COM A/P. The correlation coefficients were first calculated at zero phase lag between each pair of signals. Subsequently the two time series signals were temporally shifted relative to each other, and correlations calculated at phase lags up to 5, 2, 1 and .82 seconds corresponding to a half cycle time for the four respective frequencies, 0.1, 0.25, 0.5 and 0.61 Hz. The phase lag corresponding to the highest cross-correlation was recorded.

RESULTS

Probability of postural muscle activity

Both groups of subjects activated appropriate postural muscles for each direction of perturbation with muscle co-contractions recorded infrequently in both groups. The probability of recording activity from at least one postural muscle increased in young and old adults as platform oscillation frequency increased (Figure 2). Separate three-way ANOVA (Group X Frequency X Period) with repeated measures were performed for each direction of platform movement. There was no significant three-way interaction effect for either direction of platform movement (Forward: $F(3, 42)=.847$, $p=.4$; Backward: $F(3, 42)=.871$, $p=.463$). For forward platform oscillations, significant main effects of Frequency ($F(3, 42)=22.787$, $p<.001$), Period ($F(1, 14)=11.402$, $p=.005$) and Group ($F(1, 14)=8.598$, $p=.011$) were revealed in addition to significant interaction effects (Frequency X Group: $F(3, 42)=7.239$, $p=.002$; Frequency X Period: $F(3, 42)=6.315$, $p=.015$; Period X Group: $F(1, 14)=7.132$, $p=.018$). In contrast, for backward platform oscillations, solely a significant interaction effect of Frequency X Group ($F(3, 42)=3.026$, $p=.04$) and a significant main effect of Frequency ($F(3, 42)=10.739$, $p<.001$) were revealed.

Decomposition of the interaction effects revealed that the number of cycles where activity was recorded in at least one postural muscle: 1) was higher in the transition versus steady state period at 0.1 and 0.25 Hz in the young adults following a forward platform translation; 2) increased as the frequency of oscillation increased during steady state periods in response to forward perturbation in both young and old adults and in response to backward perturbation in young adults; 3) was higher in the old adults during steady state period at 0.1 and 0.25 Hz.

Postural muscle response complexity differed between the two groups with old adults using more postural muscles than young adults in response to platform movement at lower frequencies (Figure 3). There were no Frequency X Period interaction effects for either the young ($F(6,110)=1.547$, $p=.169$) or old ($F(6,100)=1.094$, $p=.371$) adults. Significant Frequency ($F(6,110)=8.629$, $p<.000$) and Period ($F(2,54)=846$, $p=.005$) main effects were found for the young adults. In the young adults, three and four muscle responses were recorded infrequently and only at the higher frequencies during the transition period, with the probability of recording more complex response decreasing substantially from transition to steady state periods at 0.1 and 0.25 Hz .

No significant Frequency ($F(6,110)=1.711$, $p=.125$) and Period ($F(2,54)=.147$, $p=.864$) main effects were found the old adults. In the old adults, use of three muscles was recorded even at the lowest frequency of platform oscillation and the greater complexity of the response remained obvious in both periods of perturbations. This suggests that even though they were at a constant frequency in steady state period, the task was not getting any easier for the old adults. Moreover, while young adults relied primarily on distal muscle activity to maintain balance during transition and steady state periods, old adults incorporated back and neck muscles in a greater number of responses.

Place Figure 2 near here

Place Figure 3 near here

Postural muscle onset latencies

Independent three-way ANOVAs for each muscle showed significant main effects of Frequency, Period and Group as well as significant two-way interaction effects (Frequency x Group, Frequency X Period, Group X Period; $p < .01$ for all comparisons). Compared to young adults, postural muscles were activated consistently later by the old adults for both directions of platform movement (Figure 4). Exact p values from post hoc analysis of differences in postural muscle onset latencies between young and old adults in both transition and steady state are given in Table 1.

Place Table 1 near here

There were no significant differences in muscle onset latencies between the two groups, during transition periods at 0.1 and 0.25 Hz. These two frequencies are relatively slow and both groups were successful in maintaining balance by using similar reactive mechanisms. At higher frequencies of oscillation, muscle activity during the transition period was significantly earlier in the young than the old adult (Figure 4). In steady state periods, phasic activity recorded in almost every postural muscle occurred earlier in young than old adults suggesting that the two groups employed different mechanisms of control. An anticipatory mechanism was used by the young adults with postural muscle activity related to slowing of the platform. In the old adult, a reactive mechanism was used with postural muscles onset latencies related to the slowing and change in direction of the platform.

Separate analyses of postural muscle onset latencies for each group were completed in order to determine whether there was a shift in the control mechanism used to maintain balance between the transition and steady state periods. In the old adults, transition periods were characterized by postural muscle activity at latencies close to the reversal of platform direction, either as the platform decelerated prior to or accelerated following a change in direction. There were no significant differences in the onset latencies between transition and steady state periods with two exceptions: slightly earlier postural muscle activity during the steady state periods for the G muscle at .1 Hz and the TA muscle at 0.5 Hz (see Table 2).

Young adults activated their postural muscles at or around the point of change in platform direction during the transition period at 0.1 Hz and around the point where the platform was slowing down during the transition periods at 0.25, 0.5 and 0.61 Hz (Figure 4). In contrast to old adults, steady state periods in young adults were characterized by significantly earlier activity in all postural muscles (see Table 2).

Place Figure 4 near here

Place Table 2 near here

In order to determine whether subtle differences in the postural muscle onset latencies recorded in the young and old adults were camouflaged by grouping data from sequential oscillations, data for the first and last five cycles at different perturbation frequencies are reported. Tibialis anterior and gastrocnemius muscle onset latencies (mean ± SD) from young and old subjects at 0.25, 0.5 and 0.61 Hz are represented in Figure 5.

Place Figure 5 near here

As illustrated, in the first cycle of the transition period at all frequencies, both young and old adults activated the distal postural muscles close to the time of platform change in direction. Over the subsequent cycles at 0.25, 0.5 and 0.61 Hz, TA and G muscle activity was recorded in the young adults at increasingly earlier latencies. The shift to earlier onsets continued through the transition period and distal muscle onset latencies remained stable over the remaining cycles in the steady state period. No consistent shift in either TA or G muscle onset latency was noted during the transition period in the old adults. Moreover, old adults did not reach the same values of anticipatory or early postural muscles onset latencies as the young adults even after 10, 30 or 40 cycles in the steady state periods at 0.25, 0.5 and 0.61 Hz, respectively.

Regulation of center of mass and center of pressure

The ranges of COM and COP displacements are plotted for steady state and transition periods across all frequencies for the young and old adults (Figure 6). A three-way ANOVA of the COP data revealed significant main effects of Group ($F(1,15) = 19.957$, $p < .001$), Period ($F(1,15) = 20.176$, $p < .001$), Frequency ($F(3,15) = 126.340$, $p < .001$) as well as a significant interaction effect of Frequency X Group ($F(3,15) = 4.894$, $p = .003$). There were no significant interaction effects of Frequency X Period ($F(3,15) = 2.333$, $p = .078$), Period X Group ($F(1,15) = .289$, $p = .592$) or Frequency X Period X Group ($F(3,15) = .034$, $p = .992$). For the COM, the three-way ANOVA revealed a significant interaction effect of Frequency X Group ($F(3, 15) = 11.17$, $p < 0.001$) and main effects of Frequency ($F(3,15) = 21.13$, $p < 0.001$) and Group ($F(1, 15) = 44.46$, $p < 0.001$). No other interaction or main effects reached the level of statistical significance.

Displacements of the COM A/P and COP A/P were compared between young and old subjects across oscillation frequencies and perturbation periods. For both COP and COM variables, no significant differences between the two groups were noted at .1 and .25 Hz during transition or steady state periods. During the transition periods at the higher frequencies, displacement of the COP at 0.5 Hz and COM at both 0.5 and 0.61 Hz was greater in the old than the young adult (COP at 0.5 Hz: $p=.031$, COM at 0.5 Hz and 0.61 Hz: $p=.003$, $p=.004$). The COP displacement remained significantly higher in the old adult during the steady state period at 0.5 Hz ($p=.014$). Significantly greater amplitude of COM displacement in the old adult was also recorded in the steady state period at 0.61 Hz ($p = .002$.)

Place Figure 6 near here

It was expected that COM and COP displacements would be regulated with less movement recorded during steady state than transition periods. Contrary to expectation, there was no period-dependent modulation of the COM with minimal period-dependent modulation of COP movement amplitude recorded in both groups. In the young adults, COP A/P displacement was significantly less during steady state than transition at 0.1 and 0.25 Hz ($p<.001$ and $p=.005$). In the old adults, significantly less displacement of the COP was recorded during steady state compared to transition period at 0.1Hz ($p<.001$).

In young and old adults, there were significant increases in COP A/P displacements in both transition and steady state periods as the platform frequency increased to 0.5 Hz (young adults, transition period: $p<.001$ and steady state period: $p<.001$; old adults, transition period: $p<.001$ and steady state period: $p<.001$). Increasing platform oscillation frequency to 0.61 Hz did not result in additional COP displacement in either period.

The trend for COM displacement in the young adult was consistent across transition and steady state periods. At the two lowest frequencies, COM displacement closely matched the magnitude of platform displacement (approximately 20 cm) suggestive of a "ride" pattern as reported by Buchanan and Horak (1999). As platform oscillation frequency increased, the magnitude of COM movement decreased significantly. In contrast, there was minimal modulation of COM displacement by the old adults. Specifically, a significant increase in COM was recorded during the transition period as the frequency increased to 0.5 Hz followed by a decrease in COM displacement with the platform frequency increase to 0.61 Hz. There was no modulation of the COM during steady state by the old adults.

Cross-correlation coefficients and phase lags between the platform, COP A/P and COM A/P time series were determined for the two highest frequencies of oscillation. With a zero phase lag, moderate cross-correlations coefficients between the platform, COP A/P and COM A/P time series were obtained and the values were similar in the young and the old adults for both platform frequencies. Time series signals were temporally shifted relative to each other and the phase lag with the highest cross-correlation was recorded. The movement of the COM A/P and COP A/P always lagged the platform movement. Mean cross-correlation coefficients calculated at zero phase lags, as well as maximum cross-correlation coefficients and the corresponding phase lag calculated between COP A/P and platform, COM A/P and platform, and COP A/P and

COM A/P in young adults and old adults at 0.5 Hz are presented in Table 3. Similar results were obtained at 0.61 Hz. Analysis of variance revealed no significant effect of Frequency or interaction effect of Frequency X Group for any of the three pairs of variables: COP A/P with platform ($F(1,14)=.427$, $p=.524$), COM A/P with platform (($F(1,14)=2.681$, $p=.124$) or COP A/P with COM A/P ($F(1,14)=.179$, $p=.678$).

The phase lags corresponding to the maximum correlation between two time series signals were significantly longer in old than young adults: COP A/P with platform ($F(1,14)=11.904$, $p=.004$), COM A/P with platform (($F(1,14)=.179$, $p=.678$) and COP A/P with COM A/P ($F(1,14)=13.520$, $p=.002$)

Place Table 3 near here

DISCUSSION

This study used an oscillating platform to investigate anticipatory and reactive postural control mechanisms elicited when perturbations of comparable mechanical characteristics were used. The results from these experiments clearly show that the ability to compensate for an impending yet highly predictable perturbation decreases with aging.

Adaptation of postural response changes with aging

Young adults used two distinct patterns of postural muscle activation. During transition periods and specifically for the initial cycles following changes in platform frequency, young adults generated activity in response to the slowing and change in direction of the platform while in steady state periods, timing of muscle activity was indicative of anticipation of platform slowing. The differences were consistent for the proximal and distal postural muscles with adaptation occurring over three to five cycles at each frequency. The rapid shift in absolute timing of postural muscle activity was frequency independent. Similar adaptations of both gastrocnemius and tibialis anterior muscle patterns to sinusoidal motion of a treadmill have been reported in young adults for trials averaged over four cycles at a new frequency (Dietz et al. 1993). Successive trials of discrete backward platform translations also elicit enhanced ankle muscle responses at latencies that decrease over three to five trials (Nashner 1976).

Two components have been identified in the adaptation response to repeated perturbation (Hansen et al. 1988). First, the initial change between the first and subsequent trials has been attributed to habituation of a startle-like response. The startle response is known to attenuate quickly, and therefore, would be expected to be a non-significant factor after the first perturbation. A second more gradual change reflecting actual adaptation occurs over the subsequent series of perturbations. Recent work has demonstrated that the amplitude of postural responses is constantly modulated, even when they are appropriate (Pavol and Pai 2002). Woollacott et al. (1988) examined the responses of adults to repeated translational platform movements and found that with repeated exposure to movements, subjects swayed less and showed smaller amplitude responses. Thus, with repeated exposure to a given task, subjects refine their response characteristics to optimize response efficiency.

In the current experiment, no adaptation was recorded in the old adults even after 50 cycles. During both transition and steady state periods, although the same postural muscles were used, muscle onset latencies were consistent with a reactive mechanism of control with old adults responding to the slowing down and change in direction of the platform. The lack of adaptation may reflect age-related changes in interactions between postural control and higher level neural processes Experimental evidence suggests that the time course of sensorimotor adaptation is moderately degraded with age (Bock and Schneider 2002). There is cumulating evidence of age-related declines in sensorimotor performance such as stimulus discrimination, simple reaction time and the utilization of pre-cues (Cerella 1990, Hale et al. 1987). It was expected that the continued oscillation of the platform could or would work like a pre-cue to augment alertness and thus facilitate responses. Old adults may take longer to consolidate newly gained information into long-term motor memory.

Stiffness as an anticipatory compensatory mechanism for low frequency perturbations

When platform movement is consistent over multiple cycles, the mechanical perturbation induced is predictable and should be more easily managed than a discrete perturbation. Subjects can anticipate the effects of both the perturbation and their postural corrections and should be able to exploit multiple means of maintaining balance with the least effort.

The low probability of recording discrete bursts of postural muscle activity at low frequencies (0.1 and 0.25 Hz) suggests the use of alternate control mechanisms such as the use of muscle stiffness and/or body inertia. At low translation frequencies, body displacement mirrored platform motion with similar average displacements of COP and COM in the young and old adults. Under these circumstances, body kinetic energy is reduced. Smaller and even delayed generation of active forces together with the intrinsic stiffness of the body are possibly sufficient to counteract the effect of sequential perturbations. Our results correspond with those of Corna et al. (1999) who reported that at low frequency translations (0.2 Hz) young adults "followed" the platform with little body movement.

When the frequency of the platform increases however, this strategy is no longer sufficient for maintaining balance. The most functionally appropriate strategy is rather to pursue and comply with movement of the platform, mobilizing the different body links to an appropriate extent (Corna et al. 1999). At higher frequencies of platform translations, young adults activated the appropriate muscles indicating anticipatory response to the perturbations. A similar strategy was reported at 0.6 Hz in young adults who exploited body inertia, with the malleolus and hip segments consistently phase-lagged relative to the head segment (Buchanan and Horak 1999, Corna et al. 1999).

In old adults, the probability of muscle activation was very high at both slow and fast translation frequencies. Old adults activated the same group of muscles as the young adults; however the timing and complexity of muscle pattern activity was different. The use of proximal muscles such as back extensors, neck flexors and extensors at onset latencies consistent with a reactive mechanism of control shows that, even at low frequencies, old adults tried to actively stiffen the body by muscle activation and failed to exploit intrinsic muscle stiffness and/or inertia to control their balance.

Decreased regulation of the relationship between the center of mass and center of pressure

The nervous system acts to control the position of the body's centre of gravity relative to the feet (Dietz et al. 1993). Controlling for the displacement of the COM by movement of the COP is a strategy that works well in quiet stance. However, in a dynamic situation one has to take into account also the velocity at which a movement takes place. It is important to consider not only how far the COM is displaced but also how fast it is moving. It is possible that the old subjects relied on a strategy taking into consideration only the displacements of the COP and COM, and not using the cues about the velocities at which these displacements occur. The neuro-physiological basis for velocity-dependent somatosensory afferent activity is well documented at the peripheral (Johansson et al. 1982, Matthews 1988) and central levels (Esteky and Schwark 1994). Jeka et al. (1997) have shown that somatosensory information from the fingertip and arm couples into the postural control system through the relative velocity of touch bar and body movement. Lack of sway velocity regulation has been shown in older adults at risk for falls. Fernie et al. (1982) examined both sway amplitude and velocity in a population of institutionalized elderly and determined that sway velocity, but not amplitude, was significantly greater for those who had fallen one or more times in a year than for those who had not fallen.

In addition to COM velocity, regulation of relative position of the COP and COM is crucial. The phase lags between platform and both COP and COM signals were consistently longer in old adults indicative of reactive postural control driven mainly by platform movement. The increased range of COP in old adults may reflect their inability to correctly predict how far the COP has to move relative to COM. Winter et al. (1998) described the algebraic difference between "COP-COM" displacements as the error in the postural system. One explanation for the increased range in COP A/P may be the age-related loss of plantar sensory function (Maki and McIlroy 1996, Perry et al. 1999). Perry et al. (1999) suggested that inadequate or delayed detection of the need for a compensatory reaction due to sensory loss may place the old adult at risk of being unable to compensate for disturbance of their balance and that augmenting plantar surface information may facilitate response or predictive ability.

CONCLUSION

These data suggest that the anticipatory postural mechanism was not used by old adults for regulating balance in this paradigm. Rather, old adults responded to a predictable postural challenge using reactive postural adjustments independent of the frequency of platform oscillation, the direction of perturbation and without adapting over multiple trials. The use of a reactive mechanism in steady state periods may be a consequence of an improper reactive response in the transition period. Before a switch to the anticipatory mechanism is possible, a certain level of postural stability may be required. The role of the reactive mechanism inside the transition period, as well as throughout the stable state, could be to achieve this stability which would permit a subsequent switch to anticipatory mechanisms. It is possible that because of a lack of the ability to initially successfully integrate the multiple sensory sources and generate appropriate responses, old adults never achieved this level of stability. Providing increased warning of an impending perturbation and augmenting sensory information to allow for earlier detection of destabilization may improve postural responses in the old adult.

Acknowledgements

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Table 1. P values from post hoc analyses of differences in postural muscle onset latencies between young and old adults. Comparisons reported for transition and steady-state periods.

	Transition period				Steady state period			
	TA	G	Q	H	TA	G	Q	H
Frequencies								
0.1 Hz	.537	.229			.013	**<.001**		
0.25 Hz	.029	.111	.468	.030	**<.001**	**<.001**	**.003**	**<.001**
0.5 Hz	**.001**	**.001**	.039	**.001**	**<.001**	**<.001**	**<.001**	**<.001**
0.61Hz	**<.001**	**.003**	**.001**	**.001**	**<.001**	**<.001**	**<.001**	**<.001**

Statistically significant comparisons (p<.006) are indicated in bolded text. No analysis was performed for Q and H muscles at 0.1 Hz as there was no activity recorded in the young adults.

Table 2. P values from post hoc analyses of differences in postural muscle onset latencies between transition and steady-state periods. Comparisons reported for young and old adults.

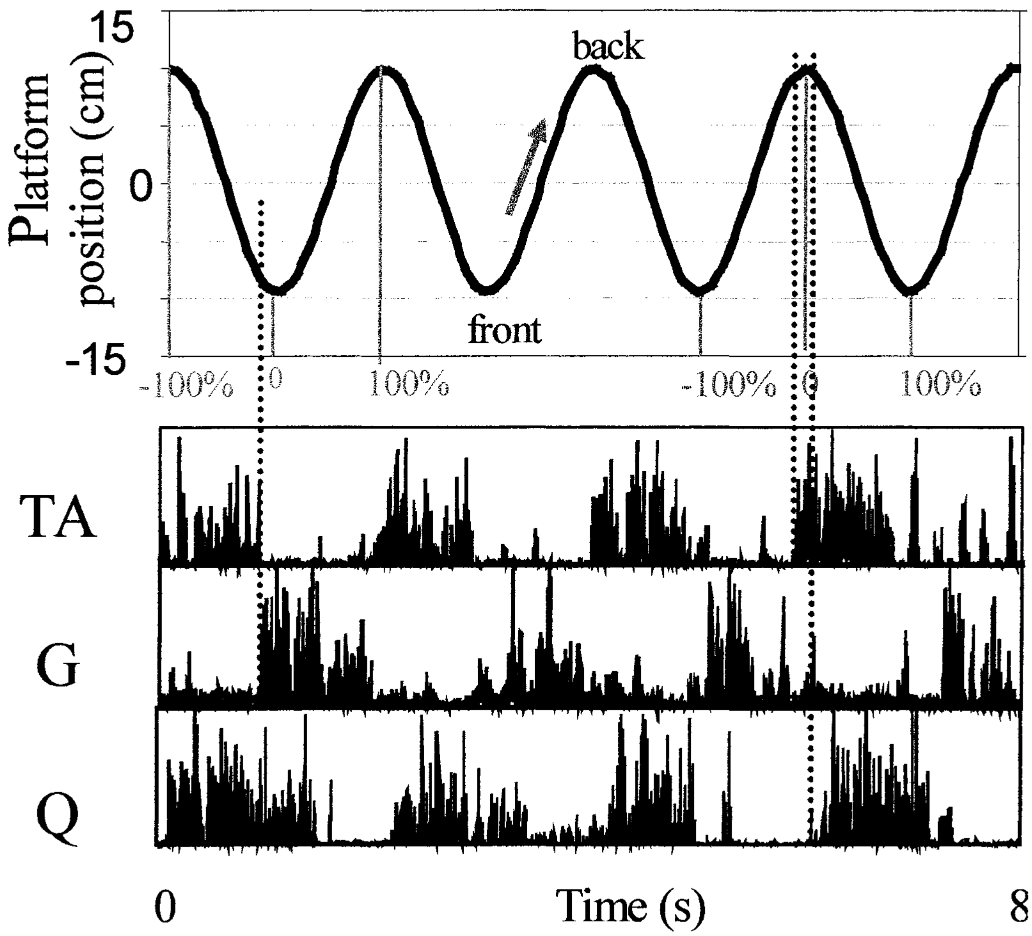
	Young adults				Old adults			
	TA	G	Q	H	TA	G	Q	H
Frequencies								
0.1 Hz	**.005**	**.002**			.805	**.006**	.364	.05
0.25 Hz	**.001**	**< .001**	**.004**	**<.001**	.32	.184	.546	.077
0.5 Hz	**<.001**	**<.001**	**.001**	**.003**	**.004**	.403	.336	.023
0.61Hz	**<.001**	**.001**	**<.001**	**.005**	.058	.447	.248	.911

Statistically significant comparisons ($p<.006$) are indicated in bolded text.

Table 3. Cross correlation coefficients and phase lags between time series displacements of COP A/P, COM A/P and platform during steady state at 0.5 Hz in young and old adults.

	Young adults			Old adults		
	COP A/P with platform	COM A/P with platform	COP A/P with COM A/P	COP A/P with platform	COM A/P with platform	COP A/P with COM A/P
Cross correlation coefficients obtained at zero phase lag	0.63 ±0.19	0.95 ±0.02	0.75 ±0.11	0.53 ±0.30	0.87 ±0.11	0.69 ±0.17
Maximum cross correlation coefficients	0.78 ±0.12	0.96 ±0.02	0.88 ±0.07	0.74 ±0.14	0.90 ±0.09	0.82 ±0.13
corresponding phase lag (ms)	-128 ±52.5	- 43.5 ±22	-78 ±16	-227 ±102	-84 ±22.5	-178 ±93.5

Fig. 1 Examples of platform movement and activity in tibialis anterior (TA), gastrocnemius (G) and quadriceps (Q) muscles recorded from an old adult during four cycles of platform oscillation in steady state period at 0.5Hz. The arrow indicates backward platform translation. Zero represents the time at which the platform changed direction, while -100% and +100% represent the half cycles preceding and following the change in direction, respectively. Examples of coding postural muscle onset latencies are indicated with vertical lines. For each muscle, relative onset latencies were determined as a percentage of half cycle time, with a positive or negative value if the burst occurred after or before time zero, respectively.



15
0
-15
Platform position (cm)
back
front
-100%
0
100%
-100%
0
100%
TA
G
Q
0
Time (s)
8

Figure 1

Fig. 2 Percentage of perturbations where activity was recorded for each postural muscle in young (grey bars) and old (black bars) adults. The error bars represent ±1 SD around the mean. Values for tibialis anterior (TA), quadriceps (Q), neck flexor (NF), gastrocnemius (G), hamstring (H), back extensor (BE), and neck extensor (NE) muscles at two frequencies of platform translation (0.25 and 0.5Hz), during the transition (A, B) and the steady state periods (C, D) are presented.

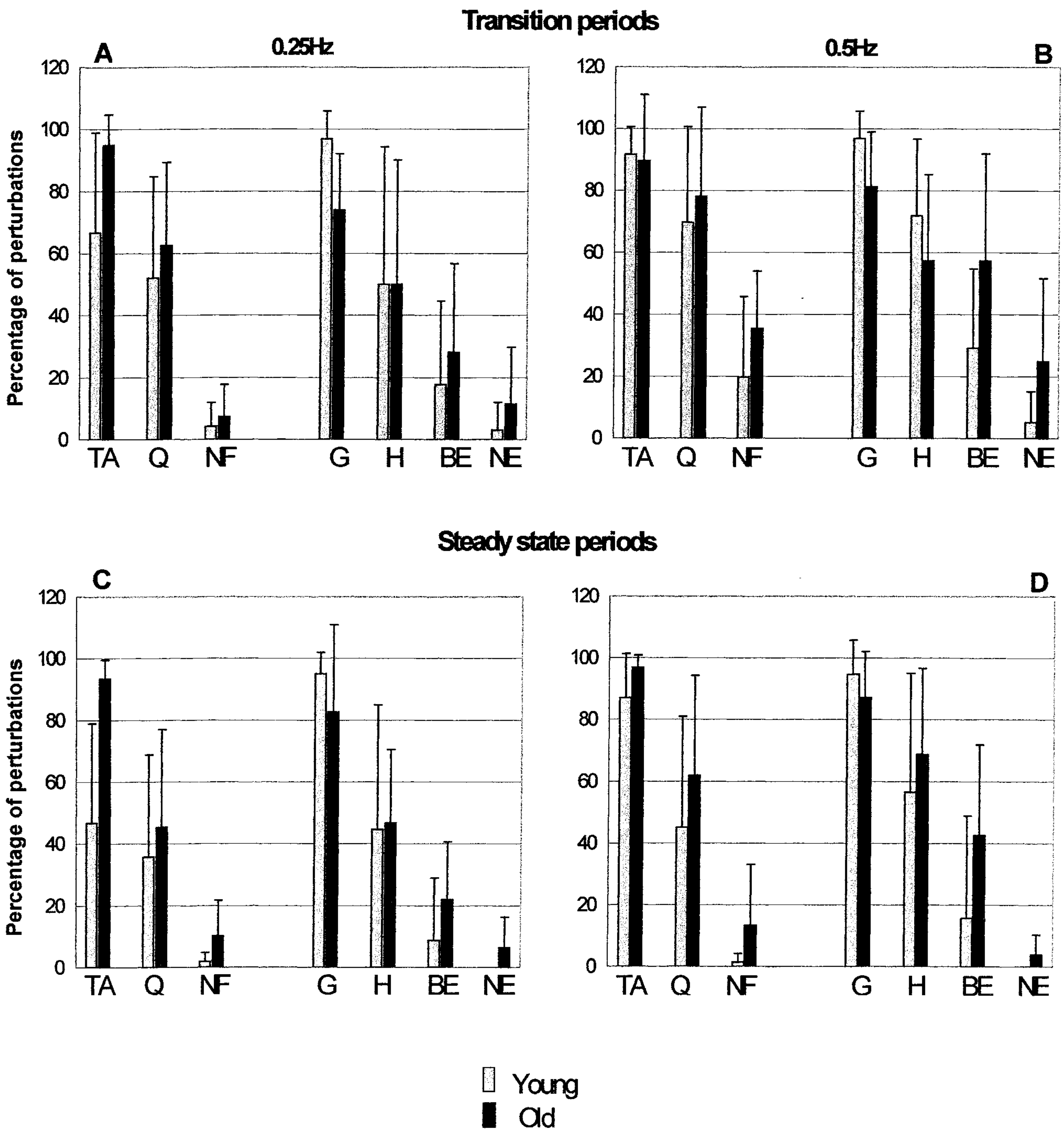

Transition periods
A
0.25Hz
0.5Hz
B
Percentage of perturbations
120
100
80
60
40
20
0
TA
Q
NF
G
H
BE
NE
Steady state periods
C
D
Young
Old

Figure 2

Fig. 3 Percentages of platform oscillations where phasic bursts of activity were recorded in 1, 2, 3 or 4 postural muscles following a forward perturbation (left panels) or a backward perturbation (right panels) for all four frequencies of platform oscillations. Data for transition (top panels) and steady state periods (bottom panels) are plotted. Bars at the left and right within each pair represent data from young and old adults, respectively.

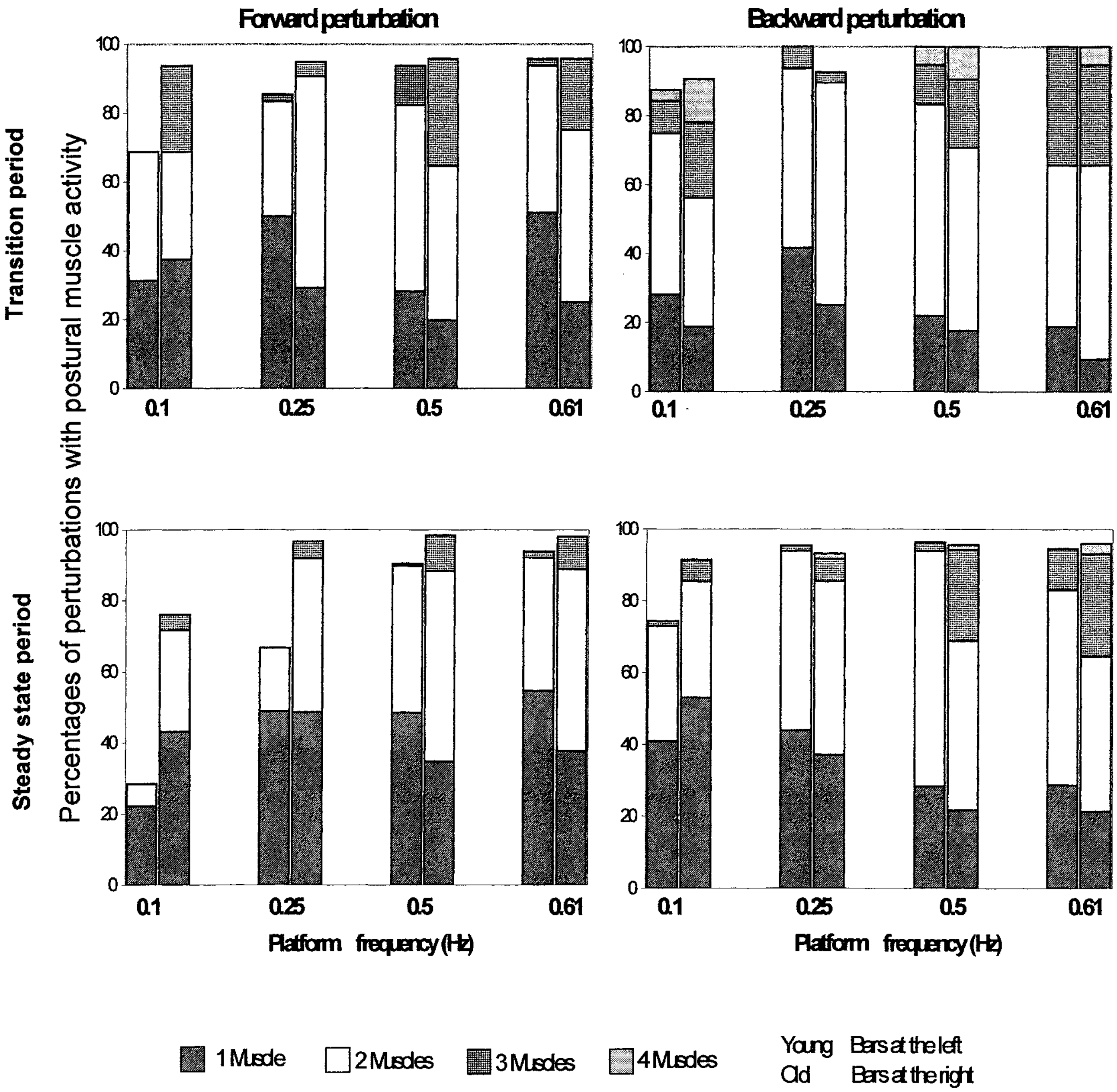
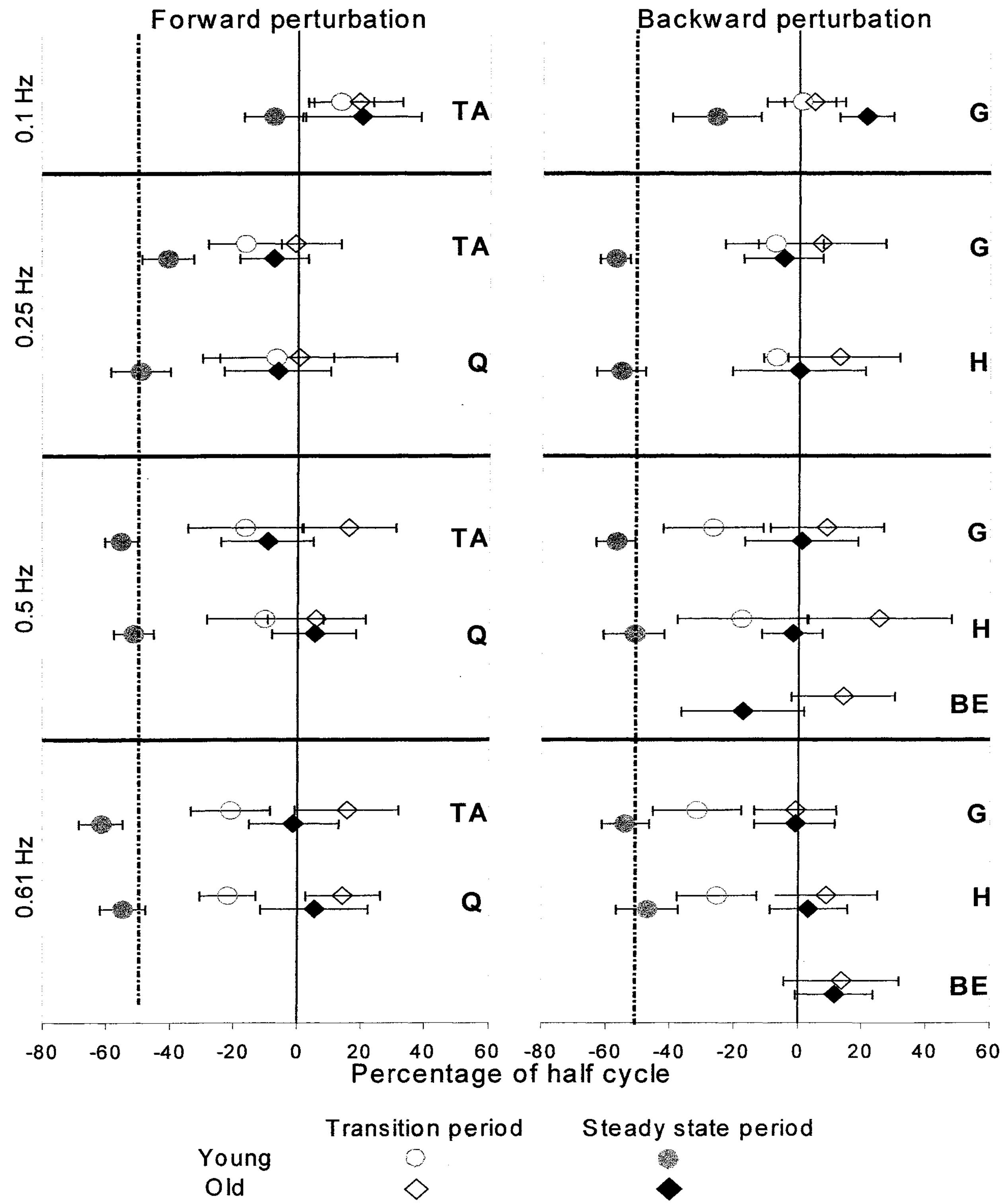

Forward perturbation
Backward perturbation
Transition period
Steady state period
Percentages of perturbations with postural muscle activity
100
80
60
40
20
0
0.1
0.25
0.5
0.61
Platform frequency (Hz)
1 Muscle
2 Muscles
3 Muscles
4 Muscles
Young Bars at the left
Old Bars at the right

Figure 3

Fig. 4 Postural muscle onset latencies (mean ± SD) of young adults (circle icons), and old adults (diamond icons) at the four frequencies of platform translation 0.1, 0.25, 0.5 and 0.61 Hz. Onset latencies are expressed as a percentage of half cycle time for muscles normally associated with a forward perturbation (TA, and Q; left panel) and for muscles normally associated with a backward perturbation (G, H, and BE; right panel). Zero represents the time at which the platform changed direction. For both forward and backward directions of motion, the platform began to slow down after the -50% mark indicated with a dashed line. Open and filled icons represent data from transition and steady state periods, respectively. For clarity purposes, values for the transition periods are offset on the *y* axis. Onset latencies of the BE are illustrated only for old adults since, in the young adults, this muscle was activated in less than 50% of the trials.



Forward perturbation
Backward perturbation
0.1 Hz
0.25 Hz
0.5 Hz
0.61 Hz
TA
Q
G
H
BE
-80
-60
-40
-20
0
20
40
60
Percentage of half cycle
Transition period
Steady state period
Young
Old

Figure 4

Fig. 5 Tibialis anterior (left panels) and gastrocnemius (right panels) muscle onset latencies (mean ± SD) for young adults (circle icons), and old adults (diamond icons) at three frequencies of platform translation, 0.25, 0.5, and 0.61 Hz. Values from the first five trials following the increase in oscillation frequency (trials 1 to 5; transition period) and from the last five trials at each frequency (trials 16 to 20 at 0.25 Hz, 36 to 40 at 0.5 Hz, 46 to 50 at 0.61 Hz; steady state period) are represented. Note the difference in scale of the abscissa (time, ms) due to different absolute cycle times across frequencies. Zero represents the time at which the platform changed direction.

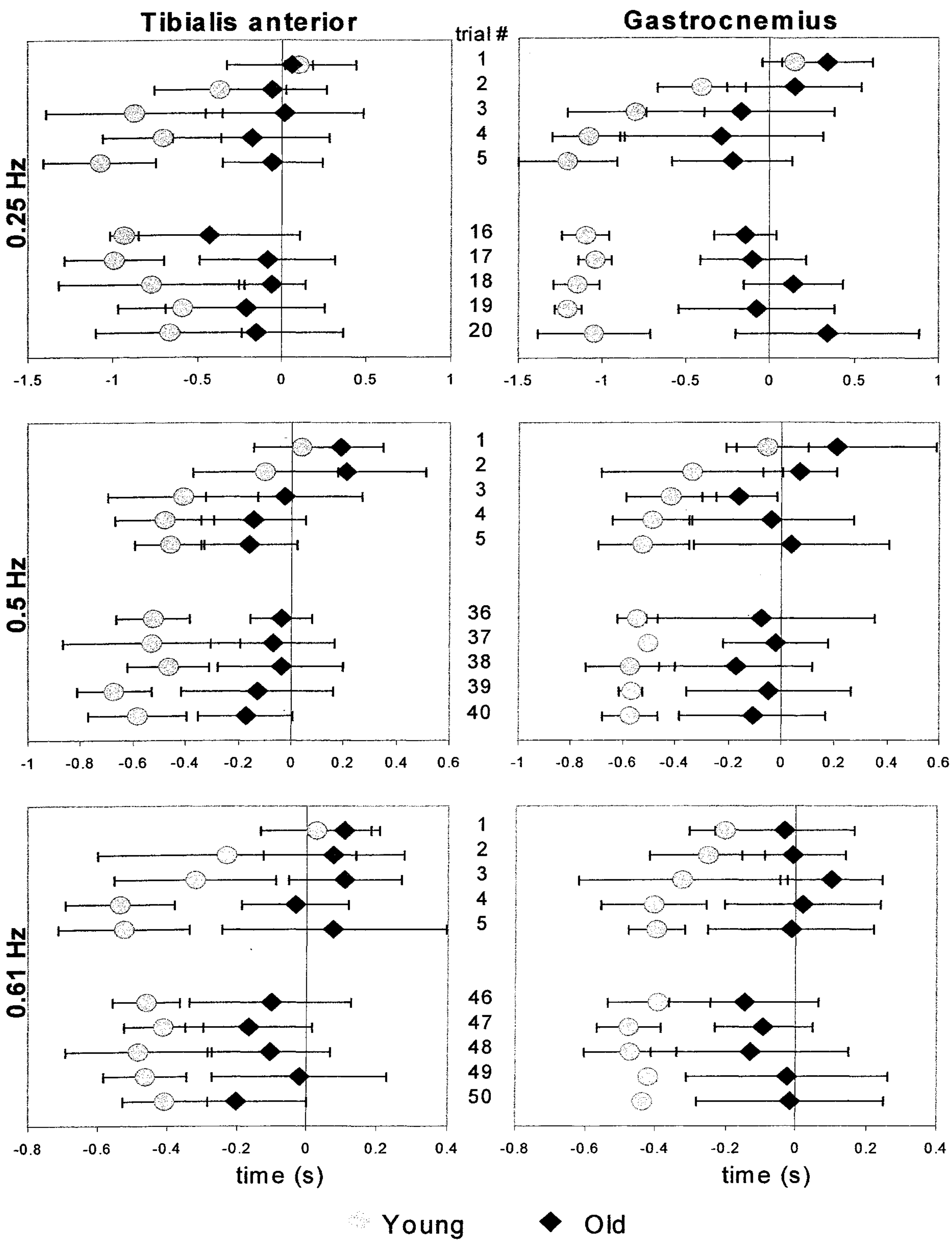
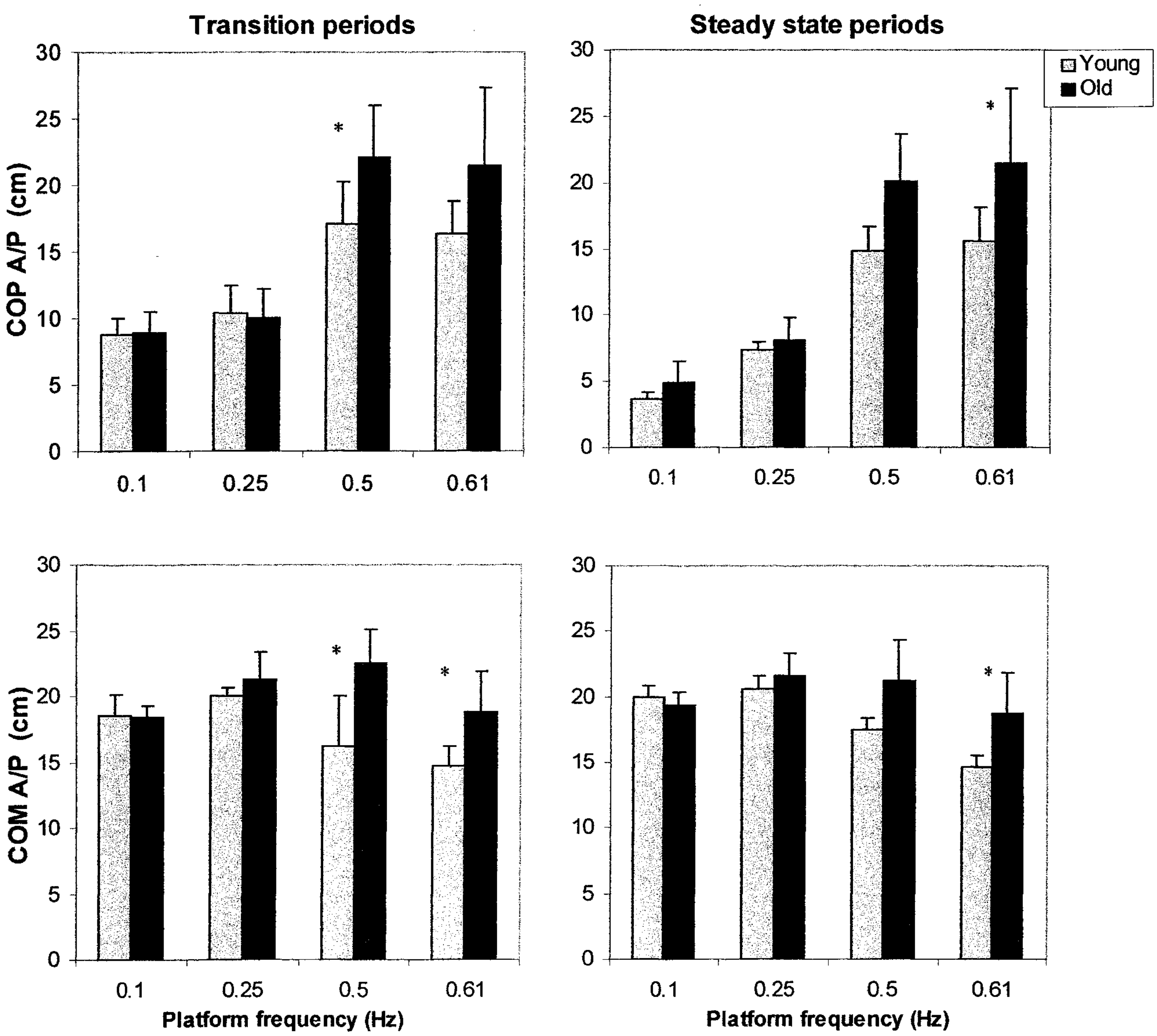

Tibialis anterior
Gastrocnemius
trial #
0.25 Hz
0.5 Hz
0.61 Hz
1
2
3
4
5
16
17
18
19
20
36
37
38
39
40
46
47
48
49
50
time (s)
time (s)
Young
Old

Figure 5

Fig. 6 Group means (± SD) of COP A/P (top panels) and COM A/P (bottom panels) range of displacement from old (black bars) and young (grey bars) adults. Data from transition (left panels) and steady state periods (right panels) at four frequencies of platform translations are presented.



Transition periods
Steady state periods
Young
Old
COP A/P (cm)
COM A/P (cm)
0.1
0.25
0.5
0.61
Platform frequency (Hz)
*

Figure 6

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CHAPTER 3

Age-related changes in postural responses to externally- and self-triggered continuous perturbations

ABSTRACT

The purpose of this study was to determine whether aging disrupts the anticipatory adjustments in response to continuous externally-triggered perturbations (ETP) and self-triggered perturbations (STP) in the same manner. Healthy young and old adults were exposed to continuous anterior/posterior (A/P) sinusoidal ETP and STP. The 20 cm peak-to-peak displacements were delivered at successively higher frequencies of 0.1, 0.25, 0.5 and 0.61 Hz. Step numbers, centre of pressure (COP) and postural muscle activity (EMG) were analyzed. Young adults used anticipatory adjustments in both ETP and STP. The old adults' use of anticipatory adjustments, characterized by earlier postural muscle onset latencies, fewer steps, tighter coupling of the COP and platform movements and smaller A/P COP excursions, were recorded in STP but not ETP. However, COP range remained larger and was located in less safe regions at the boundaries of the base of support (BOS) for more time in old compared to young adults. In older adults, self-triggering postural perturbations may have: i) primed the CNS to attend to proprioceptive information thus permitting the old adult to decrease the threshold for detecting changes in platform speed resulting in earlier postural muscle activity; ii) increased arousal/alertness facilitating incorporation of anticipatory postural strategies; and iii) decreased anxiety associated with postural threats permitting use of appropriate control mechanisms.

Keywords: Balance, Aging, Platform perturbation, Electromyogram, Center of Pressure, Stance

INTRODUCTION

Human movements are performed in a dynamic environment, with both predictable and unpredictable perturbations that are compensated with anticipatory and reactive control mechanisms. Anticipatory adjustments typically precede predictable perturbations, whether self- or externally generated, counteracting the expected destabilizing effects (Massion 1992, Toussaint et al. 1997, Shiratori and Latash 2001). Precise and correct anticipatory adjustments, based on adaptive internal representations of the system and expected external conditions (Wolpert 1995), can greatly reduce the magnitude of required reactive responses (Pavol and Pai 2002).

With expected disturbances of the BOS, when characteristics of platform displacement are known and signalled (Horak et al. 1989, Nashner 1976, Horak and Nashner 1986), subjects make appropriate adjustments: shift of body centre of mass (Pavol and Pai 2002, Cordo and Nashner 1982), changes in initial ankle torque responses (Horak et al. 1989), changes in postural muscle reflex gains (Wolpaw 1985), and decreased body displacement. Postural responses are also shaped by adjustments in central set (Horak et al. 1989, Hansen et al. 1988) resulting in modifications based on prior experience with perturbation characteristics and effectiveness of prior responses. Efficient and effective responses result when stimuli are predictable but responses are inappropriate when stimuli characteristics change unexpectedly.

Anticipatory control clearly operates when a disturbance is directly generated by the individual's own movements (Dufosse et al. 1985). McChesney et al. (1996) demonstrated that prior knowledge, either specific or non-specific of a forthcoming balance perturbation, decreased postural muscle onset latency, possibly by evoking alertness. With successive trials of backward support surface movement, the ankle muscle response is enhanced with the latency reduced over three to five trials (Nashner 1976, Hansen et al. 1988). In young adults, similar adaptations in ankle muscle activity occur between three and five (Bugnariu and Sveistrup 2001, Dietz et al. 1993) cycles after an unpredictable change in sinusoidal platform oscillation frequency.

In general, the central nervous system (CNS) also attempts to compensate for forthcoming perturbations of unpredictable magnitude or occurrence through anticipatory adjustments (Shiratori and Latash 2001, Pavol and Pai 2002). A continuous dynamic process of adjustment, based on the conditions and outcomes of the previous execution, takes place over two to three trials (Thoroughman et al. 2000, Scheidt et al. 2001). Responses of young healthy adults to perturbations of uncertain occurrence during a sit-to-stand task suggest that the CNS makes short-term anticipatory adjustments to reduce the likelihood of balance loss based on the conditions last experienced (Pavol and Pai 2002). Over a longer term, the CNS adapts to acquire an "optimal" movement strategy that decreases the overall probability of balance loss and reduces dependence on reactive responses to maintain balance in unpredictable conditions (Pavol and Pai 2002).

Deterioration of balance control systems (Lord et al. 1994, Maki and McIlroy 1996a) and/or psychological factors like fear (Tinetti et al. 1994, Vellas et al. 1997, Maki et al. 1991, Maki et al. 1994) may lead to alterations in postural control in old adults. For example, we have shown that old adults do not adapt and use anticipatory postural mechanisms in response to continuous ETP (Bugnariu and Sveistrup 2001). The purpose of this study was to determine whether aging disrupts the anticipatory adjustments in response to continuous externally-triggered perturbations (ETP) and self-triggered perturbations (STP) in the same manner.

Young and old subjects underwent continuous perturbations created by a translating platform that oscillated sinusoidally at successively higher frequencies. We hypothesized that the capacity of subjects to take advantage of an anticipatory mechanism of control would be reflected in earlier muscle onset latencies, shorter phase lags between platform and COP position time series, smaller amplitudes of COP displacement, and fewer steps in response to STP versus ETP.

METHODS

Subjects

Experimental procedures were approved and performed in accordance with the Tri-Council Policy Statement on Ethical Conduct for Research Involving Humans (Canada). Healthy volunteers with no history of falls, musculoskeletal or neurological problems participated including eight young adults recruited from the university population and eight older adults recruited from community social support and recreational programs. An equal number of men and women were included in each group. Mean (± SD) age, height, weight, and foot length were: 22.1 ± 2.3 years, 173.5 ± 8.3 cm, 71.3 ± 9.9 Kg and 27.9 ± 2.3 cm for the young adults and 70.1 ± 4.6 years, 167.3 ± 6.9 cm, 69.2 ± 8.1 Kg, and 27.3 ± 2.9 cm for the old adults, respectively. Foot plantar surface light touch threshold was tested with Semmes-Weinstein Monofilaments (North Coast Medical, Inc) at the level of the metatarsal heads and heel. Each monofilament is individually calibrated to deliver a target force within a 5% standard deviation. Foot plantar surface light touch thresholds were (mean ± SD) 2.9 ± 0.3 and 3.9 ± 0.7 for the young and old adults, respectively. Detecting the filament marked 3.61 delivering a target force of 0.4g represents the norm for foot plantar thresholds. Detection of a monofilament size 3.84 to 4.31, delivering pressures of 0.6 to 2 grams respectively, indicates diminished light touch. Based on product specification and more recent investigation (Voerman et al. 1999), the old adults' thresholds were highly functional.

Three clinical tests further characterized balance abilities of the old adults: Community Balance & Mobility Scale (CB&MS), Berg Balance Scale (BERG) and Activity Balance Confidence Scale (ABC). Mean ± SD scores were: 68 ± 7.8, 54.6 ± 0.9, 93.1 ± 8.4 out of maximum scores of 96, 56 and 100 for the CB&MS, BERG, and ABC, respectively.

Task and procedures

Participants stood erect, eyes open, barefoot with feet shoulder width apart on a movable platform that was driven by an electric motor. They were asked to maintain their balance and to avoid taking steps unless absolutely necessary. If a step was taken, they were instructed to bring their feet back to the initial position. Additional support was provided when necessary through a loose harness attached to the ceiling and by an assistant standing beside the platform.

The sinusoidal 20 cm peak-to-peak anterior/posterior (A/P) platform oscillation started at 0.1 Hz. At intervals of 80-100 seconds, the frequency was increased successively to 0.25 Hz, 0.5 Hz and 0.61 Hz. Trials consisted of 10 cycles at 0.1 Hz, 20 cycles at 0.25 Hz, 40 cycles at 0.5 Hz and 50 cycles at 0.61 Hz. Subjects completed two trials of ETP and STP, each. In ETP, the frequency of the platform was suddenly and unexpectedly increased. In STP, the subjects themselves increased the frequency of the platform movement using a hand-held device. The initial three cycles at 0.1 Hz and the first five cycles at 0.25 Hz, 0.5 Hz and 0.61 Hz were considered transition periods and were analyzed separately. The remaining cycles at each frequency of platform translation constituted steady state periods during which the platform motion was constant and predictable.

A Kistler force plate (Type 9286, Kistler Instrument Corp) was placed in the center of the moving platform. The ground reaction force and platform position signals were sampled at 600 Hz. Subjects started all trials standing centered on the force plate and the exact position of their feet relative to the force plate was marked. Surface electrodes were used to record activity of the tibialis anterior (TA), gastrocnemius (G), quadriceps (Q), hamstring (H) and back extensor (BE) muscles of the left side of the body. A ground electrode was placed on the left iliac crest. Raw EMG signals were preamplified, sampled at 600 Hz and full-wave rectified.

Kinematics

The COP A/P displacements were calculated using standard methods (Henry et al. 1998). The length of the base of support surface from heel to big toe was divided into 5 equal regions called the heel (0-20 %), central (20-40% and 40-60 %), metatarsal (60-80 %) and toe (80-100 %) regions. The heel and metatarsal regions are considered the extremes. The percentage of time the COP was located in each region was calculated.

Cross-correlation coefficients and phase lags between the platform and COP time series were determined for the two highest frequencies of oscillation. Time series signals were temporally shifted relative to each other and the phase lag with the highest cross-correlation recorded. Although COP excursions do not match COM excursions, the traditional view is that COP can be used as a biomechanical measure of the stabilizing postural reactions since the COP is the variable used to control the COM (Winter et al. 1998, Rietdyk et al. 1999) and in standing balance the trajectory of the COM is maintained within the extremes of the COP positions. Patton et al. (1999) demonstrated that under normal conditions, when subjects maintain balance, the COP safety margin (minimum distance of the COP to either the heel or the toe) is also a valid measure of relative stability because it directly measures how large a perturbation would need to be to initiate a fall. Thus, reductions in COP excursions and localization of the COP in central regions of the BOS close to the ankle joint likely reflect increased stability.

Postural muscle activity

Postural muscle activity was identified as the first burst of activity associated with a perturbation that was greater than two standard deviations above the baseline and that lasted more than 50 ms. Phasic activity in muscles associated with postural responses to a perturbation of the support surface were coded relative to the beginning of each backward and forward platform translation. To be included in calculations of group postural muscle onset latencies, dynamic responses had to be triggered in at least 50 % of the directionally specific perturbations at each frequency. The sole exception was for the TA and G muscles in young adults who, at 0.1 Hz, recruited these muscles during 35 % of the perturbations.

Since absolute cycle duration varied as a function of frequency, muscle onset latencies were determined as a percentage of half-cycle time. A half-cycle was considered to be the movement of the platform from one extreme position to the other extreme position. Latencies were coded positive if muscle activity began after time zero and negative if activity began before time zero.

Data analysis

T-tests were used to identify significant differences between ETP and STP at each frequency and period, for both young and old adults. The dependent variables tested were: postural muscle onset latencies, COP A/P ranges, percentage of time COP was located inside specific regions of BOS, and phase lags between COP and platform time series. An accepted significance level of 0.05/number of comparisons to correct for multiple tests was used for all dependent variables. For phase lag data, the accepted significance level was $p<0.025$ while for remaining dependent variables the accepted significance level was $p<0.006$.

RESULTS

Stepping Responses

The number of young and old subjects who stepped (Table 1 in bold), the total number of steps, along with the minimum and maximum number of consecutive steps per person (Table 1 in brackets) in each condition are reported. For example, during the transition period at 0.5 Hz, following ETP, 3 young adults took 1 or 2 steps for a total of 4 steps. During the same transition period, 6 old adults stepped between 3 and 8 times for a total of 26 steps.

Place Table 1 near here

Following ETP, additional support was provided to three young adults during the transition to 0.5 Hz and two young adults during the steady state period at 0.61 Hz. Each support period ranged from 2 to 4 seconds. Following STP, no external support was required by young adults.

The old adults exhibited a greater need for external support. Transition periods during ETP resulted in 2, 12, and 14 support periods as the frequency of translation was increased to 0.25, 0.5, and 0.61 Hz, respectively. The steady state periods were also characterized by 7, 23 and 18 periods of external support at oscillation frequencies of 0.25, 0.5 and 0.61 Hz respectively. The length of each external support period ranged from 2 to 10 seconds. During STP, no external support was required by old adults. One old adult used arm movements for stabilization at 0.61Hz.

Anterior/posterior centre of pressure

Oscillation frequencies of 0.1 and 0.25 Hz were characterized by minimal COP A/P displacements in both groups for both perturbation types (Figure 1). Externally-triggered and STP resulted in greater COP A/P displacements during transition and steady state periods at 0.5 Hz compared to 0.1 and 0.25 Hz (all comparisons: $p<.001$). Increasing platform oscillation frequency to 0.61 Hz did not result in additional COP A/P displacement.

Place Figure 1 near here

Decreased COP A/P displacement was expected in steady state compared to transition periods. In the young adults, significantly less COP A/P displacement was recorded during steady state than transition at 0.1 and 0.25 Hz ($p<.001$ and $p=.002$) in ETP and at 0.1, 0.5, 0.61 Hz during STP ($p<.001$, $p=.005$, $p=.004$). This modulation was not observed in the old adults in either type of perturbation. In fact, with one exception there were no differences in COP A/P displacement between transition and steady state at any frequency in the old adults. The sole exception was a significantly lower displacement of COP A/P in steady state compared to transition period at 0.1Hz in both types of perturbations ($p<.001$).

Controlling perturbation onset was also expected to result in decreased COP A/P movement. Young adults generated significantly less displacement during STP than ETP in the transition period at 0.5 Hz ($p=.003$) and during steady state periods at 0.5 and 0.61 Hz ($p=.001$, and $p=.004$). In old adults, STP resulted in significantly less COP A/P movement during transition at 0.5 Hz ($p=.001$). Although the old adults were able to somewhat limit the COP displacement following STP, their COP A/P excursions remained larger than those of young adults during steady state periods at 0.5 and 0.61 Hz ($p=.001$ and $p=.002$). Examples of COP displacements from a young and an old adult following a self-triggered perturbation of the platform at 0.5 Hz are shown in Figure 2.

Place Figure 2 near here

The percentage of time the COP was located within each region of the BOS following STP is illustrated in Figure 3. Young adults consistently maintained their COP in the central regions of the BOS for the majority of time during both transition and steady state periods at all frequencies. In the old adults, the COP was located in extreme regions of the BOS especially when platform oscillation frequency increased. At 0.5 and 0.61 Hz, during both transition and steady states periods, the COP of the old adults remained within extreme regions of the BOS for significantly longer percentages of time than for young adults (all comparisons $p<.002$).

Place Figure 3 near here

The COP position always lagged platform position during steady state periods. In young adults, phase lags between platform and COP time series ranged from 125 to 146 ms during ETP and STP at 0.5 and 0.61 Hz. In old adults, the phase lags between the platform and COP time series were significantly less during STP compared to ETP at 0.5Hz ($p=.002$) and 0.61 Hz ($p<.001$).

Place Figure 4 near here

Postural muscle onset latencies

In young adults, STP resulted in few differences in muscle onset latencies during transition periods. Specifically, the TA at 0.1 Hz, G and H at 0.25, and Q at 0.5 Hz, were activated earlier in response to STP versus ETP. Steady state periods however were characterized by similar postural onset latencies regardless of perturbation type.

Place Figure 5 near here

In old adults, transition periods following STP were characterized by significantly earlier postural muscle onset latencies compared to ETP for all muscles at 0.5 and 0.61 Hz and for G at 0.25 Hz. Postural muscle onset latencies during steady state periods were significantly earlier following STP as compared to ETP for G at 0.1 Hz, for G, Q and H at 0.5 Hz and for TA, G, Q, and H at 0.61 Hz. Results of comparisons of postural muscle onset latencies between perturbation types for both young and old adults are given in Table 2.

Place Table 2 near here

To illustrate subtle differences in TA and G muscle onset latencies, data for the first and last five cycles at 0.61 Hz are illustrated for young and old adults (Figure 6). Similar results were recorded at all frequencies. Following ETP, young adults shifted from a reactive to an anticipatory mechanism during the first three cycles, with muscle onset latencies remaining stable over the remaining cycles. A similar shift was not noted during the transition period for the old adults. Old adults activated postural muscles primarily in response to and never in anticipation of the change in direction of the platform. Moreover, old adults did not reach the same values of anticipatory or early postural muscle onset latencies as the young adults even after 10, 30 or 40 cycles in the steady state periods at 0.25, 0.5 and 0.61 Hz, respectively.

Following STP, young adults shifted from a reactive to an anticipatory mechanism within the first or second cycle of the transition period with postural muscle onset latencies remaining stable over the remaining cycles. Although delayed compared to young adults, earlier postural muscle activity was recorded from old adults in transition and steady state periods following STP versus ETP.

Place Figure 6 near here

DISCUSSION

As expected, young adults responded differently in transition periods to STP versus ETP with earlier postural muscle onsets and decreased COP A/P displacements. In addition, young adults took advantage of platform movement predictability following a frequency increase by adapting to the new frequency and switching to anticipatory mechanisms of control after three to five cycles of ETP and within one or two cycles of STP. Similar results have been reported for subjects who adapted anticipatory control of a whole-body lifting task to an expected load magnitude as it became more predictable (Toussaint et al. 1998). There were no differences in steady-state responses between the two perturbation types. Since young adults were able to achieve stability within transition periods, a consistent mechanism of control was likely used during steady state periods regardless of perturbation type.

Old adults clearly struggled to maintain their balance during ETP while STP provided access to a safer mechanism of control. In ETP, old adults responded to changes in platform direction with muscle onset latencies consistent with a reactive mechanism of control. In STP, although reactive postural mechanisms were still used, they were consistent with responses to the slowing down and not the change in direction of the platform. The decrease in platform speed is the first indication of an upcoming perturbation and reversal in the direction of platform movement. In STP, old adults were able to make use of this information potentially by decreasing the threshold for detecting changes in platform speed thus permitting earlier postural muscle activity and limiting the amount of destabilization triggered by the perturbation. Kerr and Worringham (2002) showed that velocity perception is more accurate when both distance and timing cues are available, indicating that all available cues are used to make judgements of movement velocity. Our results correspond with those of Blouin et al. (2003a, 2003b) who in a similar reactive versus predictive perturbation paradigm showed that neck muscle activity was decreased 50-100 ms after platform movement onset in the predictive condition relative to the reactive condition, and that neck and head postural responses were modulated by previous experience of the acceleration. Together these results suggest that knowledge of the perturbation timing allows anticipatory control to scale the appropriate motor output.

Compared to young adults, old subjects demonstrated less efficient and less consistent responses to sinusoidal platform oscillations by displaying large amplitudes of COP A/P excursion and a greater number of steps. The magnitude of COP A/P excursion is indicative of a subjects' control and thus the subjects' ability to respond and prevent a fall. Although the old adults were able to somewhat limit COP A/P movement following STP, the maximum range of COP A/P movement was similar to that recorded in the young adults following ETP. The lack of significant differences in COP A/P displacement between transition and steady states in old adults indicates a lack of modulation of this variable.

Moreover, the old adults' COP A/P was located in less safe regions at the boundaries of the base of support for greater periods of time when compared to young adults placing them at greater risk for destabilization. This was particularly notable during transition periods and with increases in platform oscillation frequency. The functional BOS, the anterior-posterior proportion of foot length used in maximal sustained forward and backward leaning, was reported to be approximately 60% and 42% of the foot length in healthy young adults and in adults over 60 years old, respectively (King et al. 1994). Balance can successfully be maintained if the COP is at the extremes of the functional BOS but the risk of destabilization is greater especially in a dynamic situation. Patton et al. (1998) introduced the notion of safety margins, the minimum distance to the boundaries, as measures of relative stability. The spatial safety margin, the minimum distance of the COP to the edges of the feet, and temporal safety margin, the minimum extrapolated time for the COP to reach the edges of the feet, describe how far a person is from an unstable condition. Time is a critical consideration since delays in postural muscle activation and increased phase lags between COP and platform movement decrease the temporal safety margins.

The higher number of steps recorded in both groups during the transition from 0.25 to 0.5 Hz can be explained by the degree of difficulty in the task since during this particular transition, the platform frequency doubled. Nevertheless, the greater destabilization observed in the old adults and their need to step was not limited to transition periods but continued throughout the periods of steady state indicating that the ability to adapt to a constant and predictable balance challenge was limited especially during ETP. In ETP, losses of balance and greater instability in the old adults were also characterized by a greater need for external support. These results correspond with data from studies of discrete perturbations, where old adults were more likely to use a step to recover balance and stepped at lower perturbation magnitudes than young adults (Jensen et al. 2001). Stepping is a risky strategy especially in old adults who tend to require multiple steps to recover balance because of the increased risk of tripping over their own feet (Maki and McIlroy 1996a).

Previous research has reported significant correlations between postural control and physiological arousal (Maki and McIlroy 1996b) suggesting arousal may act as potential modulator of postural control. Although not a cognitive task, the self-triggering of perturbations with the hand held device might have contributed to an increased arousal in participants. Determining when to self-trigger a perturbation appears to have allowed old subjects to better stabilize the body before changing oscillation frequency and facilitated earlier activation of postural muscles which translated into a closer coupling of the COP A/P displacement to the platform movement.

Self-triggered perturbations elicited steps in fewer old adults during both transition and steady state periods. In addition, the maximum number of steps taken by each subject decreased and no external support was required to maintain balance. It is possible that the level of perceived balance threat and the fear associated with it was decreased in the STP versus ETP. Although the subjects' confidence levels were relatively high as measured by the ABC scale, and conforming to the BBS scores the participants were at no evident risk of falls, one has to consider that the oscillating platform paradigm represented a novel challenge for them and that fear is a normal response in an unpredictable, uncontrollable situation. Furthermore, the results of the CB&MS, which was designed to measure individuals with high levels of functional of balance and includes tasks more challenging than the BBS or the ABC, were low. This suggests that for our participants certain tasks still impose balance challenges and possible threats to their stability. Numerous studies have demonstrated that fear modifies strategies for the control of posture (Maki et al. 1991, Maki et al. 1994, Adkin et al. 2000, Adkin et al. 2002) and fear of falling is common in old adults (Tinetti et al. 1994, Vellas et al. 1997). Fear effects on postural control have been demonstrated even in animal models where anxious mice fall more often and are less stable compared to non-anxious mice when postural control is challenged (Lepicard et al. 2000). Evidence of fear of falling effects on anticipatory postural control is clinically relevant as it may explain deficits in postural control observed in old adults and direct towards balance retraining programs which consider decreasing this fear in order to facilitate better results.

Self-regulating postural perturbations may permit the old adult to: i) decrease the threshold for detecting the change in platform speed thus permitting earlier reactive postural muscle activity limiting the amount of destabilization triggered by the perturbation; ii) increase arousal and incorporate anticipatory postural strategies in the planning stages in preparation for changes in platform oscillation frequencies; and/or iii) decrease the anxiety associated with a postural threat thus permitting the appropriate mechanisms of control to take place.

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Table 1. Stepping responses.

	Young adults					
	Transition Periods			Steady State Periods		
	0.25 Hz	0.5 Hz	0.61 Hz	0.25 Hz	0.5 Hz	0.61 Hz
Externally-triggered	--	**3** / 4	--	--	--	--
		(1 – 2)				
Self-triggered	--		--	--	--	--

	Old adults					
	Transition Periods			Steady State Periods		
	0.25 Hz	0.5 Hz	0.61 Hz	0.25 Hz	0.5 Hz	0.61 Hz
Externally-triggered	**3** / 5	**6** / 26	**4** / 6	**2** / 2	**2** / 6	**3** / 17
	(1 – 3)	(3 – 8)	(1 – 2)	(1)	(1 – 3)	(1 – 11)
Self-triggered	**1** / 1	**3** / 5	**3** / 4	--	**2** / 2	**2** / 4
	(1)	(1 – 3)	(1 – 2)		(1)	(1 – 3)

Note: Bolded text – number of individuals who stepped; regular text – total number of steps; parentheses – range of steps taken by participants.

Table 2. P values of t-tests used to test for significant effects of ETP versus STP on muscle onset latencies during transition and steady state periods.

Transition periods

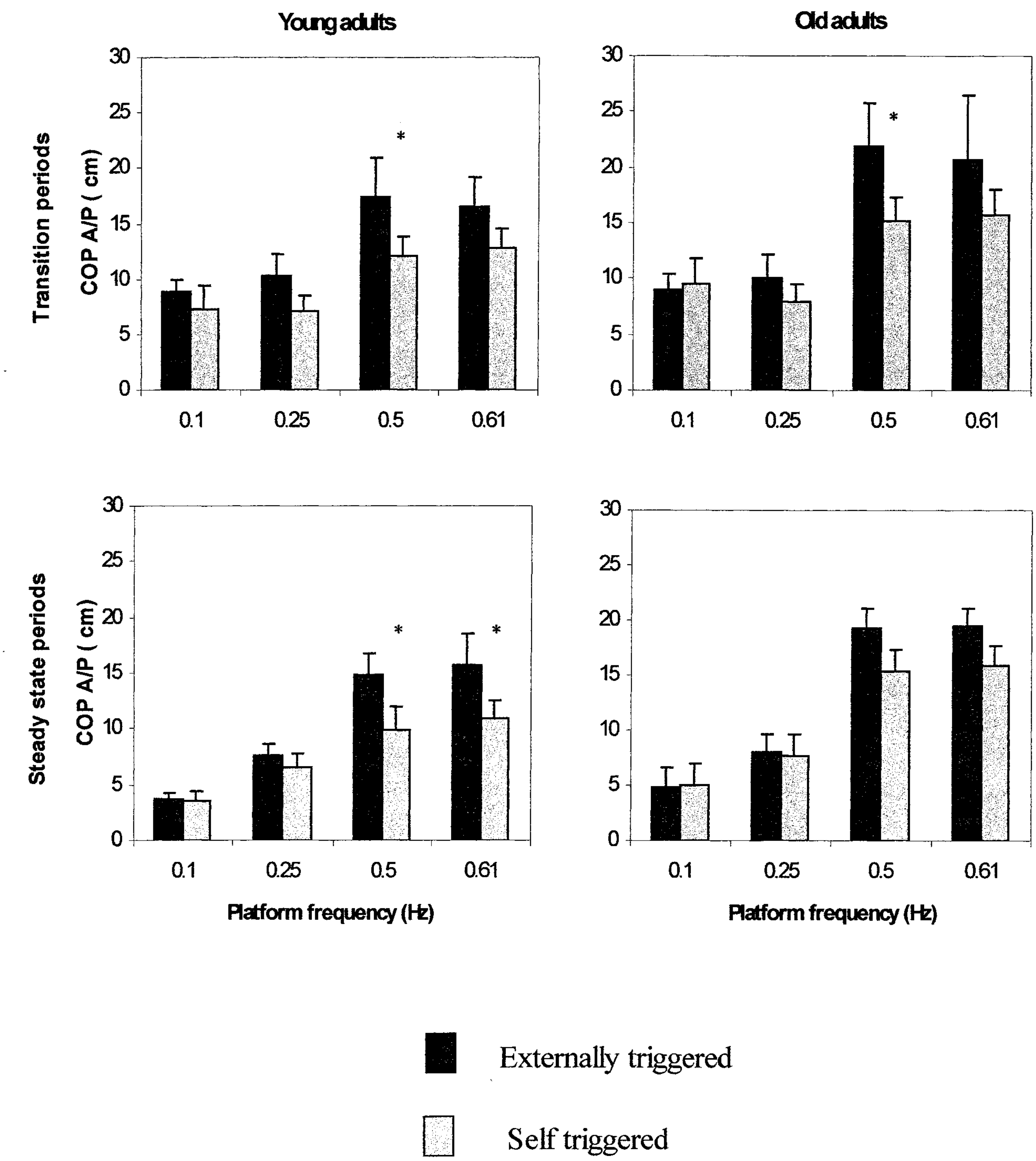
	Young				Old			
Frequencies	TA	G	Q	H	TA	G	Q	H
0.1 Hz	**.004**	.119			.033	.032		
0.25 Hz	.891	**.002**	.03	**.002**	.040	**.006**	.404	.008
0.5 Hz	.012	.008	**.004**	.024	**<.001**	**<.001**	**.002**	**<.001**
0.61Hz	.031	.019	.056	.195	**<.001**	**<.001**	**<.001**	**<.001**

Steady state periods

	Young				Old			
Frequencies	TA	G	Q	H	TA	G	Q	H
0.1 Hz	.592	.537			.016	**<.001**		
0.25 Hz	.509	.258	.067	.126	.188	.020	.246	.023
0.5 Hz	.009	.476	.599	.518	.008	**<.001**	**.002**	**.001**
0.61Hz	.160	.430	.965	.478	**<.001**	**<.001**	**<.001**	**.001**

Statistically significant comparisons (p<.006) indicated in bolded text. Note: empty cells indicate postural muscles activity was not elicited.

Fig. 1 Centre of pressure anterior/posterior (COP A/P) range (group mean ± SD, in cm) during externally-triggered (black bars) and self-triggered (grey bars) platform perturbations at four frequencies of platform translations. Data from transition periods (top panels) and steady state periods (bottom panels) from young adults (left panels) and old adults (right panels).



Young adults
Old adults
Transition periods
Steady state periods
COP A/P (cm)
30
25
20
15
10
5
0
*
0.1
0.25
0.5
0.61
Platform frequency (Hz)
Externally triggered
Self triggered

Figure 1

Fig. 2 Centre of pressure plots from a young adult (left panels) and an old adult (right panels) during transition (top panels) and steady state (bottom panels) periods following self-triggered perturbations of the platform at 0.5 Hz. Each panel illustrates the force plate on which the subjects were standing with circle icons indicating the position of the subject's feet. From top to bottom, the six circles indicate for each foot: the tip of big toe, the two widest points across the metatarsal region, the two widest points across the heel region and the back of the heel. The COP M/L position is plotted on the *x*- axis and the COP A/P position on the *y*-axis.

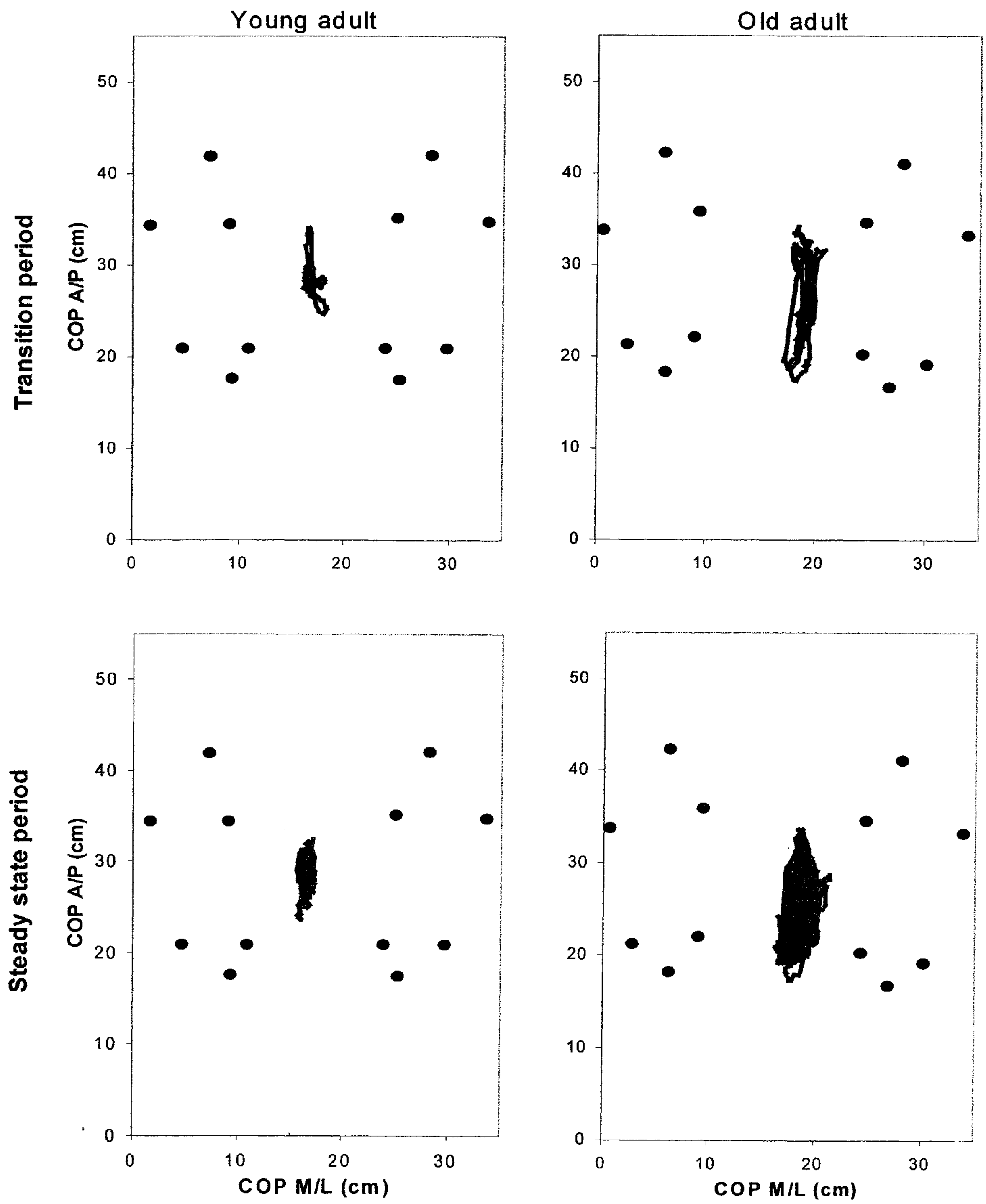
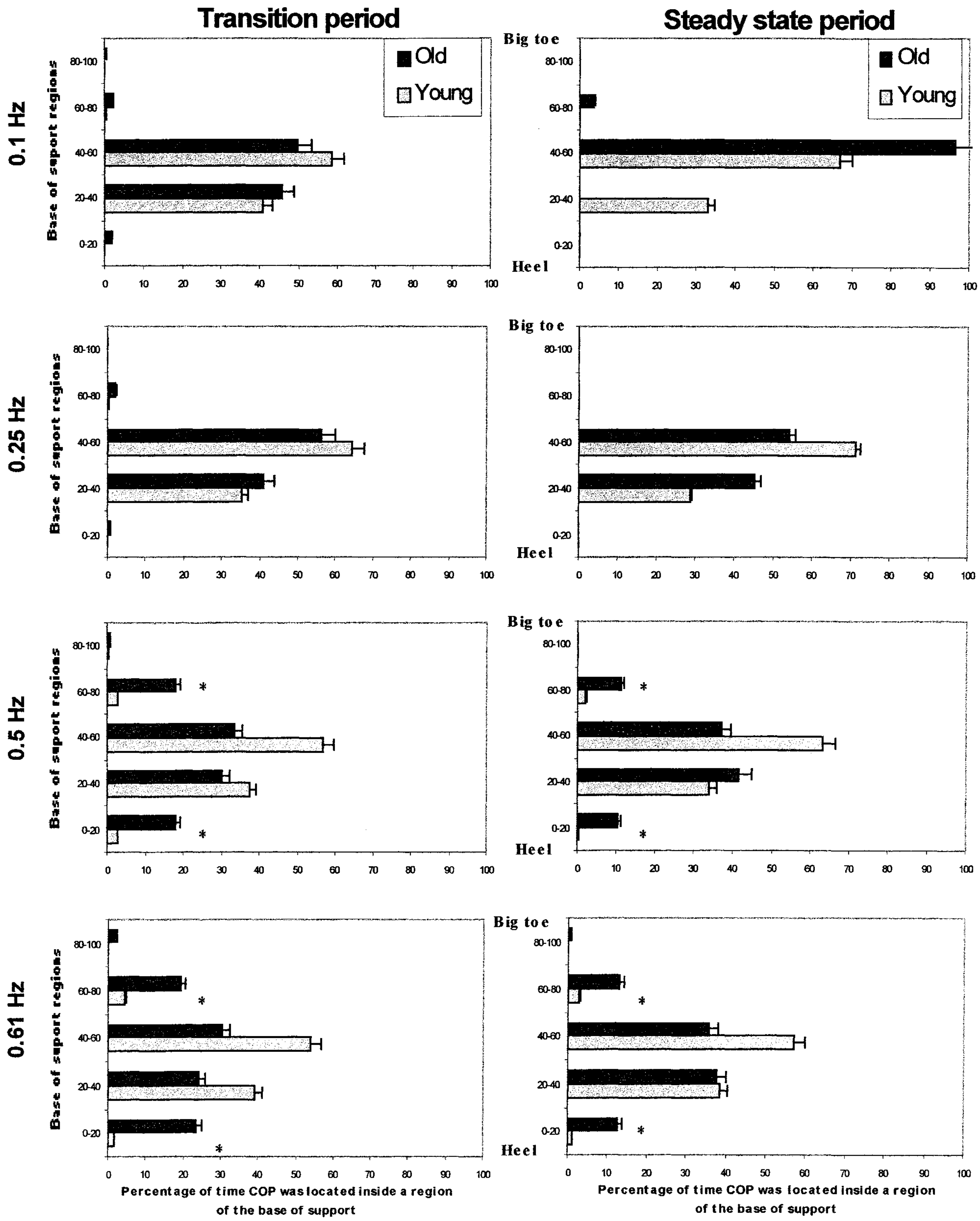

Young adult
Old adult
Transition period
Steady state period
COP A/P (cm)
COP M/L (cm)
0
10
20
30
40
50

Figure 2

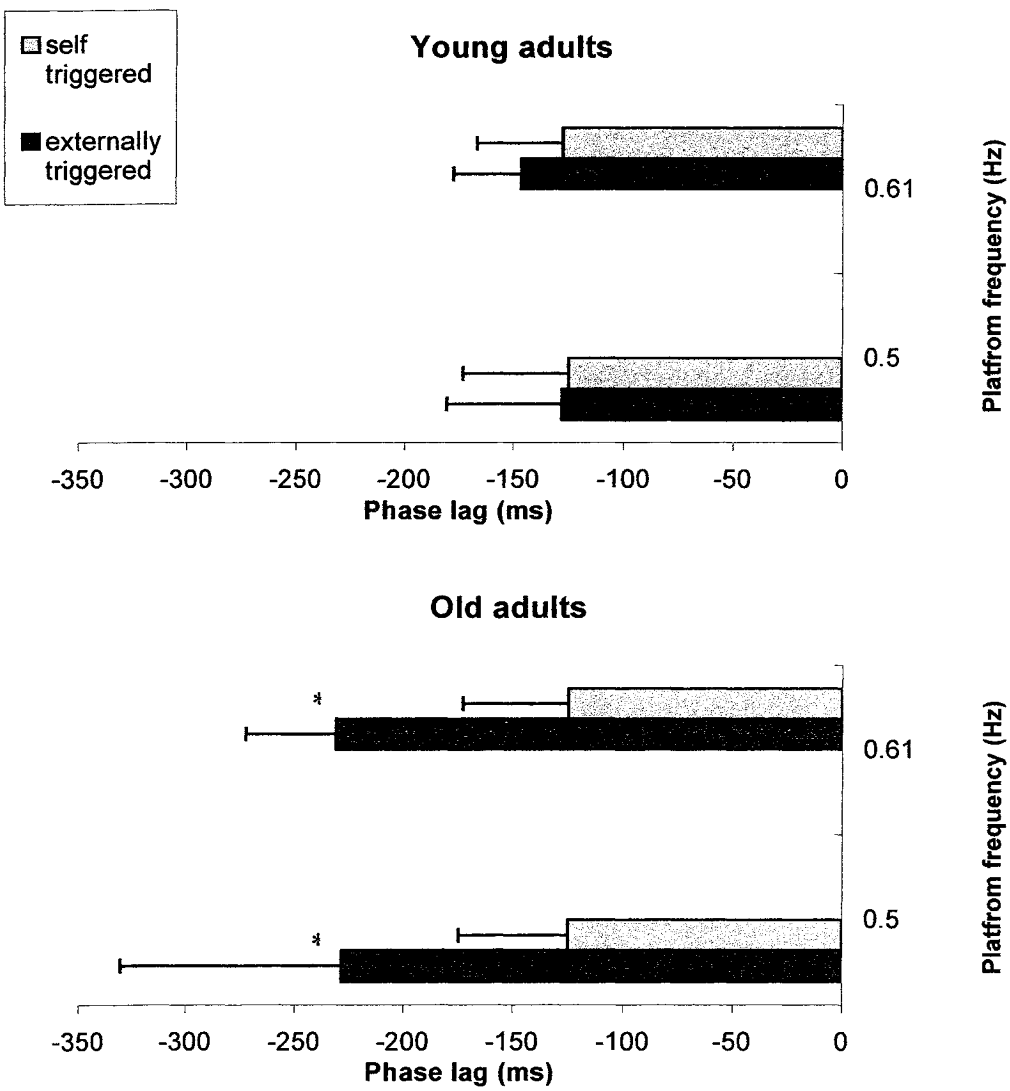
Fig. 3 Percentage of time COP was located inside a particular region of the base of support following self-triggered perturbations. Group (mean ± SD) data from transition periods (left panels) and steady state periods (right panels) at four frequencies of platform translations are presented for old (black bars) and young adults (grey bars). The base of support was divided into five equal regions, zero representing the posterior boundary delimited by the back of heel and 100 representing the anterior boundary represented by tip of the big toe. The five different regions of the BOS are represented on the *y*-axis, while the *x*-axis represents percentage of time.



Transition period
Steady state period
Old
Young
0.1 Hz
0.25 Hz
0.5 Hz
0.61 Hz
Base of suport regions
Big toe
Heel
80-100
60-80
40-60
20-40
0-20
0 10 20 30 40 50 60 70 80 90 100
Percentage of time COP was located inside a region of the base of support

Figure 3

Fig. 4 Phase lags (mean ± SD) between platform and COP time series during externally-triggered and self-triggered perturbations at 0.5 and 0.61 Hz for young and old adults. Negative values indicate that COP movement is lagging behind platform movement.



self triggered
externally triggered
Young adults
0.61
0.5
Platfrom frequency (Hz)
-350
-300
-250
-200
-150
-100
-50
0
Phase lag (ms)
Old adults
*
*
0.61
0.5
Platfrom frequency (Hz)
-350
-300
-250
-200
-150
-100
-50
0
Phase lag (ms)

Figure 4

Fig. 5 Postural muscle onset latencies (mean ± SD) of young (A, B), and old adults (C, D) at the four frequencies of platform translation. Onset latencies are expressed as a percentage of half cycle time for muscles normally associated with forward (TA and Q in panels A, C) or backward perturbations (G, H, and BE in panels B, D). Results from ETP and STP are represented by circle and triangle icons, respectively. Open and filled icons represent postural muscle onset latencies from the transition and the steady state periods, respectively. Zero represents the time at which the platform changed direction. For both forward and backward directions of motion, the platform began to slow down at the -50% mark. For clarity purposes the values for the transition periods are offset on the *y* axis. Onset latencies of the BE are illustrated only for old adults since, in the young adults, this muscle was activated in less than 50% of the trials.

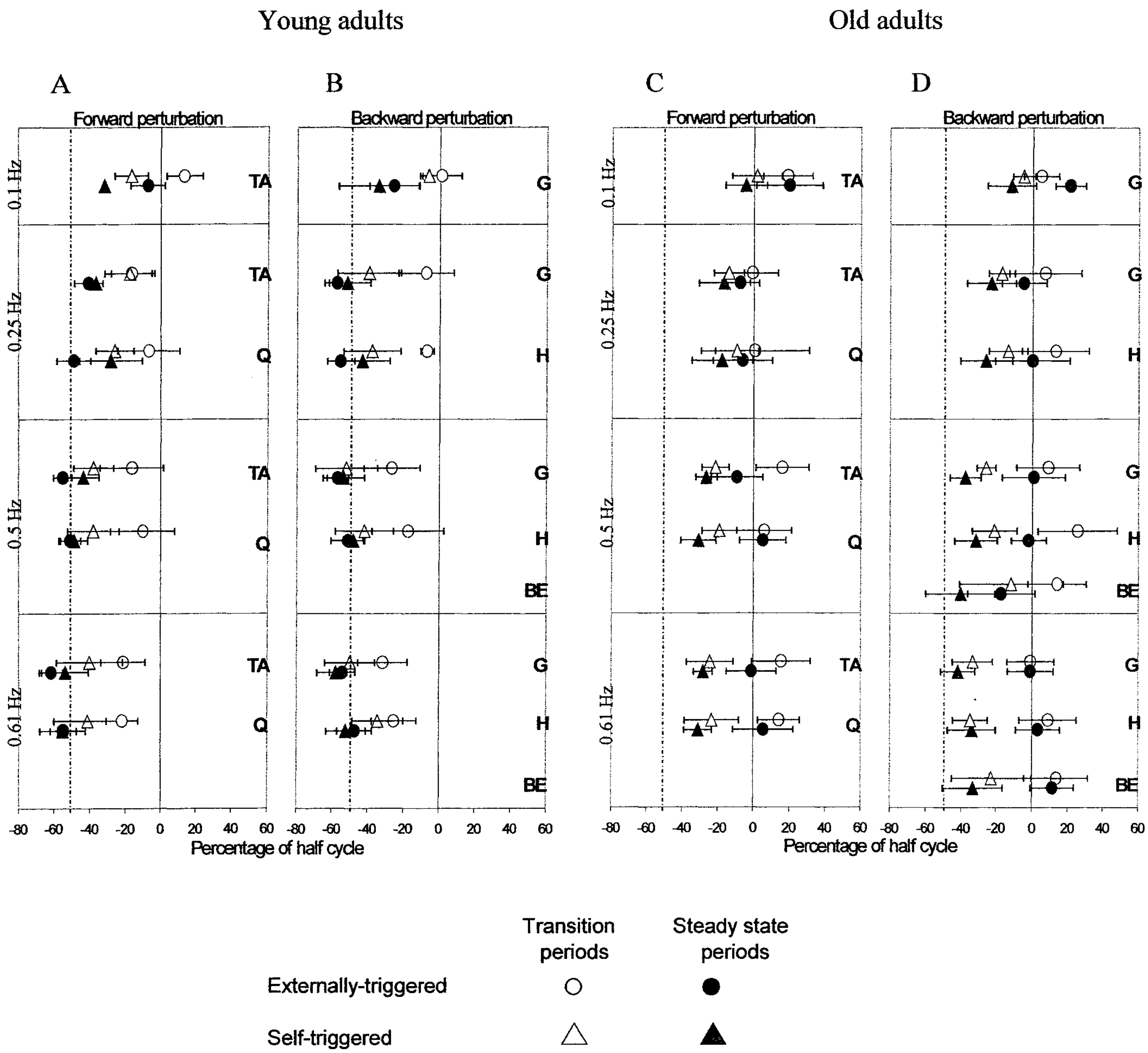
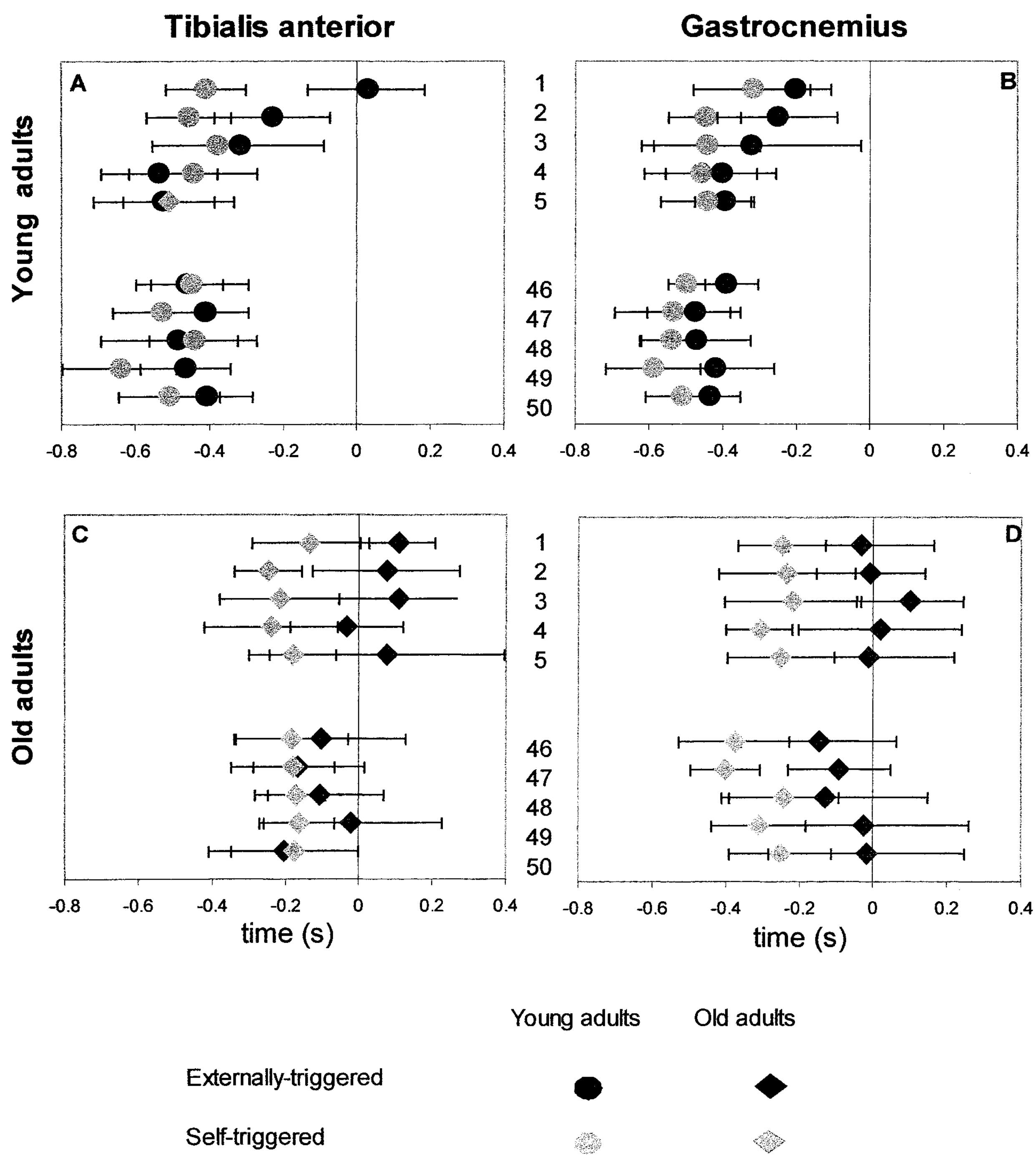

Young adults
Old adults
A
B
C
D
Forward perturbation
Backward perturbation
Forward perturbation
Backward perturbation
0.1 Hz
0.25 Hz
0.5 Hz
0.61 Hz
TA
Q
G
H
BE
-80 -60 -40 -20 0 20 40 60
Percentage of half cycle
Transition periods
Steady state periods
Externally-triggered
Self-triggered

Figure 5

Fig. 6 Tibialis anterior and gastrocnemius muscle onset latencies (mean ± SD) for young (top panels) and old adults (bottom panels) following externally-triggered (black icons) and self-triggered (grey icons) perturbations. Values from the first five cycles following the increase in oscillation frequency (transition period) and from the last five cycles (steady state period) at 0.61 Hz are represented. Zero represents the time at which the platform changed direction.



Tibialis anterior
Gastrocnemius
Young adults
Old adults
A
B
C
D
1
2
3
4
5
46
47
48
49
50
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
time (s)
Young adults
Old adults
Externally-triggered
Self-triggered

Figure 6

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CHAPTER 4

Stimulation of cutaneous mechanoreceptors from foot plantar surface boundaries improves old adults' postural responses to continuous perturbations

ABSTRACT

We have previously reported age-related differences in the use of anticipatory postural mechanisms in response to externally- and self-triggered continuous perturbations (Bugnariu and Sveistrup 2003). Evidence exists that facilitation of sensation from the foot plantar surface boundaries improves the efficacy of reactive stabilizing reactions (Maki et al. 1999). In this study, we examined whether mechanical stimulation on the foot plantar surface boundaries facilitates the use of anticipatory postural reactions in response to continuous base of support perturbations in old adults.

Old adults (n=16, 60-80 years old) were asked to maintain standing balance on a force platform that oscillated continuously 20 cm peak-to-peak in the anterior/posterior (A/P) direction at successively increasing frequencies of 0.1, 0.25, 0.5 to 0.61 Hz. All subjects completed two series of externally- and self-triggered perturbations. One half of the subjects (n=8) received additional stimulation through the means of a flexible polyethylene tube that was adhered to plantar foot surface boundaries. Centre of pressure (COP) and postural muscle activity were analyzed separately for five cycles after increases in platform frequency, transition periods, and for the remaining cycles at a constant platform frequency, steady state periods.

In old adults, mechanical stimulation of foot plantar surface boundaries improved the ability to control feet-in-place reactions, decreased center of pressure excursion and decreased the percentage of time the COP was located near the boundaries of the base of support. The additional sensory stimulation resulted in earlier postural muscle activity in response to unpredictable, externally-triggered perturbations. Furthermore, the progressive shift towards earlier postural muscle onset latencies indicates an increased ability of old adults to adapt and incorporate anticipatory postural control mechanisms. More subtle effects of the sensory stimulation were observed in the postural responses to self-triggered perturbations, indicating that the effects of predictability and sensory stimulation are not additive. The present results support the importance of cutaneous mechanoreceptors from the boundaries of feet plantar surface in the control of postural reactions evoked by unpredictable and predictable continuous perturbations.

INTRODUCTION

Various studies have shown the stabilizing influence of cutaneous information from any body part on human stance. For example, body sway was reduced by a light touch of a finger on an external support in young (Jeka et al. 1994) and old adults (Tremblay et al. 2004) or even when a passive tactile stimulus was applied at the leg or shoulder (Rogers et al. 2001). Because of their strategic location at the boundary between the body and the ground, cutaneous afferents from plantar mechanoreceptors of the feet might play an important role in controlling balance. These cutaneous afferents can provide detailed spatial and temporal information about contact pressures on the foot (Valbo and Johansson 1984, Roll 2002, Kavounoudias 1998) which can potentially be used to control posture. Maurer et al. 2001 suggested that the information provided by cutaneous afferents might be used for determining the body orientation in space and specifying the support on which the feet are resting. Furthermore, foot sole and ankle proprioceptive inputs may be co-processed and contribute jointly to postural regulation (Kavounoudias et al. 2001).

Postural regulation generally involves movements and forces at frequencies below 5 Hz. Therefore, slowly adapting type I and type II cutaneous afferent units, with Merkel cells and Ruffini endings serving as end organs, respectively, would be expected to participate in regulation of posture (Valbo and Johansson 1984, Perry et al. 2000). Both types of afferents respond to sustained skin indentation and exhibit sensitivity (albeit at different degrees) to strain components and skin deformation making them suitable to signal changes in contact force. On the other hand, a contribution of fast adapting type I afferents associated with Meissner receptors cannot be ruled out since these afferents are known to be highly sensitive to sudden changes in tangential load forces (Johnson 2001). Using microneurographic recordings in the tibial nerve, Kennedy and Inglis (2002) found both slow and fast adapting groups of mechanoreceptors with their receptive fields evenly distributed in the foot sole. It has been reported that slow and fast adapting cutaneous mechanoreceptors of the border of human foot code static and dynamic pressures (Vedel et al. 1982, Ribot-Ciscar et al. 1989, Birznieks et al. 2001).

The postural function of cutaneous afferents from the foot sole has been investigated through ankle ischemia and anesthesia of foot soles (Diener et al. 1984, Magnusson et al. 1990 a, Perry et al. 2000), through stimulation of the foot skin by means of vibration (Kavounoudias et al. 1998, 1999, Roll et al. 2002), and by means of raised "indentors" (Okubo et al. 1980, Watanabe and Okubo 1981, Maki et al. 1999). Results of these protocols support the important contribution of sensory information from the foot plantar surface in the control of various aspects of balance. Manipulation of plantar sensation was reported to have an effect on afferent nerve activation and postural sway, feet in place stabilizing reaction, compensatory stepping reactions, as well as perceptual illusory responses of whole-body leaning in stabilized subjects (Okubo et al. 1980, Watanabe and Okubo 1981, Do et al. 1990, Magnusson et al. 1990, Hamalainen et al. 1992, Wu and Chiang 1997, Maki et al. 1999, Perry et al. 2000, Kavounoudias et al. 1999, Roll et al. 2002).

Kavounoudias et al. (1998) showed that the tactile afferents from the feet provide the CNS with information about the body position with respect to the vertical axis. Changes in skin pressure under the sole signal how far the body is leaning and how it has to be straightened. The centre of mass (COM) position and velocity, relative to the base of support (BOS), is thought to be a critical variable that is controlled by the central nervous system (CNS) in maintaining upright stance (Dietz et al. 1992, Pai et al. 1997, 2000). Maki et al. (1999) proposed that "promoting sensation specifically from the plantar-surface boundaries could play an important role within the CNS, in determining proximity of the COM to the stability boundaries of the BOS established by the feet". Patton et al. (1999) demonstrated that under normal conditions, when subjects maintain balance, the centre of pressure (COP) safety margin (minimum distance of the COP to either the heel or the toe) is also a valid measure of relative stability because it directly measures how large a perturbation would need to be to initiate a fall.

Although varied and complex mechanisms contribute to the effect of aging on postural control, deterioration in cutaneous sensory function is likely to be an important factor (Maki and McIlroy 1996, 1999, Lord et al. 1991). Lower limb sensory deficits are known to affect ability to maintain balance under challenging circumstances. First, the restriction of foot sole pressure sensation and/or ankle proprioception has been shown to increase postural sway during upright stance (Fitzpatrick and McCloskey 1994, Diener et al. 1984, Magnusson et al. 1990). Second, and probably more relevant for the geriatric population, age-related loss of cutaneous sensation is well documented in old adults (Kenshalo 1986) and appears to correlate with impaired control of postural sway (Lord et al. 1991, Brocklehurst et al. 1982), as well as with increased risk of falling (Lord et al. 1994). Furthermore, mild to moderate peripheral neuropathy, often present and impairing foot and ankle sensory information in elderly (van den Bosch et al. 1995), substantially decreases unipedal balance control (Richardson et al. 1996b) and is thought to contribute to the six fold increase in injurious falls recorded with aging (Richardson et al. 1992,1996a).

This study examined the effect of mechanical stimulation of cutaneous afferents at the foot plantar surface boundaries on postural responses to predictable and unpredictable perturbations. Old adults with small changes in light touch threshold of plantar cutaneous surface participated. Feet-in-place responses evoked by continuous sinusoidal anterior-posterior (A/P) platform motion were analyzed.

We tested the effect of mechanical stimulation of plantar surface boundaries when all other sensory information related to balance were available to subjects. Evaluating the importance of cutaneous sensation when vision or vestibular information is absent is a valid question for basic science and may be relevant to situations where visual information is compromised as a result of visual impairment or poor environmental lighting, or when vestibular information is compromised as result of pathology. However, eliminating one source of information forces the system to reweigh the others (Speers et al. 2002). The presence of all sensory systems is a more natural paradigm. If improvements in old adults' postural control along with decreases in their risk of falls are expected from this type of facilitation, and use of mechanical stimulation in footwear is to be considered as a possible intervention, the remaining sensory information must remain intact.

We have previously reported decreased ability of old adults to use anticipatory postural mechanisms in response to externally-triggered perturbations (Bugnariu and Sveistrup 2001). Knowledge of perturbation timing facilitated the use of anticipatory reactions in response to self-triggered continuous perturbations in old adults (Bugnariu and Sveistrup 2003). In the current study, we hypothesized that stimulation of cutaneous sensation from the plantar foot boundaries would lead to increased stability and would enable the old adults to use anticipatory mechanism in both types of perturbations.

Increased stability would reflect an improvement in determining the proximity of the body's COM to the stability boundaries of the BOS, reduced excursion of the COP toward the BOS boundaries, decreased percentage of time with the COP located in extreme regions of the BOS, and improved ability to resist stepping. The ability to use anticipatory mechanisms would be manifested as earlier activation of postural muscles and decreased phase lags between the platform and COP movement.

METHODS

Subjects

Sixteen adults between 62 and 78 years of age gave their informed consent to participate in this study. Experimental procedures were approved and performed in accordance with the Tri-Council Policy Statement on Ethical Conduct for Research Involving Humans (Canada). All participants were healthy volunteers with no history of falls, musculoskeletal or neurological problems. They were living independently in the community and were recruited from social support and recreational programs in community centers. An equal number of men and women participated.

Mean (± SD) and range of subject characteristics, age, height, weight, foot length and light touch threshold, along with results of clinical balance tests are presented in Table 1. Foot plantar surface light touch threshold was tested with Semmes-Weinstein Monofilaments (North Coast Medical, Inc) at the level of metatarsal heads and heel. Each monofilament is individually calibrated to deliver a target force within a 5% standard deviation. Based on product specification, detecting the filament marked 3.61 (corresponding to a 0.4g force) represents the norm for foot plantar thresholds. Detection of monofilament sizes 3.84 to 4.31, delivering pressures of 0.6 to 2 grams respectively, indicates diminished light touch. More recent investigations have revealed that the norms provided by the product manufacturer are in fact too low, at least for the cervical dermatomes. For example, based on product specifications, the filament marked 2.83 delivering a 0.07 g force, is considered to represent normal threshold for pressure detection in the hand, but the norm is actually more within the range of forces covered by the filaments marked 3.84 and 4.08, 0.6 and 1 g, respectively (Voerman et al. 1999). Considering that norms for foot plantar thresholds are higher than those for the hand, detection of monofilament sizes 3.84 to 4.31 is still highly functional. To further characterize balance abilities of the subjects, three clinical tests were administered: the Community Balance & Mobility Scale (CB&MS), Berg Balance Scale (BERG) and the Activity Balance Confidence Scale (ABC). The maximum scores for the three tests are 96, 56 and 100 for the CB&MS, BERG, and ABC, respectively.

Place Table 1 near here

Task and procedures

Participants were asked to stand erect, eyes open, barefoot with feet shoulder width apart on a movable platform that was driven by an electric motor. They were asked to maintain their balance and to avoid taking steps unless absolutely necessary. If a step was taken, they were instructed to bring their feet back to the initial position. In order to prevent falls, subjects wore a loose harness attached to the ceiling while an assistant provided them with additional support if they were unable to maintain their balance. The platform oscillated sinusoidally 20 cm peak to peak in the anterior/posterior (A/P) direction. Platform oscillation started at a frequency of 0.1 Hz and after intervals of 80-100 seconds the frequency was increased successively to 0.25 Hz, 0.5 Hz and 0.61 Hz. Trials consisted of 10 cycles at 0.1 Hz, 20 cycles at 0.25 Hz, 40 cycles at 0.5 Hz and 50 cycles at 0.61 Hz. Each subject completed two five-minute trials. In externally-triggered perturbations, the frequency of the platform was increased suddenly and without warning to the subject. In the self-triggered perturbations, the subjects themselves increased the frequency of the platform movement using a hand-held device. The initial three cycles at 0.1 Hz and the first five cycles at 0.25 Hz, 0.5 Hz and 0.61 Hz were considered transition periods and were analyzed separately. The remaining cycles at each frequency of platform translation constituted the steady state periods during which platform motion was constant and predictable.

Subjects were divided into two experimental groups. For the purpose of concise and clear report, in this paper, sensory stimulation (STIM) refers to mechanical stimulation of cutaneous afferents from the boundaries of feet plantar surface. The two groups of subjects are referred to as "STIM" and "NO STIM" accordingly. The STIM group received additional mechanical stimulation during experiments. A flexible polyethylene tube (3 mm outer diameter, 1 mm inner diameter) was adhered to the boundaries of the foot plantar surface with hypoallergic tape designed for human skin, as per Maki et al. (1999). Figure 1 illustrates tube placement. During balance testing, subjects reported that they could perceive the tubing without discomfort and no loosening of the adhesive was discovered at the end of testing.

A Kistler force plate (Type 9286, Kistler Instrument Corp) was placed in the center of the moving platform. The ground reaction force and platform position signals were sampled at 600 Hz. Subjects started all trials standing centered on the force plate and the exact position of their feet relative to the force plate was marked.

Surface electrodes were used to record activity of the tibialis anterior (TA), gastrocnemius (G), quadriceps (Q), hamstring (H) and back extensor (BE) muscles of the left side of the body. A ground electrode was placed on the left iliac crest. Raw electromyographic (EMG) signals were preamplified, sampled at 600 Hz and full-wave rectified.

Place Figure 1 near here.

Data reduction

Kinematics

The vertical component of ground reaction force (F_z) was derived from summing the forces from the four piezoelectric crystals mounted in the corners of the force plate. The COP A/P displacements were calculated using standard methods (Henry et al. 1998). In addition, the length of the BOS surface from heel to big toe was divided into five equal regions (Figure 1) referred to as: heel (0-20 %), central (20-40% and 40-60 %), metatarsal (60-80 %) and toe (80-100 %) regions. the heel and metatarsal regions are referred to as the "extreme regions" of the BOS. The percentage of time the COP was located in each particular region was calculated.

Cross-correlation coefficients between the platform and COP time series were determined for the two highest frequencies of oscillation at zero phase lag. Time series signals were then temporally shifted relative to each other and the phase lag corresponding to the highest cross-correlation was recorded. We used COP rather than COM excursions as the indicators of stability largely because of the methodological constraints. Previously we have reported that in a continuous sinusoidal A/P translation paradigm the COM and COP time series displayed moderate to high correlations (r= 0.65 to 0.88, Bugnariu and Sveistrup 2004a). Although COP excursions do not exactly match COM excursions, the traditional view is that COP can be used as a biomechanical measure of stabilizing postural reactions since the COP is the variable used to control the COM (Winter et al. 1998, Rietdyk et al. 1999) and for standing balance to occur the trajectory of the COM must be maintained within the extreme COP positions. To prevent a fall, the COP must travel beyond the COM at least for an instant to generate torques that accelerate the COM away from the stability limits. Hence, for tasks in which balance is fully recovered, as in the present study, COP can be a sensitive indicator of relative stability and reductions in COP excursions and localization of the COP in central regions of the BOS close to the ankle joint for increased percentages of time reflect increased stability.

Postural muscle activity

Postural muscle activity was identified as the first burst of activity that was greater than two standard deviations above the base line and that lasted more than 50 ms. Phasic activity in all postural muscles associated with postural responses to a perturbation of the support surface were coded relative to the beginning of each backward and forward platform translation. In order to be considered a dynamic postural response triggered by the surface perturbations and to be included in calculations of group postural muscle onset latencies, a muscle had to be active in at least 50 % of the directionally specific perturbations at each frequency. Postural muscle onset latencies were coded initially in milliseconds relative to the point of change in direction of the platform corresponding to extremes in the platform position. Since the absolute duration of a cycle varied as a function of cycle frequency, relative muscle onset latencies were determined as a percentage of half-cycle time. A half-cycle was considered to be the movement of the platform from one extreme position to the other extreme position. For each postural muscle, onset latencies were coded positive if the bursts occurred after time zero and negative if the bursts occurred before time zero.

Data analysis

Descriptive statistics were used to characterize the subject sample. Three way analysis of variance (ANOVA) was used to test for significant differences in the COP (Perturbation type (externally- versus self-triggered) X Sensory stimulation (STIM versus NO STIM) X Period (transition versus steady state). Three way ANOVA was used to test for significant differences in the percentages of time the COP was located inside central or extreme regions of the BOS

(Frequency X Sensory stimulation X Period). Multivariate ANOVA was used to test for significant differences in postural muscle onset latencies. All ANOVAs were performed with an accepted significance level of $p<.05$. P-values for all univariate post-hoc analyses were corrected according to the number of post-hoc comparisons made ($p=.05$ / number of comparisons). When t-tests were used for post-hoc comparisons, the Levene's test for equality of variances was conducted first to confirm equality of variances between groups. For phase lag data, the accepted significance level was $p< .025$; for all other dependent variables the accepted significance level was $p< .006$.

RESULTS

Subjects with sensory stimulation took fewer steps in both types of perturbations. In all externally-triggered perturbations without sensory stimulation, a total of 37 and 25 steps were recorded during transition and steady state periods, respectively. In all externally-triggered perturbations with sensory stimulation, a total of 6 steps were recorded during transition and 1 step in steady state periods. In all self-triggered perturbations without sensory stimulation, a total of 10 and 6 steps were recorded during transition and steady state periods, respectively. In all self-triggered perturbations with sensory stimulation, a total of 2 steps were recorded during transition and 2 steps in steady state periods.

Place Figure 2 near here

The 0.1 and 0.25 Hz platform oscillation frequencies were characterized by minimal displacements of the COP A/P for both STIM and NO STIM groups, during both types and periods of perturbations (see Figure 2). Significant main effects of STIM on COP A/P displacements were present at 0.5 and 0.61 Hz ($F(1,28)=12.651$, $p=.001$ and $F(1,28)=5.684$, p=.024). At both 0.5 and 0.61 Hz, no significant main effects were revealed for period (transition: $F(1,28)=3.652$, $p=.066$ and steady state: $F(1,28)=.248$, $p=.623$) or perturbation type (externally-triggered: $F(1,28)=3.442$, $p=.074$ and self-triggered: $F(1,28)=3.058$, $p=.091$). At 0.5 Hz, significant interactions between Perturbation type X Sensory stimulation ($F(1,28)=4.921$; $p=.035$), and Sensory stimulation X Perturbation type X Period ($F(1,28)=6.546$; $p=.016$) were present. No significant interactions were revealed at the 0.61 Hz frequency.

Decomposition of the interaction effects revealed that sensory stimulation significantly reduced the COP A/P displacement in externally-triggered perturbations at 0.5Hz during transition and steady states ($p<.001$ and $p<.001$) and at 0.61 Hz during transition and steady states ($p=.005$ and $p=.003$). In self-triggered perturbations, the sensory stimulation significantly reduced the COP A/P displacement only during the steady state period at 0.5 Hz ($p=.001$). In the NO STIM group, the self-triggered perturbations significantly reduced the COP A/P displacement during the transition ($p<.001$) and steady state ($p=.006$) periods at 0.5 Hz when compared to externally- triggered perturbations. In the STIM group, the type of perturbation (externally- versus self- triggered) had no significant effect on COP A/P displacement during either transition or steady state periods at any frequency.

Examples of COP excursions inside the base of support following externally and self-triggered perturbations at 0.5 Hz are shown in Figure 3. Data from STIM and NO STIM subjects are illustrated.

Place Figure 3 near here

Place Figure 4 near here

The percentage of time the COP was located inside a particular region of the BOS following self-triggered perturbations for STIM and NO STIM groups is illustrated in Figure 4.

Significant main effects of Sensory stimulation ($F(1,14)=25.479$; $p<.001$), Frequency ($F(3,12)=29.801$; $p<.001$) and Period ($F(1,14)=23.323$; $p<.001$) over the percentage of time the COP was located inside the extreme regions of the BOS were present. Significant interactions were found between Frequency X Sensory stimulation ($F(3,12)=8.388$; $p=.003$), Frequency X Period ($F(3,12)=6.037$; $p=.010$) and Period X Sensory stimulation ($F(1,14)=10.190$; $p=.007$) No three way significant interactions were revealed.

Post-hoc analysis revealed that following both types of perturbations, consistent and similar behaviour was noted in both groups at the 0.1 and 0.25 Hz frequencies of platform translation ($p=.819$). Subjects maintained their COP in the central regions of the BOS for the majority of time during both transition and steady state periods at these two slowest frequencies. With increases in platform oscillation frequency, the COP was recorded in the extreme regions of the BOS with significant differences between the two slow and the two fast frequencies ($p<.001$). However, sensory stimulation resulted in an increase of percentage of time the COP was located in central regions of the BOS. Subjects from the STIM group maintained their COP in central regions of the BOS for significantly longer percentages of time at 0.5 Hz during both transition and steady states periods ($p<.001$ and $p=.003$) and at 0.61 Hz during transition periods ($p=.002$) compared to the NO STIM group.

Separate analysis of the two extreme regions of the BOS revealed that following self-triggered perturbations, sensory stimulation significantly reduced the percentage of time COP was located in the heel region in transition and steady state periods at 0.5 Hz ($p=.001$ and $p=.003$) and at 0.61 Hz ($p=.001$ and $p=.002$). However, no significant differences were found in the percentage of time the COP was located in the metatarsal region with and without STIM at

0.5 Hz during transition and steady state (p=.021 and p=.286) and at 0.61 Hz during transition and steady state periods (p=0.105 and p=.695)

In the STIM group, the percentage of time the COP was located in extreme or central regions of the BOS was not significantly different between externally- and self-triggered perturbations at 0.5 and 0.61 Hz (p=0.123, p=0.108) nor between transition and steady state periods at 0.5 and 0.61 Hz (p=.061, p=.356). In the NO STIM group, following self-triggered perturbations, the percentage of time COP was located in extreme regions of the BOS was significantly lower in steady state compared to transition periods at 0.5 Hz (p=.007) and at 0.61 Hz (p=.004)

Cross-correlation coefficients and phase lags between the platform and COP A/P time series were determined for the two highest frequencies of platform oscillation, for the two groups of subjects during both types of perturbations. The maximum correlation between the two variables ranged from 0.71 ± 0.11 to 0.81 ± 0.12, with no significant differences between the two groups (p=.467), the two types of perturbations (p=.56) or the two frequencies (p=.525). However, with sensory stimulation, in externally-triggered perturbations, the phase lag between the platform and COP A/P time series significantly decreased from -228 ± 102 ms to -90 ± 90.5 ms (p=.011) at 0.5 Hz and from -231 ± 41.5 ms to -100 ± 50 ms (p=.007) at 0.61 Hz (Figure 5). In self-triggered perturbations, the phase lag between the platform and COP A/P time series ranged from -70 ± 65ms to -128.5 ± 52.5ms with no significant difference whether sensory stimulation from the feet plantar surface boundaries was present (p=.166 at 0.5Hz and p=.147 at 0.61 Hz)

Place Figure 5 near here

Place Figure 6 near here

Postural muscle onset latencies of subjects with STIM and NO STIM during externally-triggered and self-triggered perturbations are presented in Figure 6 A and B, respectively. For forward perturbations (TA and Q muscles), the multivariate ANOVA revealed significant main effects of Sensory stimulation ($F(2,16)=37.680$; $p<.001$), Perturbation type ($F(2,16)=18.389$; $p<.001$) and Period ($F(2,16)=31.533$; $p<.001$) along with a significant interaction effect of Perturbation type X Sensory stimulation ($F(2,16)=12.001$; $p=.001$). For backward perturbations (G and H muscles), the multivariate ANOVA revealed significant main effects of Sensory stimulation ($F(2,18)=12.077$; $p<.001$), Perturbation type ($F(2,18)=84.341$; $p<.001$) and Period ($F(2,18)=9.274$; $p=.002$) along with a significant interaction effect of Perturbation type X Sensory stimulation ($F(2,18)=14.282$; $p=.001$).

Post-hoc analyses revealed that in externally-triggered perturbations, STIM resulted in earlier postural muscle onset latencies in the majority of muscles across all frequencies and phases. In contrast, in self-triggered perturbations, the sensory stimulation decreased the muscle onset latencies for a minority of muscles, with no evident pattern across frequencies or phases. Exact p values for all post hoc t-tests used to test the effect of stimulation in externally- and self-triggered perturbations during transitions and steady state periods are given in Table 2.

Place Table 2 near here

Furthermore, post-hoc analyses revealed that compared to externally-triggered, the self-triggered perturbations elicited significantly earlier postural muscle onsets in majority of muscles at 0.5 and 0.61 Hz in the NO STIM group, but with one exception made no difference in the STIM group at any frequency. Exact p values for all post hoc t-tests used to test the effect of perturbation type in NO STIM and STIM groups during transition and steady state periods are given in Table 3.

Place Table 3 near here

In order to determine whether subtle differences in postural muscle onset latencies recorded in the two groups were camouflaged by grouping data from sequential oscillations, data for the first and last five cycles at different perturbation frequencies are reported. Tibialis anterior and gastrocnemius muscle onset latencies (mean ± SD) from subjects with and without sensory stimulation, during both types of perturbations at 0.25, 0.5 and 0.61 Hz are represented in Figure 7.

Place Figure 7 near here

In the STIM group, a progressive shift towards earlier onset was noted (triangular markers) during the first five cycles of a new frequency in externally-triggered perturbations. A similar trend was noted during the self-triggered transition periods although this was not as consistent across frequencies. For the last five cycles in the steady state periods, the earlier muscle onset latencies were maintained, although more variability was present in externally- versus self-triggered perturbations.

DISCUSSION

Based on clinical tests our subjects had high functional balance skills, were at no risk of falls, had high confidence in their balance and had only minimal diminished light touch sensation of the plantar surface. Regardless, the STIM effects were present despite available sensory information from all systems. Mechanical stimulation of foot plantar surface boundaries improved the ability of the old adults to control feet-in-place reactions and decreased COP excursion and the percentage of time COP was located near the boundaries of the base of support. The sensory stimulation resulted in earlier postural muscle activity in response to unpredictable, externally-triggered perturbations indicating improvement of reactive postural responses. Furthermore, the progressive shift during transition periods towards earlier postural muscle onset latencies and the earlier muscle activation during steady state periods indicate the increased ability of the STIM group to adapt and incorporate anticipatory mechanisms. This is of particular importance since, without sensory stimulation similar responses were not observed in old adults. In contrast to the effects with STIM, we reported that old adults displayed no shift in postural muscle onset latency during transition period and did not reach the same values of early postural muscles onset latencies even after 10, 30 or 40 cycles in the steady state periods at 0.25, 0.5 and 0.61 Hz, respectively in response to identical externally- triggered perturbations (Bugnariu and Sveistrup 2001, 2003).

Importantly, more subtle effects of the sensory stimulation were observed in the postural responses to self-triggered perturbations compared to those recorded following externally-triggered perturbations, possibly because of an already less threatening condition resulting from the control and predictability of perturbations (Bugnariu and Sveistrup 2004b). It is important to note that the effects of self-triggered and of sensory stimulation were not additive. In the subjects with sensory stimulation, the postural responses were not substantially different in self-triggered as compared to externally-triggered perturbations, as reflected by relative similar muscle onset latencies, COP ranges and percentages of time the COP was inside one particular region of the BOS.

Although the effect of sensory stimulation on the ability to resist stepping was not the primary focus of this study, the reduction in the total number of steps seen with STIM in both types of perturbations, supports the hypothesis that increased information about BOS stability boundaries, due to the mechanical stimulation, improves the ability to maintain the COM within the BOS. This is in line with results reported by Maki et al. (1999) where facilitation appeared to improve the ability to control "feet-in-place" reactions, young subjects being more able to avoid stepping when instructed to do so in response to transient instability in the backward direction. The same study reported that in old adults, facilitation of plantar sensation decreased the frequency of multiple forward-step reactions.

Regulation of Center of Pressure

In line with the effect on postural muscle onset latencies, the additional information provided by the mechanical stimulation of the boundaries of the plantar surface resulted in decreased phase lags between platform and COP movement and decreased excursions of the COP A/P during steady state periods. Again, these effects were especially evident for externally-triggered perturbations. Our results are complementary to reports of increased body sway induced by sinusoidal low frequency (0.3 Hz) displacement of the supporting surface when an ischemic block of afferent fibers was applied above the ankles (Diener et al. 1984, Mauritz and Dietz 1980). In the present study, sensory stimulation not only reduced the absolute range of COP, but also the percentage of time the COP was located in the extreme, less safe regions of the BOS. For example, in self-triggered perturbations, although a significant effect of sensory stimulation on absolute range of COP was present only at 0.5 Hz, the percentage of time the COP was located inside the extreme regions of the BOS was significantly decreased not only at 0.5 but at 0.61 Hz as well. It is important to note that the expression "COP located inside a region of BOS" does not refer to a static location, since during the present perturbations the COP was not static but constantly moving and having to change direction in order to travel beyond the COM for at least an instant to generate torques that accelerate the COM away from the limits of stability. Thus, decreasing the percentage of time the COP was located in extreme regions of the

BOS and decreasing the phase lags between COP and platform movement, through sensory stimulation increased stability by improving both spatial and temporal safety margins as defined by Patton et al. (1999).

Furthermore, directional specificity of the sensory stimulation effect was observed. In self-triggered perturbation trials, sensory stimulation reduced the percentage of time COP was located in the extreme heel region of the BOS, but had no significant effect on the percentage of time COP was located inside the anterior metatarsal region of the BOS. These findings correspond to results of experiments in which facilitation of plantar cutaneous sensation reduced the extent to which the COP approached the back of the foot during continuous perturbations (Maki et al. 1999). The absence of similar effects in the anterior direction may relate to the availability of information from proprioceptive receptors in the joints and muscles of the toes as proposed by Maki et al. (1999) and Perry et al. (2000). The main effect on COP appears to support the hypothesized contribution of plantar mechanoreceptors information to an internal representation of the stability limits, especially the posterior limit.

In general, across all dependent variables, significant effects of sensory stimulation were noted at the fastest platform oscillation frequencies, 0.5 and 0.61 Hz. Maki et al. (1999) also showed effects of plantar facilitation on COP displacement only at high magnitude perturbations similar to the ones in the 0.5 and 0.61 Hz conditions of the present study. One possible explanation may be that minimal destabilization and necessary postural adjustments were recorded at 0.1 and 0.25 Hz. This behaviour, reminiscent of upright stance, was characterized as a "ride" of the platform (Buchanan and Horak 1999). Since at the two slowest oscillation frequencies, the displacements of COP were small and the COP was located mainly in the central regions of the BOS, the pressure levels at the boundaries of the foot where the tube was adhered may not have changed substantially and consequently did not stimulate the cutaneous afferents. Another explanation may come from the adaptation characteristics of cutaneous receptors which may facilitate the perception of the rate of change of a stimulus. It has been shown that old women sense slow changes in standing posture less consistently than rapid changes (Thelen et al. 1998). As the frequency of platform oscillation increases, so does the velocity of the perturbations, the back and forth rate of the COM displacement over the BOS (Buchanan and Horak 2001) and consequently the rate with which the COP moves in the sagittal direction along the length of the BOS.

Role of cutaneous afferents

Effects of mechanical stimulation of cutaneous afferents from feet plantar surface boundaries were present despite available visual, vestibular and proprioceptive information, indicating that the cutaneous mechanoreceptors provide distinct information not substituted by other inputs. These results are in accordance with reported increased instability following hypothermic anesthesia of the foot soles, which removes cutaneous information, in subjects with access to visual, vestibular and proprioceptive information (Perry et al. 2000).

Cutaneous receptors are present in large numbers in the main contact areas of the heels, metatarsal zones, and external border of the feet. The receptors lack spontaneous activity in unloaded position and when no stimulation is applied to the soles (Kennedy and Inglis 2002). Further support of the role of cutaneous mechanoreceptors in balance comes from the evidence showing that in old women thresholds for successful detection of ankle movements are lower in condition of weight bearing (Thelen et al. 1998) compared to non weight-bearing ankle (Berenberg et al. 1987, Gurfinkel et al. 1982). Considering that cutaneous afferents are co-processed with proprioceptive information, a possible explanation for this improved detection may be the successful use of pressure cues from weight-bearing plantar receptors.

When standing on a continuous oscillating platform, the pressure levels in a given sole area change continuously. Vedel and Roll (1982) reported that slow adapting pressure receptors are able to code the static pressures applied to their receptive fields as well as their dynamic changes. By inducing oriented postural responses from localized vibration of the foot skin of standing subjects Kavounoudias et al. (1999) showed that cutaneous afferents from the feet provide the CNS with information about the body position with respect to the vertical axis. These afferents are encoded in a pressure scale and decoded as spatially relevant cues about whole-body orientation (Roll et al. 2002). For example, an increase in pressure distribution in the heel region compared to the metatarsal area would indicate that the body is leaning backward and would give rise to a compensatory postural reaction to cancel the pressure difference. In response to sudden toes-up rotation of a platform, both medium and long latency responses in ankle muscles were well correlated with the time derivative of the pressure difference between the forefoot and the rear foot region, as well as with the static pressure in the antagonist foot region (Wu and Chiang 1997). Finally, illusory perceptions of whole-body leaning in stabilized subjects were reported by Roll et al. (2002). Both orientation and amplitude of these perceptions were dependent on the stimulation pattern, further supporting the idea that foot sole inputs contribute to spatial representation of body posture.

CONCLUSION

The present results support the importance of cutaneous mechanoreceptors from boundaries of feet plantar surface in the control of postural reactions evoked by unpredictable and predictable continuous perturbations. Since decreased plantar sensation is often associated with aging, the present results suggest that even small decreases may contribute to the impaired control exhibited by old adults when recovering balance and may lead to interventions to counteract these difficulties.

Acknowledgements

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Table 1. Subject characteristics

	STIM group	NO STIM group
Gender	4 males, 4 females	4 males, 4 females
Age (years)	69.3 ± 5.7 (62 - 78)	70.1 ± 4.6 (62 - 77)
Weight (Kg)	69.9 ± 8.6 (60 - 83.9)	69.2 ± 80.1 (56 - 80)
Height (cm)	168 ± 5.6 (160 - 176)	167.3 ± 6.9 (158 - 176)
Foot length (cm)	27. 6 ± 2.8 (24.2 - 28.5)	27.3 ± 2.9 (24.5 - 28.1)
Foot plantar surface light touch threshold (filament number and target force)	4.01 ± 0.4 (3.61- 4.56) (0.4g – 4g)	3.9 ± 0.7 (2.83 - 4.56) (0.07g – 4g)
Community Balance & Mobility Scale	72 ± 13.7 (44 - 80)	68 ± 7.8 (55 - 80)
BERG Balance Scale	54.8 ± 1.3 (53 - 56)	54.6 ± 0.9 (53 - 56)
Activity Balance Confidence Scale (ABC)	96.7 ± 2.17 (93.17 - 100)	93.1 ± 8.4 (77.5 – 100)

Note: Group Means ± 1 standard deviation are presented with group ranges in parentheses.

Table 2. P values from post hoc analyses of differences in postural muscle onset latencies between the STIM and NO STIM groups. Comparisons reported for perturbation type and periods. Statistically significant comparisons (p<.006) indicated in bolded text.

Externally-triggered

	Transition				Steady state			
	TA	G	Q	H	TA	G	Q	H
Frequencies								
0.1 Hz	**.006**	.014	.018	**.005**	.091	**<.001**	**.001**	.010
0.25 Hz	.049	**.017**	.210	.039	**.001**	**.001**	**.005**	.038
0.5 Hz	**<.001**	**.002**	**.009**	**<.001**	**<.001**	**<.001**	**.001**	**.001**
0.61Hz	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**

Self-triggered

	Transition				Steady state			
	TA	G	Q	H	TA	G	Q	H
Frequencies								
0.1 Hz	.108	.106	.351	.844	.371	.636	.800	.995
0.25 Hz	.367	**.008**	.059	**.004**	.200	**.001**	.532	.259
0.5 Hz	**.003**	.216	.106	.700	**.001**	.107	.165	.094
0.61Hz	.014	.224	.315	.615	**<.001**	.644	**.006**	.368

Table 3 P values from post hoc analyses of differences in postural muscle onset latencies between externally- and self-triggered perturbations. Comparisons reported for groups and periods. Statistically significant comparisons (p<.006) indicated in bolded text.

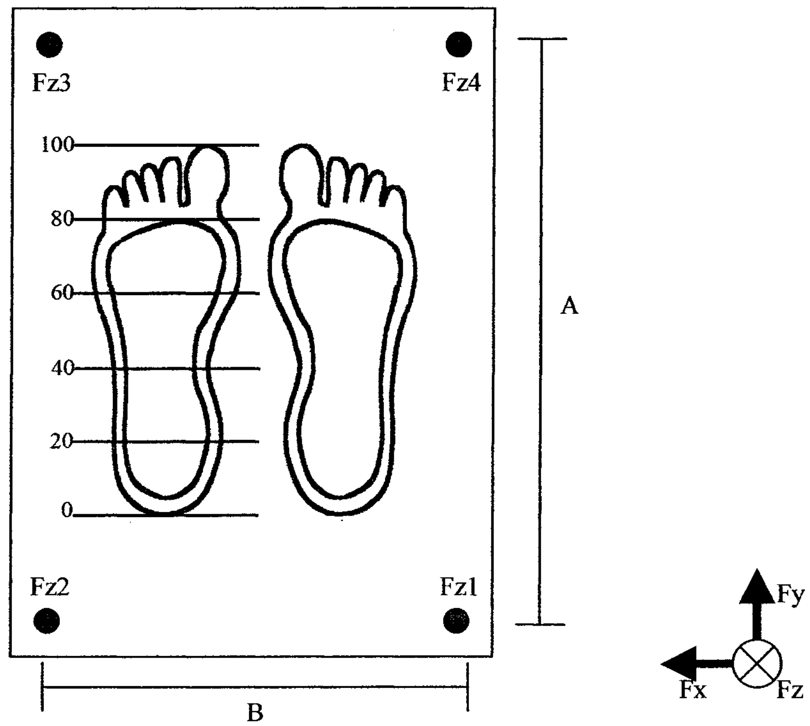
NO STIM

	Transition				Steady state			
	TA	G	Q	H	TA	G	Q	H
Frequencies								
0.1 Hz	.033	.032	.075	.016	.016	**<.001**	**.002**	.014
0.25 Hz	.040	**.006**	.404	.008	.188	.020	.246	.023
0.5 Hz	**<.001**	**<.001**	**.002**	**<.001**	.008	**<.001**	**<.001**	**.001**
0.61Hz	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**	**.001**

STIM

	Transition				Steady state			
	TA	G	Q	H	TA	G	Q	H
Frequencies								
0.1 Hz	.874	.454	.961	.529	.137	.023	.252	.158
0.25 Hz	.770	.519	.410	**.006**	.574	.059	.057	.466
0.5 Hz	.018	.770	.117	.737	.148	.534	.375	.365
0.61Hz	.659	.293	.271	.273	.638	.941	.936	.595

Fig. 1 Schematic of the Kistler force plate and the equations for calculating the COP. The placement of the polyethylene tube adhered to foot plantar surface boundaries and used to mechanically stimulate cutaneous afferents is illustrated. The BOS was divided into five equal regions from heel to big toe. The percentage of time the COP was located inside each region during perturbations was calculated for each oscillation frequency.



$$Fz = Fz_1+Fz_2+Fz_3+Fz_4$$
$$COP\ (A/P) = (Fz_3+Fz_4) - (Fz_1+Fz_2) * A/Fz$$
$$COP\ (M/L) = (Fz_3+Fz_2) - (Fz_1+Fz_4) * B/Fz$$

Figure 1

Fig. 2 Group (mean ± SD) COP A/P displacement amplitudes of old adults with STIM (grey bars) and NO STIM (black bars) during perturbations at four frequencies of platform translation. Data from transition periods (top panels) and steady state periods (bottom panels) following externally-triggered perturbations (left panels) and self-triggered perturbations (right panels) are shown. Statistically significant differences between groups are indicated with an asterix (*). Note: corrected p-values for multiple comparisons $p < .00625$.

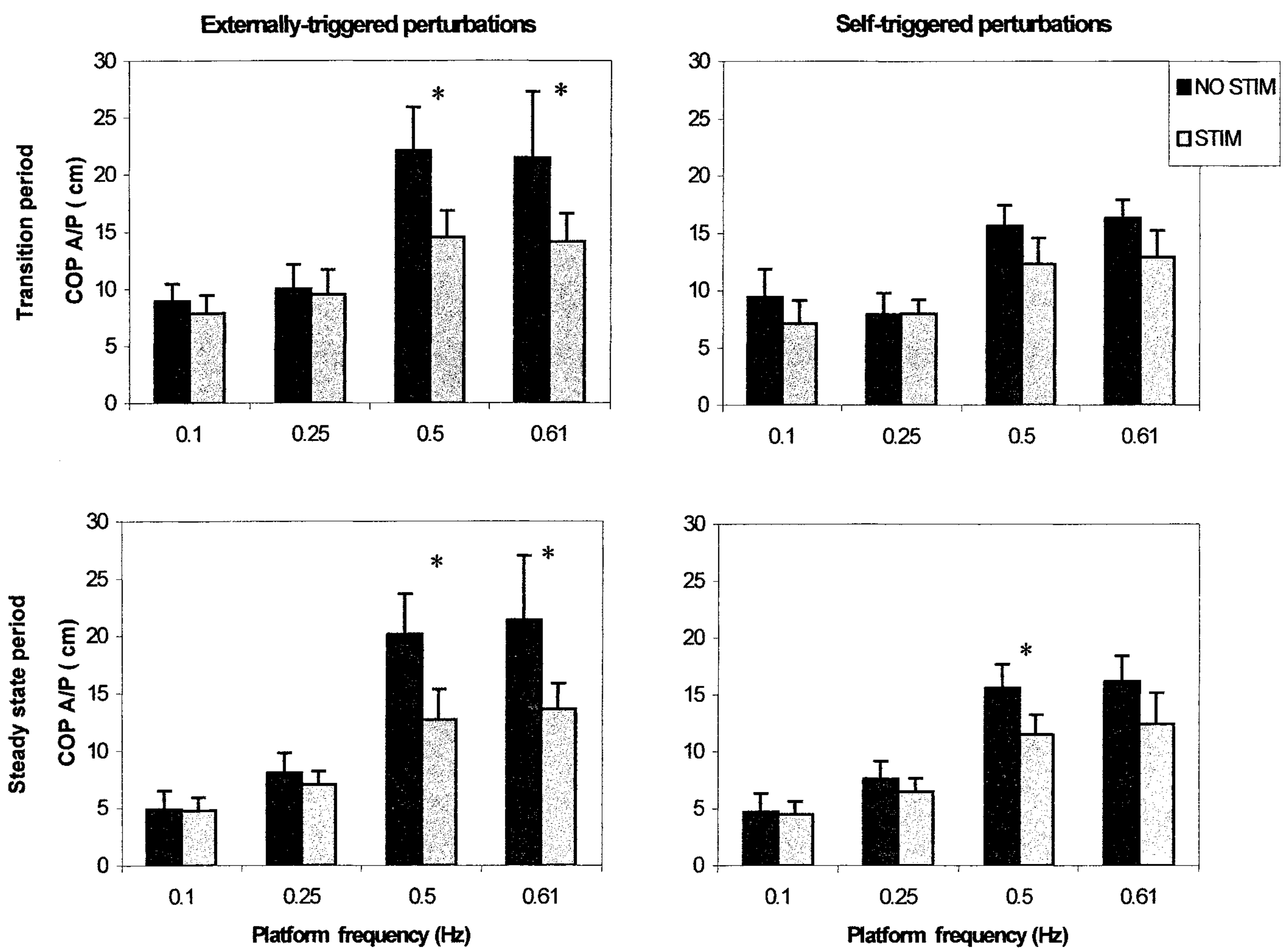
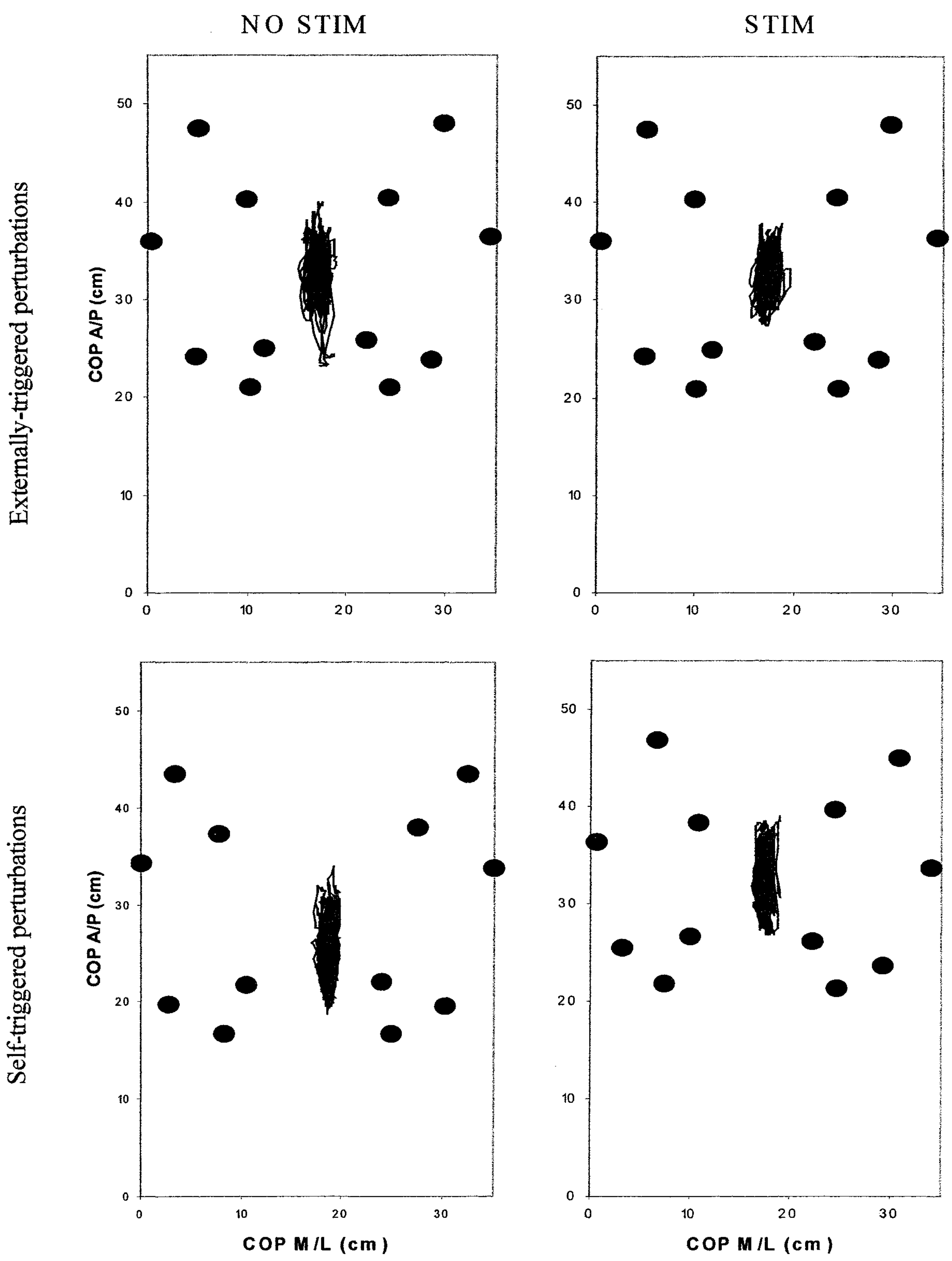

Externally-triggered perturbations
Self-triggered perturbations
Transition period
COP A/P (cm)
Steady state period
COP A/P (cm)
NO STIM
STIM
0.1
0.25
0.5
0.61
Platform frequency (Hz)
Platform frequency (Hz)
*
*
*
*
*
30
25
20
15
10
5
0

Figure 2

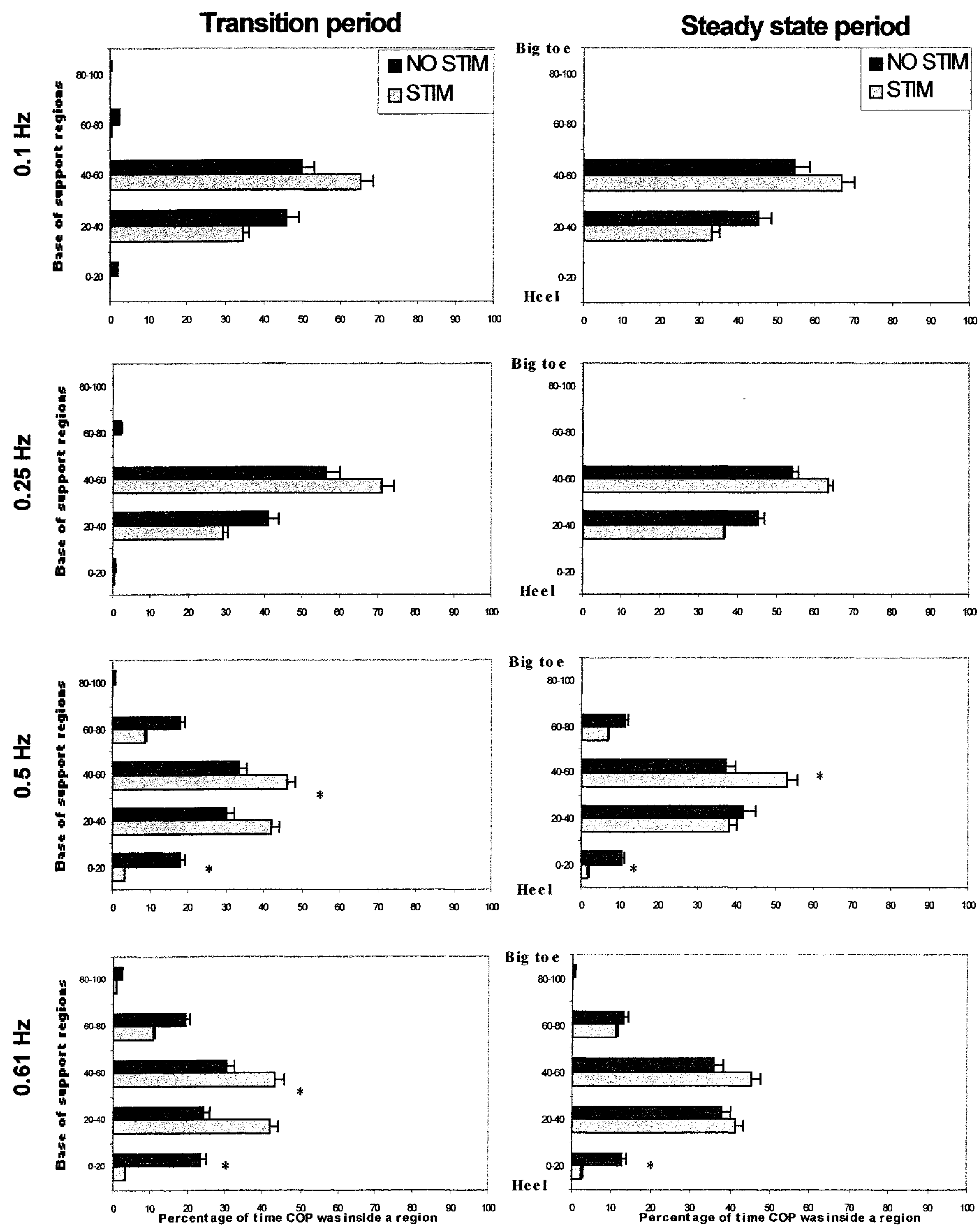
Fig. 3 Examples of COP displacements from subjects with NO STIM and STIM (left and right panels, respectively) during externally- and self-triggered perturbations (top and bottom panels respectively) during steady states at 0.5 Hz. Each panel illustrates the dimensions (in cm) of the force plate on which the subjects were standing, with the circle icons indicating the position of subject's feet. From top to bottom, the six icons indicate for each foot: the tip of big toe, the two widest points across the metatarsal region, the two widest points across the heel region and the back of the heel. The COP M/L excursion is plotted on the x-axis and the COP A/P excursion on the y-axis.



NO STIM
STIM
Externally-triggered perturbations
Self-triggered perturbations
COP A/P (cm)
COP M/L (cm)

Figure 3

Fig. 4 Percentage of time the COP was located inside a particular region of the base of support for subjects with STIM (grey bars) and NO STIM (black bars). Group (mean ± SD) data from transition (left panels) and steady state periods (right panels) at four frequencies of platform translation are presented. The base of support was divided into five equal regions, zero representing the posterior boundary delimited by the back of heel and 100 representing the anterior boundary represented by tip of the big toe. The five different regions of the BOS are represented on the *y*-axis, while the *x*-axis represents percentage of time.



Transition period
Steady state period
NO STIM
STIM
0.1 Hz
0.25 Hz
0.5 Hz
0.61 Hz
Base of support regions
Big toe
Heel
80-100
60-80
40-60
20-40
0-20
0 10 20 30 40 50 60 70 80 90 100
*
Percentage of time COP was inside a region of the base of support

Figure 4

Fig. 5 Phase lags (mean ± SD) between platform and COP A/P time series from STIM and NO STIM groups during steady state periods following externally- and self-triggered perturbations at 0.5 and 0.61 Hz. Statistically significant differences between groups are represented with an asterix (*). Note: corrected p-values for multiple comparisons $p < .0125$

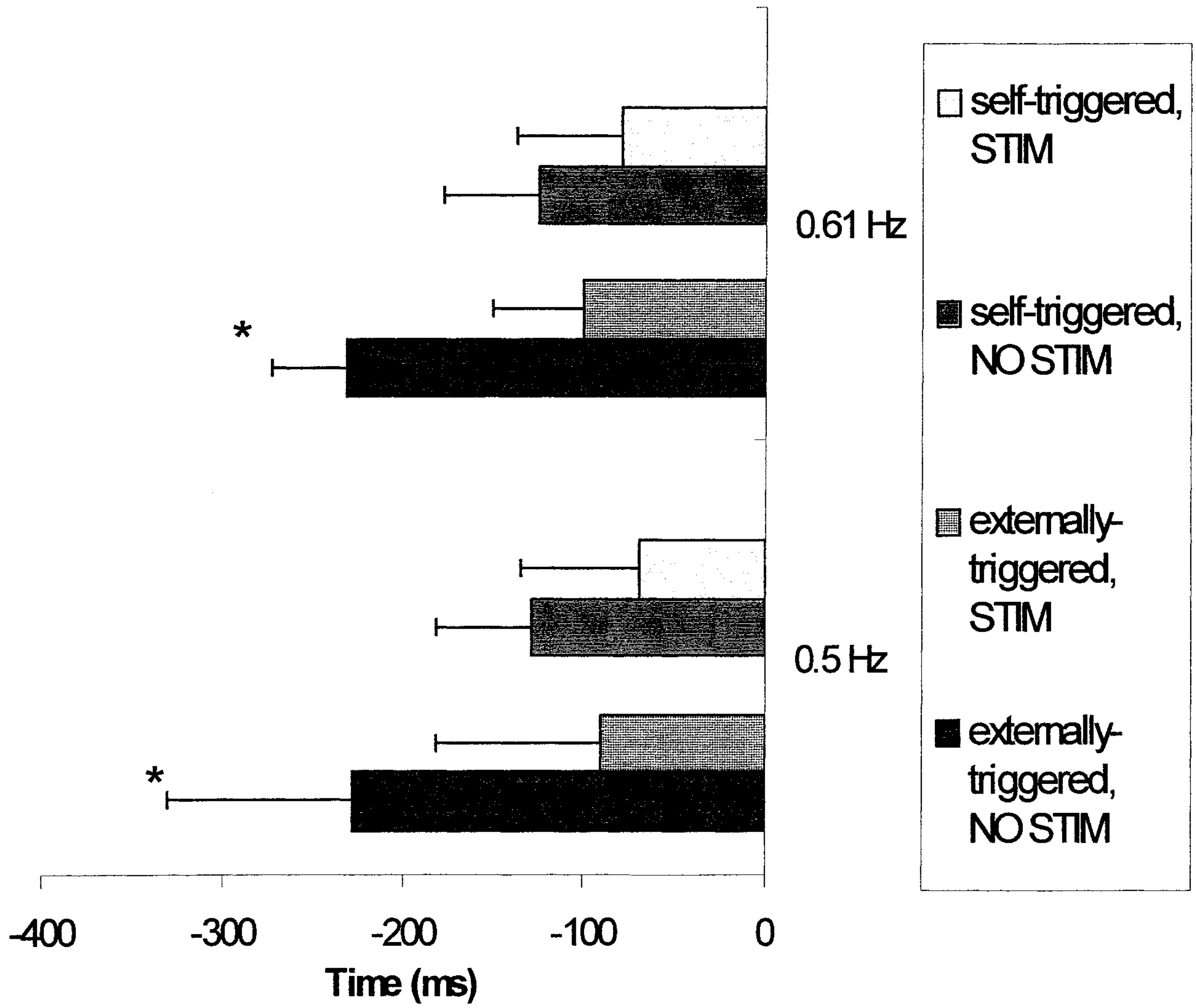
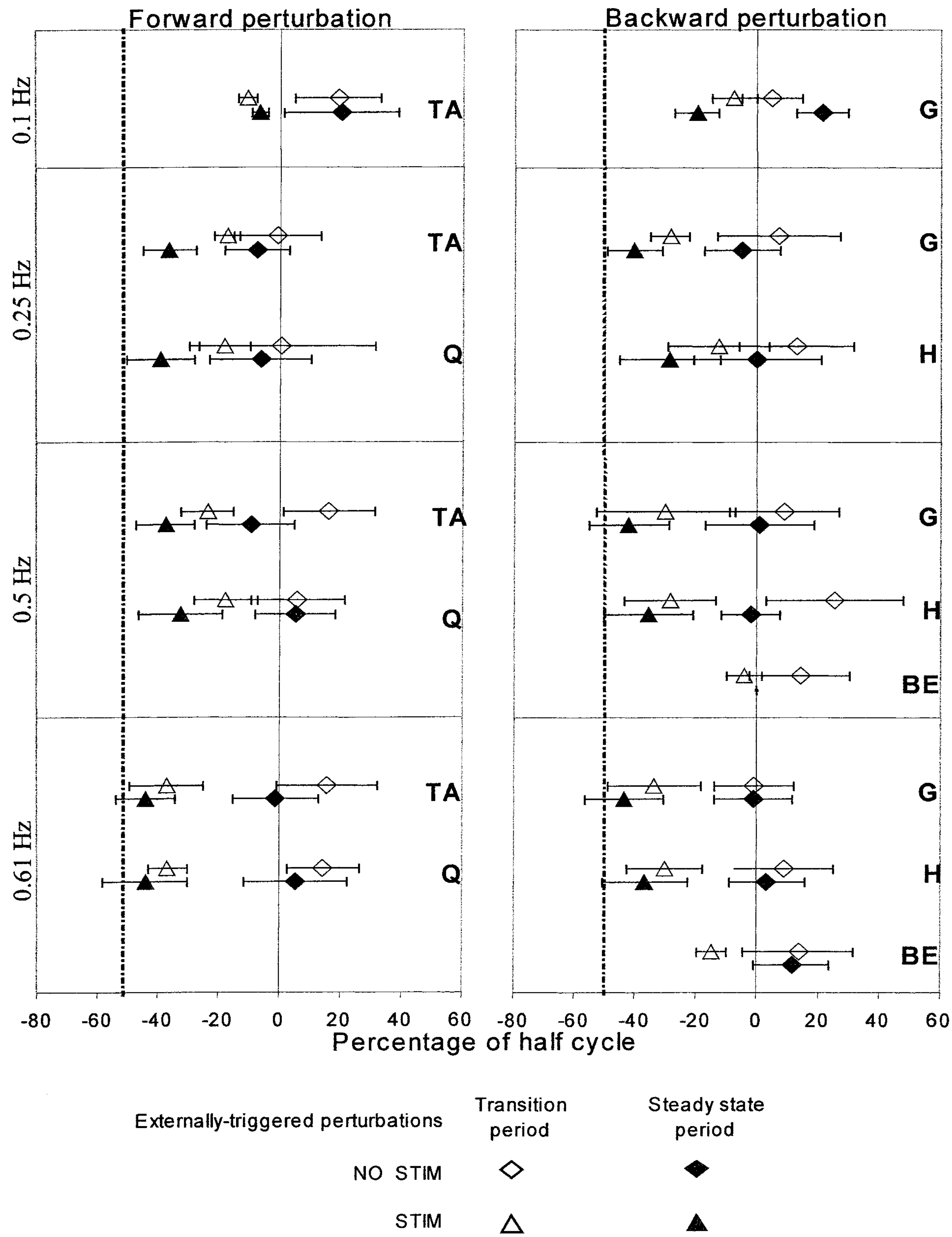

self-triggered, STIM
self-triggered, NO STIM
externally-triggered, STIM
externally-triggered, NO STIM
0.61 Hz
0.5 Hz
*
*
-400
-300
-200
-100
0
Time (ms)

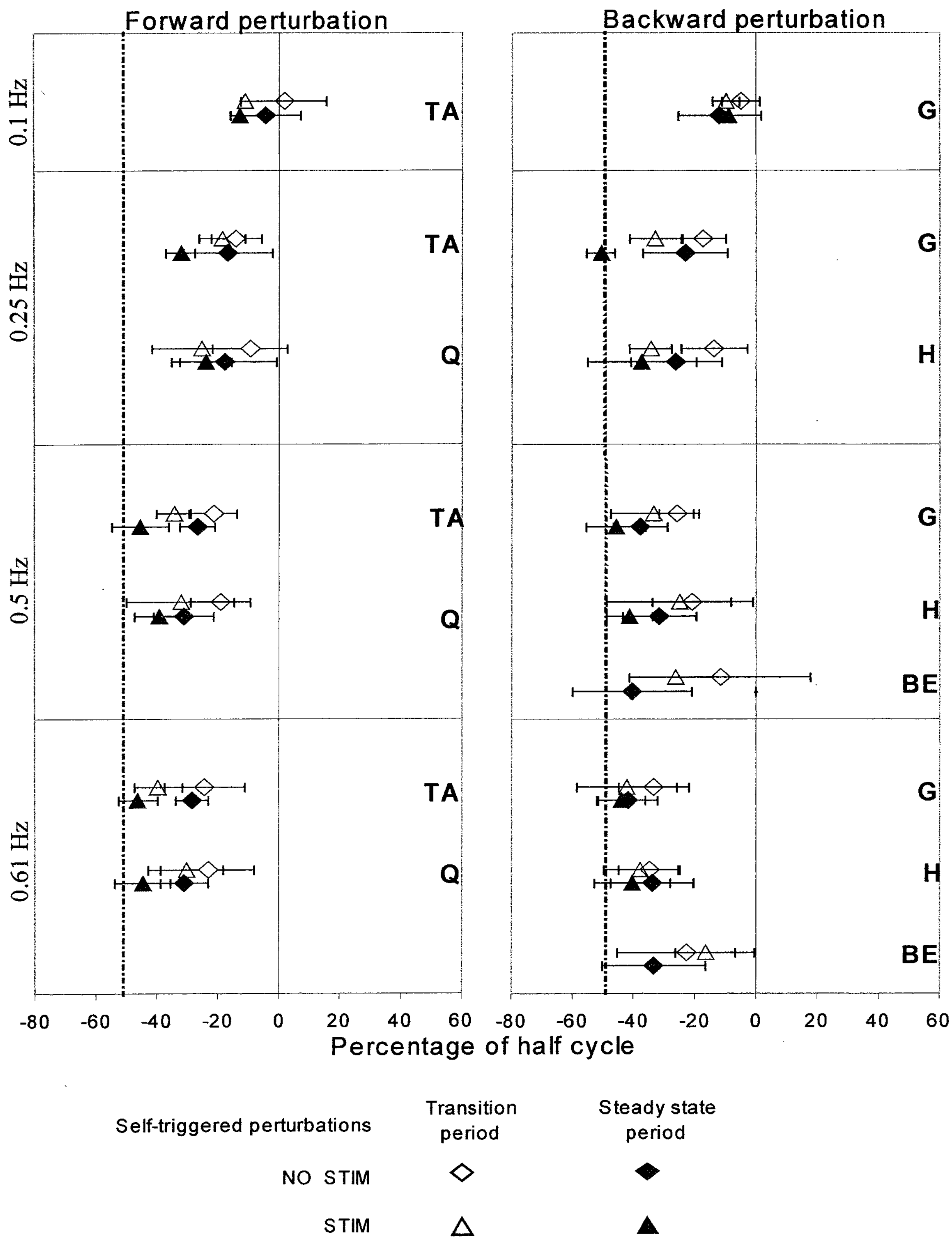
Figure 5

Fig. 6 A and B Postural muscle onset latencies (mean ± SD) of subjects with STIM (triangle icons) and NO STIM (diamond icons) at four frequencies of platform translation 0.1Hz, 0.25Hz, 0.5Hz, and 0.61 Hz in externally-triggered perturbations **(6A)** and in self-triggered perturbations **(6B)**. Onset latencies are expressed as a percentage of half cycle time for muscles normally associated with a forward perturbation (TA and Q) and for muscles normally associated a with backward perturbation (G, H, and BE). Open and filled icons represent postural muscle onset latencies from the transition and the steady state periods, respectively. Zero represents the time at which the platform changed direction. For both forward and backward directions of motion, the platform began to slow down after the -50% mark. For clarity purposes the values for the transition periods are offset on the *y* axis. Onset latencies of the BE are not illustrated for steady states in trials with STIM since the muscle was activated in less than half of the trials.



Forward perturbation
Backward perturbation
0.1 Hz
0.25 Hz
0.5 Hz
0.61 Hz
TA
Q
G
H
BE
-80 -60 -40 -20 0 20 40 60
Percentage of half cycle
Externally-triggered perturbations
Transition period
Steady state period
NO STIM
STIM

Figure 6 A



Forward perturbation
Backward perturbation
0.1 Hz
0.25 Hz
0.5 Hz
0.61 Hz
TA
Q
G
H
BE
-80 -60 -40 -20 0 20 40 60
Percentage of half cycle
Self-triggered perturbations
Transition period
Steady state period
NO STIM
STIM

Figure 6 B

Fig. 7 Tibialis anterior and gastrocnemius muscle onset latencies (mean ± SD) from subjects with STIM (triangles icons) and NO STIM (diamond icons), during externally- and self-triggered perturbations. Values from the first five cycles following the increase in oscillation frequency (transition period) and from the last five cycles of the steady state period at 0.25, 0.5 and 0.61 Hz are represented. Zero represents the time at which the platform changed direction.

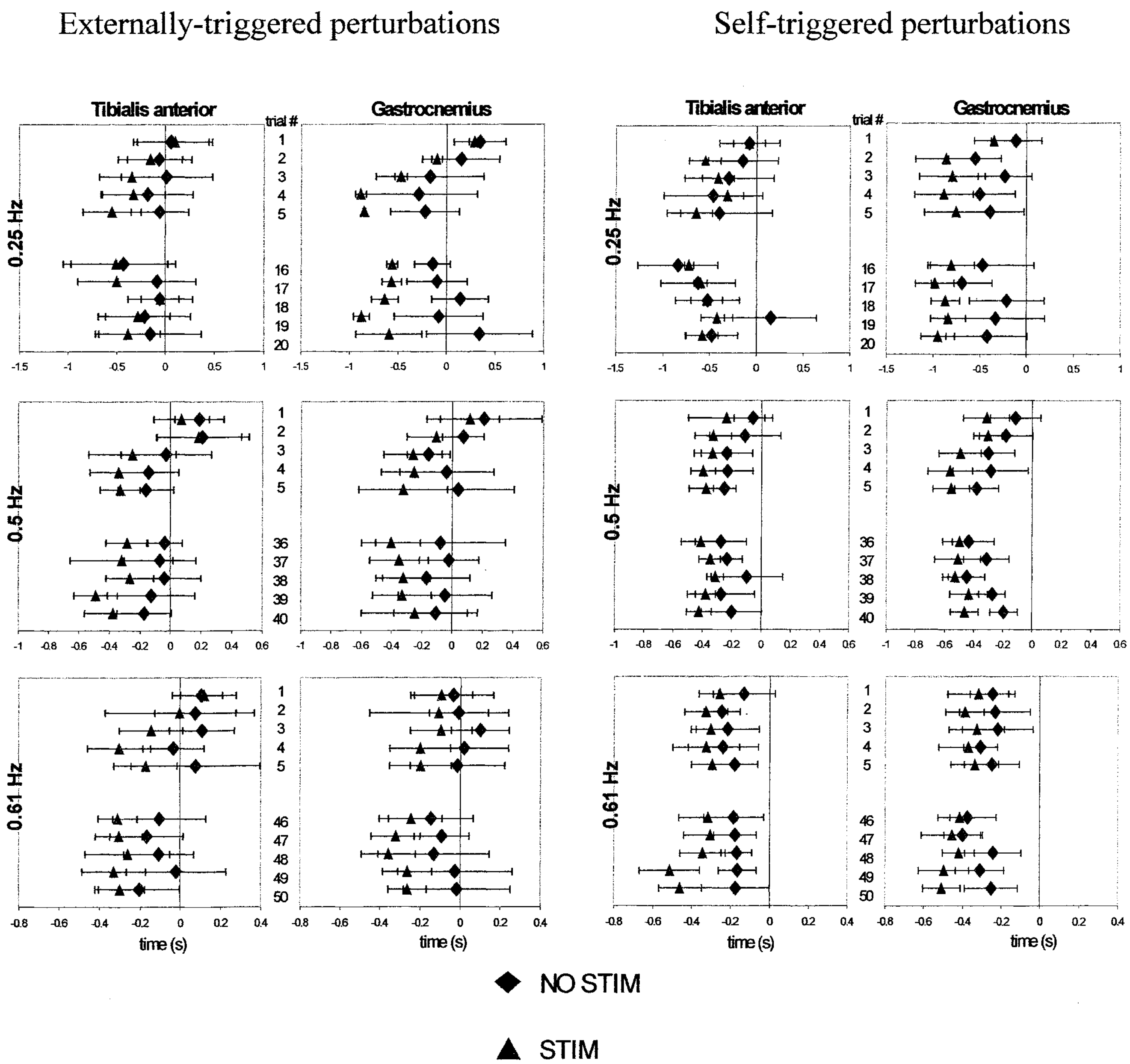

Externally-triggered perturbations
Self-triggered perturbations
Tibialis anterior
Gastrocnemius
trial #
0.25 Hz
0.5 Hz
0.61 Hz
time (s)
NO STIM
STIM

Figure 7

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CHAPTER 5

Development of a model explaining age-related differences in postural responses to continuous perturbations

ABSTRACT

A model was developed to explain age-related differences in postural responses to continuous perturbations. The model was used to: 1) investigate the impact of noise and neural delay on standing balance in young and old adults perturbed by a constantly sinusoidal platform translation; and 2) evaluate predictions with regards to stepping responses. Experimental data were obtained from young (22.3 ± 2.1 years old, n=8) and old (70 ± 4.2 years old, n=8) adults who maintained their balance on a platform that oscillated sinusoidally 20 cm peak-to-peak in the anterior/posterior (A/P) direction at 0.5 Hz. A mathematical model representing body motion in response to continuous sinusoidal platform perturbations was implemented. An initial two segment model (foot and inverted pendulum) proposed by Pai and Patton (1997) focussing only on mechanical constraints and simulating only anterior movement, was expanded to include neural constraints and applied to sinusoidal anterior-posterior movement. The neural constraints incorporated noise and time delays. The time delay reflected the time required for all processes from the moment a signal indicated a deviation from the vertical to the time where the restoring force produced the necessary torque. Simulations were run at the same frequency of platform translation as the experimental data. Time delay and noise parameters were tuned to obtain best representation of experimental data. Stability boundaries for successful control of feet-in-place

standing balance on the oscillating platform were calculated based on a dynamic concept of stability.

The inverted pendulum model provided a good approximation of the experimental data, with a correlation coefficient of 0.89 ± 0.03 and 0.83 ± 0.02 for the young and old individuals respectively. The age-related difference in the control of standing balance on a continuous oscillating platform recorded in experimental data can be partially explained through increased levels of sensory noise and neural delays in the simulated data of old adults. Old adults crossed more often the regions of stability boundaries compared with young adults. Our data support the concept of dynamic stability limits (Pai et al. 1997, 1999, 2000) according to which, both the horizontal position and velocity of the center of mass (COM) with respect to the base of support (BOS) provide critical information pertaining to one's ability to control balance. We also demonstrated that the acceleration parameters of a perturbation have to be taken into account when calculating stability limits and we derived for the first time the equations for calculating these stability limits related to continuous translations of the BOS.

INTRODUCTION

Adequate postural control is essential to the successful execution of activities of daily living. Recent efforts have been directed toward deriving novel measures and modeling approaches to provide more insight into mechanisms underlying postural control. Contrary to experimental settings which are difficult to manipulate especially with human subjects, mathematical models provide a framework allowing systematic manipulation of parameters and can thus assist in characterizing experimental conditions and explaining experimental results. Moreover, when models achieve a good representation of experimental data, their predictive ability can be used to extend results to similar populations in different paradigms. Such predictions may provide guidance for developing intervention programs for improving stability when perturbed.

The static concept of stability limits considers only the position of the centre of mass (COM) with respect to the base of support (BOS). More recently, extensive work with mathematical modeling defined a new dynamic concept of stability limits (Pai et al. 1997, 1998, 2003) which simultaneously considers both the relative position and velocity between the COM and the BOS. Combining empirical approaches with mathematical modeling, Pai et al. demonstrated that, in fact, the position of COM can be outside of the BOS and not result in a loss of balance if the COM velocity has the appropriate magnitude and direction (Pai et al. 1997, 1998). Mathematical modeling has been used to: i) simulate the anterior movement of a simple pendulum connected to a stationary BOS and to identify a feasible stability region for safely terminating the movement (Pai and Patton 1997); ii) identify thresholds for step initiation induced by discrete support surface translations (Pai et al. 2000); and iii) estimate the impacts of reductions in ankle strength or in functional BOS on balance and stability (Pai and Patton 1997).

A simple inverted pendulum model of human stance and stability in the sagittal plane may include only two segments, one representing the symmetrical placement of the feet and the other representing the rest of the body. This type of model, where body rotation occurs only at the ankle is appropriate for simulating movement in the sagittal plane. The musculature of the ankle is responsible for controlling the displacement of COM while muscles of more proximal joints, such as knee, hip and spine are responsible of maintaining a rigid body (Winter et al. 1996). Despite the limitations introduced by a simplified model of the human body that makes the assumption that all corrective responses are located at the ankle joint and that the rest of the body behaves as a unit, the inverted pendulum model has been used extensively with appreciable results (Pai et Patton 1997, Pai et Iqbal 1999, Pai et al. 2000, Stirling and Zakynthinaki 2004). A multiple segment model of the human body may be more realistic; however, the mathematical equations representing motion for multiple link models are complex, nonlinear and highly coupled and often do not have analytical solutions (Iqbal and Pai 2000).

To successfully maintain balance and counter the mechanical effects of a perturbation generated by a moving platform, the central nervous system (CNS) makes adaptive adjustments to improve the stability of the body COM state, its velocity and position. Such control relies on accurate internal representations of body orientation and stability limits. The stability limits are a function of anatomical, physiological, and environmental constraints and therefore can be calculated based on physical laws of motion (Pai et al. 2003). In human stance control, the CNS receives delayed information from a multisensory system and uses this information to estimate body orientation relative to the environment. An exact estimation of body orientation is not possible because all sensory information is received with a certain time delay and the sensory signals may not always be reliable as, for instance, in old adults with age-related sensory losses

(Skinner et al. 1984, Horak et al. 1990, Speers et al. 2002). In addition, the estimation of body orientation involves an integration of different sensory systems each with its own coordinate frame (Mergner et al. 1997). Thus, the CNS can only provide a best possible estimate of body orientation and base the corrective response on this estimate. A multisensory integration model of human stance control based on optimal estimation theory proved that despite transient external perturbations, a controller was able to stabilize a model of an inherently unstable standing human with neural time delays of 100 ms (van der Kooij et al. 1999).

The purpose of the study was: 1) to investigate the impact of noise and neural delay on standing balance in young and old adults perturbed by a constantly sinusoidal platform translation; and 2) to evaluate model predictions with regards to stepping responses. A mathematical model representative of body motion in response to continuous sinusoidal platform perturbations has been implemented. The stability boundaries for successful control of feet-in-place standing balance on the oscillating platform were calculated based on a dynamic concept of stability. It was hypothesized that the age-related difference in the control of standing balance on a continuous oscillating platform recorded in experimental data would be partially explained through increased levels of noise and neural delays in the simulated data of old adults. It was also hypothesized that compared to younger adults, older adults would more often cross the safety boundaries of the stability limits predicted by a dynamic model.

METHODS

Experimental

The experimental data used to compare and test the model predictions were collected in a previous study (Bugnariu and Sveistrup 2004 a). In summary, the study involved sixteen adults who gave their informed consent to participate. The experimental procedures were approved and performed in accordance with the Tri-Council Policy Statement on Ethical Conduct for Research Involving Humans (Canada). All participants were healthy volunteers with no history of falls, musculoskeletal or neurological problems. Eight young adults and eight old adults participated with an equal number of men and women included in each group. Mean (± SD) age, height, weight, and foot length were: 22.3 ± 2.1 years, 170.9 ± 5.5 cm, 71.4 ± 10.8 Kg and 26.9 ± 1.2 cm for the young adults and 70 ± 4.2 years, 165.1 ±13.8cm, 70.2 ± 14.7 Kg, and 26.9 ± 1.1 cm for the old adults.

Task and procedures

Participants were asked to stand erect, eyes open, barefoot with feet shoulder width apart on a movable platform that was driven by an electric motor. They were asked to maintain their balance and to avoid taking steps unless absolutely necessary. If a step was taken, they were instructed to bring their feet back to the initial position. In order to prevent falls, subjects wore a loose harness attached to the ceiling while an assistant provided them with additional support if they were unable to maintain their balance. The platform oscillated sinusoidally 20 cm peak-to-peak in the anterior/posterior (A/P) direction. Platform oscillation started at a frequency of 0.1 Hz and after intervals of 80-100 seconds the frequency was suddenly and unexpectedly increased successively to 0.25 Hz, 0.5 Hz and 0.61 Hz. Each subject completed two five-minute trials. The present analyses are restricted to the perturbations cycles at 0.5 Hz (80 cycles of anterior-posterior continuous translations per subject). We chose to focus our analysis on the perturbations at 0.5 Hz because our previous analyses showed that: i) at 0.1 and 0.25 Hz the majority of subjects ride the platform with minimal displacements of the COM relative to the BOS; ii) the increase in platform frequency from 0.25 to 0.5 Hz proved to be the most challenging transition of the paradigm, eliciting the highest number of stepping responses across all four frequencies from both young and old subjects; iii) significant differences in postural responses of young and old adults were evident at 0.5 Hz in numerous variables used to characterize postural reactions including postural muscle onset latencies, COP and COM displacements and phase lags relative to platform movement; and iv) postural responses at 0.5 and 0.61 Hz proved to be statistically similar (Bugnariu and Sveistrup 2004 a, b, c). At 0.5 Hz, the characteristics of continuous sinusoidal platform translations in the A/P direction were: displacement: ±0.1m, velocity: ±0.314m/s, and acceleration: ±0.987 m/s^2.

A Kistler force plate (Type 9286, Kistler Instrument Corp) was placed in the center of the moving platform and the subjects started all trials standing centered on the force plate. The ground reaction force and platform position signals were sampled at 600 Hz. Reflective markers were placed on the left side of the body over the following landmarks: cathi of left eye, lateral mandibular joint, seventh cervical vertebra, acromion, greater trocanter, lateral femoral condyle, lateral malleolus, heel, and fifth metatarsophalangeal. A reflective marker was also placed on the moving platform. A high resolution video camera, sampling at 60 Hz, recorded the position of the left side of the body in a sagittal view. A motion analysis system (APAS, Ariel Performance Analysis System) provided position information for calculation of total COM kinematics. The two-dimensional co-ordinates of body markers were filtered at 6Hz. A bilaterally symmetrical six-link body segment model composed of the feet, shanks, thighs, trunk, arms and head was used to estimate the total body COM position, velocity and acceleration in the anterior-posterior direction (Vaughan et al. 1991). The position, velocity and acceleration of the platform were subtracted from the COM corresponding parameters. Thus, COM position, velocity and acceleration data relative to a coordinate system fixed to the moving platform were obtained.

The number of stepping responses and incidences of additional support offered by an assistant were recorded during the experiments. The presence of a step and actual time of additional support were confirmed by video recordings.

Model

A typical inverted pendulum model (Figure 1) was used to simulate the movement of the body in sagittal plane. The motion equation of the inverted pendulum was determined using Euler-Lagrangian dynamics (Eq. 1).

$$\tau = -\tfrac{4}{3} m l^2 \ddot{\theta} + m l (g \sin\theta - \ddot{x}_p \cos\theta) \qquad \text{(Eq. 1)}$$

Place figure 1 near here

The inverted pendulum is controlled by a nonlinear model-based control law (Eq.2) derived from Eq.1, which cancels the nonlinearities of the inverted pendulum model (Craig 1989). This reduces the system to a linear system, which can be controlled using a typical proportional-derivative servo (Eq. 3)

$$\tau_r = -\tfrac{4}{3} m l^2 \ddot{\theta}_r + m l (g \sin\theta_e - \ddot{x}_p \cos\theta_e) \qquad \text{(Eq. 2)}$$

$$\ddot{\theta}_r = \ddot{\theta}_d + k_v(\dot{\theta}_d - \dot{\theta}_e) + k_p(\theta_d - \theta_e) \qquad \text{(Eq. 3)}$$

where τ_r is the restoration torque equivalent to the subjects' dorsiflexor and plantarflexor torques; l is half of the subject's height and represents location of the model COM; m is body mass; g is the gravitational acceleration; $\ddot{x}_p$ is the platform acceleration; $\ddot{\theta}$, $\dot{\theta}$, θ are the body angular acceleration, velocity and position. $\ddot{\theta}_d$, $\dot{\theta}_d$, θ_d are the desired body angular acceleration, angular velocity and angular position; θ_e and $\dot{\theta}_e$ are the estimated angular position and velocity of the body as perceived by the subject's sensory system; $\ddot{\theta}_r$ is the linear proportional-derivative servo; and k_p and k_v are the position and speed controller gains, respectively.

The inverted pendulum model for body dynamics is integrated into a broader system model (Figure 2) representative of the postural control system. The goal of the system is to maintain a certain desired trajectory of the body best fitted for the specific postural task. In our system model we assumed that the goal was the maintenance of upright stance with null desired body angular acceleration and angular speed ($\ddot{\theta}_d = \dot{\theta}_d = 0$). Based on this desired trajectory for the body, the controller, representing the central nervous system, sends the appropriate posture control commands to the muscles, which generate the torques producing the body dynamics simulated here by the inverted pendulum. The output of the inverted pendulum model, the real angular position and velocity, representing the body kinematics, are detected by multiple sensors and fed back to the controller as an estimated angular position and velocity. In this paper, the estimated angular position was generated from the real angular position perturbed by noise and delay. Various combinations and levels of noise and/or delays can be added into a simulation at numerous components of the system affecting different elements, such as sensory inputs, control gains and/or motor outputs. Perturbing the control gains with noise will, as a consequence, change the robustness of the system; possibly leading to instability (the model will "fall down"). In our simulated model, white noise with different magnitudes was added to the sensors, sensory noise, and to the output torque, torque noise. Delays were introduced for the generation of restoring torque, torque delay, as well as for the time required to perceive, transmit and integrate sensory information for estimation of the body position, sensory delay. In our model, the sensory delay and torque delay represent the total neural delay.

Place figure 2 near here

Simulations

A Matlab simulation fifth order Runge-Kutta method with a fourth-order step size control was used to integrate the equation of motion (Eq. 1) and perform each simulation. Parameters such as mass, height, and foot length for the inverted pendulum model were taken directly from measurements of subjects that participated in the study. These parameters were in accordance with previously published data (Winter 1990). The simulation output included time histories of the kinematic states, angular position and velocity for the inverted pendulum segment, from which COM position and velocity were derived. Eighty second simulations were run with various combinations of sensory noise and delays. For the initial implementation, torque noise was set to 1.5 Nm and torque delay to 50 ms for both young and old adults. Numerous simulation trials were run, in which the sensory noise level and delay were adjusted sequentially, with the purpose of reproducing COM trajectories in the position and velocity space that matched the experimental results. Time series of COM position and velocity from simulations were compared to corresponding experimental data. The COM position was normalized to foot length and the COM velocity was normalized to height. The time series of COM trajectory were divided into 40 cycles each corresponding to one cycle of platform oscillation. Averaging across the 40 cycles we obtained an "averaged COM trajectory" for each experimental or simulated trial. The "averaged COM trajectories" from simulated and experimental data were cross-correlated. The simulated data were considered to be an accurate representation of the experimental data when: i) the simulated COM trajectories had similar shapes to the experimental trajectories; ii) the ranges of simulated COM position and velocity were within ±3.5 % of the experimental data; and iii) the correlation between the averaged simulated and average experimental trajectories was greater than 0.8.

Stability boundaries

Simulation of body movement on the platform was followed by computation of stability boundaries. The common method previously used to identify the stability boundaries for a given system and perturbation was an iterative process (Pai et al. 1999, 2000). This consisted in numerous simulations and optimization processes in order to determine the maximum and minimum COM velocities that would still permit the task to be completed successfully (Pai and Patton 1997).

The boundaries of the dynamic stability region are dependent on the platform acceleration and system parameters (e.g. body anthropometrics). There is a significantly increased degree of complexity introduced when studying dynamic continuous translations compared to discrete perturbations. In order to identify the appropriate stability boundaries under continuous sinusoidal translation of the platform, two stability boundaries were identified for each discrete value of perturbing acceleration. Using an iterative process, this implies a high number of simulations. Therefore, we exploited the reversible dynamics of the modeled inverse pendulum for a more rapid and precise determination of the stability boundaries. The use of reversible dynamics was possible because of the negligible air friction forces. The dynamic equations and stability constraints for calculating the stability boundaries are presented in Appendix A.

For each system parameter and discrete perturbing acceleration there are two stability boundaries. For each COM starting position, these boundaries represent the minimum and maximum COM velocities for which balance can be maintained with the COP at either of the BOS extremes, heel or toe (Figure 3 A). Beyond the right side of the right boundary, the subject will certainly fall backwards, while beyond the left side of the left boundary, the subject will fall forward.

As specified earlier, for a given system, the stability boundaries are dependent on the perturbation acceleration at a specific moment in time. Therefore, the stability region illustrated in Figure 3A, corresponding to one particular platform acceleration, represents only one slice of a three-dimensional stability space. Taking into consideration the specific platform perturbation accelerations in our study that ranged from +0.987 to -0.987 m/s^2, stability boundaries corresponding to 40 platform accelerations between the minimum and maximum were generated. Stability boundaries corresponding to all other platform accelerations values were interpolated. Together, these stability boundaries form the stability boundaries planes in the space of stability (Figure 3B). The system is stable as long as the COM position-velocity trajectory remains between the two planes.

Place figure 3 near here

For each subject, the experimentally-derived and the simulated COM trajectories were plotted independently with the computed stability boundaries at all platform accelerations. Stepping was considered to be necessary or unnecessary depending on whether the respective COM trajectory (i.e., experimental or simulated) crossed or did not cross the stability boundary planes. We evaluated the model predictions by determining whether the subjects stepped or received external support when the model predicted a step and whether the subjects kept their feet stationary when the model did not predict a step.

Data analysis

Descriptive statistics were used to describe the subject sample, the number of steps and incidence of external support. Independent t-tests were used to identify significant differences between young and old adults in levels of noise and neural delays from the most accurate simulations. An accepted significance level of $p<0.05$/ number of comparisons to correct for multiple tests and a 95 % confidence interval was used for all dependent variables. The accepted significance level was $p<0.025$.

RESULTS

The inverted pendulum model provided a good approximation of the experimental data. Figure 4 represents examples of simulated and experimental data from a representative young and old adult. Cross-correlation coefficients between the average COM trajectories of simulated and experimental data were 0.89 ± 0.03 and 0.83 ± 0.02 for the young and old adults, respectively.

Place figure 4 near here

For each simulation data set that respected the criteria to be considered a good representation of experimental data, the noise and delay parameters were recorded. For young adults, the simulation parameters that resulted in the best representation of experimental data were: i) average neural delay times of 94.25 ± 3.06 ms with values ranging from 90 to 100 ms, corresponding to average sensory delays of 44.25 ± 3.06 ms; and ii) sensory noise magnitudes of 0.3 ± 0.08 deg. with values ranging from 0.2 to 0.4 deg. For old adults, the simulation parameters that resulted in the best representation of experimental data were: i) average neural delay times of 130.38 ± 7.63 ms with values ranging from 120 to 145 ms, corresponding to average sensory delays of 80.38± 7.63 ms; and ii) sensory noise magnitudes of 1.01 ± 0.21 deg. with values ranging from 0.8 to 1.5 deg. Compared to young adults, in old adults the average sensory delay was significantly longer ($p<.001$) and the sensory noise levels significantly larger ($p<.001$).

Subjects were instructed to keep their feet in place and avoid stepping unless absolutely necessary. During experimental trials, a total of 4 steps and 3 external support periods lasting from 2 to 4 seconds were recorded from the young adults. In contrast, for the same number of experimental trials, a total of 32 steps and 37 external support periods lasting between 2 and 10 seconds were recorded in the old adults.

In all experimental trials of both young and old subjects when no steps were recorded, the model consistently predicted a no step response, i.e. the simulated COM trajectory did not cross the stability boundaries planes. A step that was at the same time recorded experimentally and predicted by the model, i.e. the simulated COM trajectory crossed the stability boundaries planes, was considered "necessary" (Figure 5 A). A step that was recorded experimentally but not predicted by the model was considered "unnecessary". A step that was predicted by the model but not recorded experimentally was considered a "false step".

Place figure 5 near here

In young adults, in simulated trials where the COM trajectory crossed the stability planes boundaries, young adults always stepped. All 4 steps recorded from young adults in experimental trials, were "necessary" steps. There were no "unnecessary" steps and no "false step" predictions in young adults. Figure 5B illustrates a simulated COM trajectory inside the stability boundary planes for a young adult.

In old adults, 23 steps were "necessary" and 9 were "unnecessary", since the subjects took steps although the experimental and simulated COM trajectories were both inside the stability space. There were 35 "false steps" predicted by the model where the simulated COM trajectory crossed over the stability planes boundaries but in the corresponding experimental period the subjects did not step. The "false step" predictions may be explained by the presence of external support given to subjects during the experimental trials. The simulation trials predicted a step but in the experimental trials the external support repositioned the COM trajectory inside the stability space before a step was taken (see Figure 5 C). It is likely that without the external support, the subjects would have either stepped at a later time or lost their balance completely and relied on the harness to break their fall. Therefore without the external support, the "false steps" may in fact be "necessary" steps. Not all periods of external support were related to a "false step" prediction; therefore one can conclude that caution on the part of the lab assistant resulted in support where in fact none was needed.

DISCUSSION

Despite certain limitations, the inverted pendulum model provided a good approximation of the body kinematics describing the behaviour of a subject standing on a continuously oscillating platform. Even when consistent torque noise and torque delay parameters between young and old adults were maintained, the model was representative of the experimental data. Furthermore the combination of simulated parameters that best reproduced the experimental results revealed age-related differences in the level of sensory noise and sensory delay. Maintaining consistent torque delays and torque noise parameters is in line with reports of other studies of reactions to anterior/posterior postural perturbations that have indicated that the muscle force required to generate these reactions is well within the capabilities of healthy older adults (Alexander et al. 1992, Luchies et al. 1994, Maki and McIlroy 1996). In addition, the maximum ankle muscle torque and rate of ankle muscle torque development have been showed to be similar between young and old healthy adults in response to backward and forward platform translations (Hall et al. 1999). Therefore, the force production characteristics are not the limiting factor in the postural control of healthy old adults.

The analysis of the current data support the hypothesis that the loss of control related to aging can be explained, in large part, by an increase in sensory noise and delay. Deterioration of sensory inputs has been cited as an important factor influencing the postural control in older adults. Reductions in proprioception (Skinner et al. 1984, Thelen 1998) and marked decrease in touch sensitivity, two-point discrimination (Bruce 1980) and vibration sense particularly in the lower limbs (Kenshalo 1986, Brocklehurst et al. 1982) have been reported in old adults. These reductions are associated with a loss in density and sensitivity of sensory receptors and innervating sensory fibers. Due to physiological characteristics and sampling frequency, the signal from each receptor contains a certain amount of variance or noise. The fluctuating environment of the sensory receptors is translated, through a process of averaging, into a smooth report received by the CNS. The message received by the CNS signalling deviation of the body from the upright position, is the mean of signals detected by the receptors. This averaging process has as a consequence, a decrease in the variance of the overall signal that is usually relayed to the brain by means of a neural frequency code. It is expected that this frequency will also, usually, encode a smoothed or average signal (Norwich 2003). Assuming independence of the sensory receptors and based on probability law, the reduction in density and sensitivity of sensory receptors associated with aging will result in more variance (noise) in the averaged signal transmitted to the CNS since the averaging process is done on fewer samples.

The conceptual model in Figure 2 is a simplified version of complex postural control. In the current model, the sensory noise and delay from all systems were represented as one parameter, when in fact multiple sensory systems provide information that contributes to the estimation of body position and velocity. Each one of these systems has its own level of noise and delay depending on the integrity of that particular system. Furthermore, the level of noise and delay can vary from one system to another and the CNS may compensate for a noisy system by changing the gain on that input. Although this strategy can help mitigate the effects of noise, there is ultimately no way to replace the information lost (Speers et al. 2002). Re-weighting also becomes problematic when multiple sensory inputs are affected by noise and delay; such as in aging. Age-related changes in the ability of older adults to activate postural muscle responses in an anticipatory manner were evident in significantly longer postural muscles onset latencies in old than young adults (Inglin and Woollacott 1988, Frank et al. 1987, Bugnariu and Sveistrup 2004 a). Experimental evidence suggests that the time course of sensorimotor adaptation is moderately degraded with age (Bock and Schneider 2002). There is accumulating evidence of age-related declines in sensorimotor performance such as stimulus discrimination and the utilization of pre-cues (Cerella 1990, Hale et al. 1987). Slower adaptation of postural control responses to various transient perturbations and task conditions has been reported in old adults (Woollacott et al. 1986, Horak et al. 1989, Peterka and Black 1990, Bugnariu and Sveistrup 2004 a, b, c). Progressive age-related loss of neurons, dendrite and reduced branching, altered transmitter metabolism (Kirshen et al. 1984) and a general slowing of information processing (Stelmach et al. 1985) in conjunction with decreased nerve conduction velocity, could detrimentally impact the generation of complex postural responses.

Combining an empirical approach with mathematical modeling, Pai et al. (2003) demonstrated that predicted stability boundaries correlated with experimental data and an internal representation of COM stability limits guided adaptive improvements in the feedforward control of COM. Future research may improve our system model by integrating this element of prediction and /or anticipation thus better estimating the desired body trajectory.

Our small sample of steps prevented us from achieving sufficient statistical power in order to test the models ability to predict stepping. However, there was a tendency for old adults to step more than young adults even when their balance was apparently stable, i.e. the COM trajectory was inside the stability space. The tendency for more "unnecessary" steps to be taken by older adults has been noted in other studies of step initiation thresholds following discrete perturbations (Pai and Iqbal 1999, Pai et al. 2000). Anxiety and fear of falling may be important determinants of whether a step will occur and may explain the "unnecessary" steps taken by the older subjects.

Based on model predictions, old adults should have stepped each time that the trajectory of the COM crossed the stability planes. The experimental data showed that in a number of occasions where "false steps" were predicted by the model, old subjects relied on external support to correct their balance. It is possible that they would have initiated a step at a later time. However, initiating a step after the COM crosses the stability planes may prove to be too late to prevent a fall. In young adults, there were no "false step" predictions; therefore the three periods of support in young adults were probably a cautionary measure by the lab assistant. The subjects would however have managed without the external support.

CONCLUSION

The inverted pendulum model provided a good approximation of the experimental data for both young and old adults. The age related differences in the control of standing balance on a continuous oscillating platform recorded in the experimental data can be partially explained through increased levels of sensory noise and neural delays in the simulated data of old adults. The COM trajectories of old adults crossed more often the regions of stability boundaries compared with those of the young adults. Our data support the concept of dynamic stability which considers not only the horizontal location of the COM with respect to the BOS, but also the magnitude and the direction of its corresponding velocity, as critical information for the ability to control balance. We demonstrated that the acceleration parameters of a perturbation must be taken into account when calculating stability limits and we derive for the first time the equations for calculating these stability limits related to continuous translations of the BOS.

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Appendix A

Eq. 1 describes the dynamics of the inverted pendulum.

$$\tau = -\tfrac{4}{3} ml^2 \ddot{\theta} + ml(g \sin\theta - \ddot{x}_p \cos\theta) \qquad \text{Eq. 1}$$

$\ddot{\theta}$, θ are the angular acceleration and position, l is half of the subject's height, m is body mass and g is the gravitational acceleration, $\ddot{x}_p$ is the platform acceleration.

The inverted pendulum model has been extended with a foot segment that provides a BOS. The additional dynamic equations and the stability conditions are listed below

$$F_x = ml\dot{\theta}^2 \sin\theta - (m + m_f)\ddot{x}_p - ml\ddot{\theta}\cos\theta \qquad \textbf{Eq. 4}$$

$$F_y = -ml\dot{\theta}^2 \cos\theta + (m + m_f)g - ml\ddot{\theta}\sin\theta \qquad \textbf{Eq. 5}$$

In addition to the previous definitions, $\dot{\theta}$ is the angular speed, m_f is the foot mass, l_f is the foot length, l_c is the distance from the foot center of mass to the ankle, l_a is the distance from the heel to the ankle, h_f is the height of the foot, h_c is the distance from the ankle to the foot center of mass, F_x, F_y are ground reaction forces $\ddot{x}_p$ is the platform acceleration, in our case the perturbing acceleration

If the system does not rotate $\sum_i \tau_i = 0$ **Eq. 6**

The system is considered to be inside the stability boundaries as long as: ground reaction forces are positive and the COM velocity can be reduced to zero relative to the BOS while maintaining

COP within the BOS at all times (Pai and Iqbal 1999). From Eq. 1, 4-6 we extract X_{COP} which is the position of the center of pressure measured from the toes.

$$x_{COP} = l_f - l_a - \frac{m_f g l_c - h_f F_x - \tau - m_f h_c \ddot{x}_p}{F_y} \qquad \textbf{Eq. 7}$$

When the system maintains the X_{COP} at the toes:

$$x_{COP} = 0 \qquad \textbf{Eq. 8}$$

and when the system maintains X_{COP} at the heel:

$$x_{COP} = l_f \qquad \textbf{Eq. 9}$$

The above conditions (Eq 8-9) applied to Eq 1,4-7 define two unique angular accelerations, resulting from maintaining the COP at each extreme of the BOS (Eq. 10-11).

$$\ddot{\theta}_{toes} = \frac{-m_f g l_c + h_f(ml\dot{\theta}^2 \sin\theta - (m+m_f)\ddot{x}_p) + ml(g\sin\theta - \ddot{x}_p\cos\theta) + m_f h_c \ddot{x}_p + (l_f - l_a)((m+m_f)g - ml\dot{\theta}^2\cos\theta)}{ml(l_f - l_a)\sin\theta + mlh_f\cos\theta + \frac{4}{3}ml^2}$$

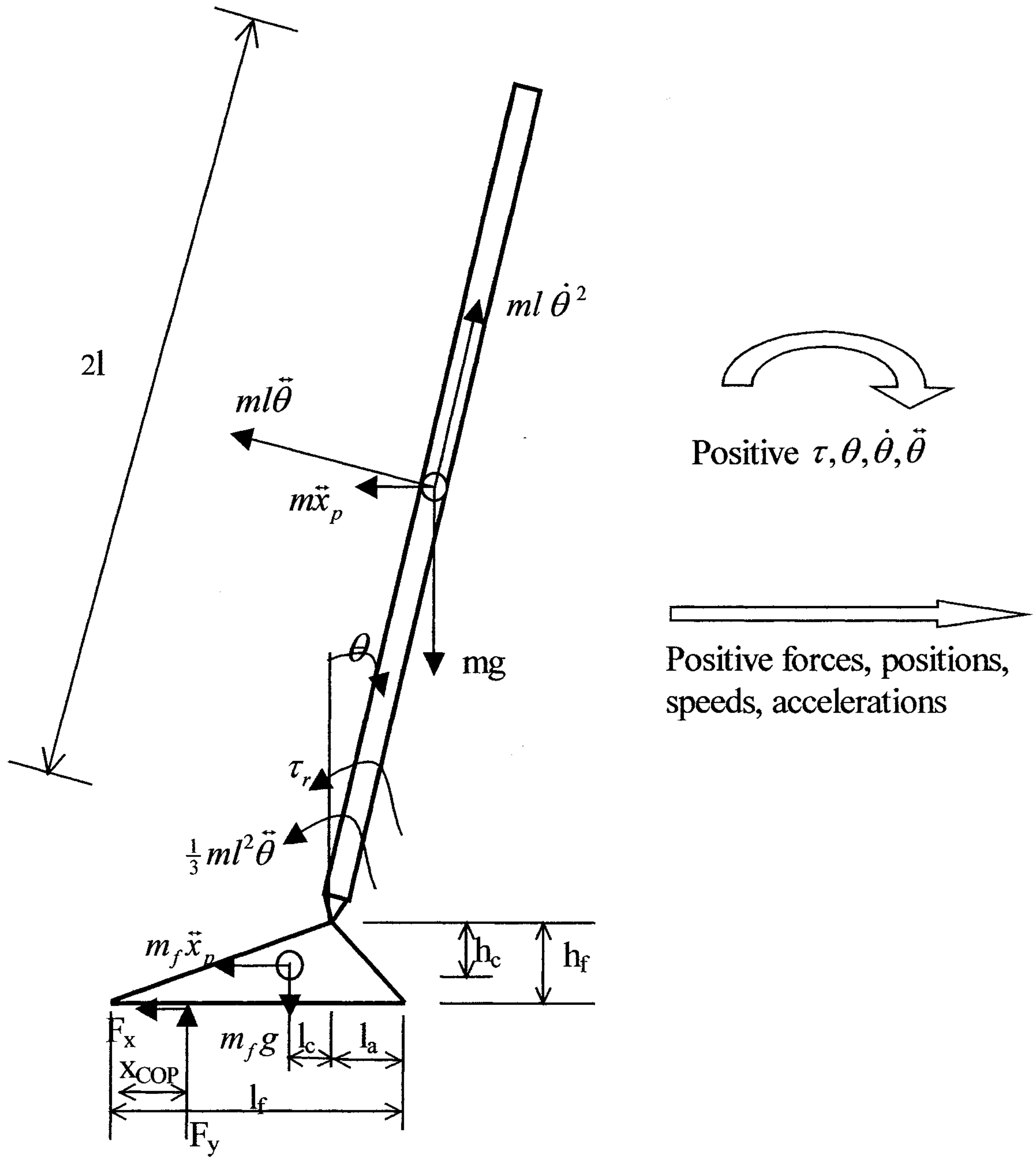
Eq. 10

$$\ddot{\theta}_{heel} = \frac{-m_f g l_c + h_f(ml\dot{\theta}^2 \sin\theta - (m+m_f)\ddot{x}_p) + ml(g\sin\theta - \ddot{x}_p\cos\theta) + m_f h_c \ddot{x}_p + (-l_a)((m+m_f)g - ml\dot{\theta}^2\cos\theta)}{ml(-l_a)\sin\theta + mlh_f\cos\theta + \frac{4}{3}ml^2}$$

Eq. 11

Using the equations Eq. 10, 11 and the reversible property of the system, the stability boundaries can be derived starting from two extreme stable states. These stable states are defined by the COP position at one of the two extremes of the BOS (toes or heel), zero angular velocity and zero angular acceleration of the body segment and COM. Using these two stable states as initial positions and by slightly increasing and decreasing the angular speed, a time dependent position and velocity are obtained. The stability boundaries are defined by the time dependent position and sign-reversed velocity data.

Fig. 1 Free body diagram of a two-segment model (foot and inverted pendulum) of the human body. The foot travels in the anterior-posterior direction with the perturbation imposed by the platform, while the body segment rotates at the joint. $\ddot{\theta}.\dot{\theta}.$,□ are the angular acceleration, speed and position, l is half of the subject's height, m is body mass, m_f is the foot mass, l_f is the foot length, l_c is the distance from the foot center of mass to the ankle, l_a is the distance from the heel to the ankle, h_f is the height of the foot, h_c is the distance from the ankle to the foot center of mass, X_{COP} is the position of the center of pressure measured from the toes, $\square_r$ is the restoring torque applied by the controller, F_x, F_y are ground reaction forces, $\ddot{x}_p$ is the platform acceleration, in our case the perturbing acceleration and g is the gravitational acceleration.



2l
$ml\dot{\theta}^2$
$ml\ddot{\theta}$
$m\ddot{x}_p$
mg
θ
τ_r
$\frac{1}{3}ml^2\ddot{\theta}$
$m_f\ddot{x}_p$
h_c
h_f
F_x
$m_f g$
l_c
l_a
x_{COP}
l_f
F_y
Positive $\tau, \theta, \dot{\theta}, \ddot{\theta}$
Positive forces, positions, speeds, accelerations

Figure 1

Fig. 2 Conceptual diagram for the system model. The controller, representing the CNS is responsible for integrating the desired trajectory of the body with the estimated sensory information and sending the appropriate posture control commands to the muscles. The muscle torques produce the body dynamics simulated by the inverted pendulum. The output of the inverted pendulum model, the real angular position and velocity, representing the body kinematics, are detected by multiple sensors and fed back to the controller as an estimated body angular position and velocity. In this paper the estimated angular position has been generated from the real angular position perturbed by noise and delay. In the simulated model, white noise was added to the sensors, sensory noise, and to the output torque, torque noise. Delays were introduced for the generation of restoring torque, torque delay, as well as for the time required to perceive, transmit and integrate sensory information for estimation of the body position, sensory delay. In this system model the sensory delay and torque delay represent the total neural delay.

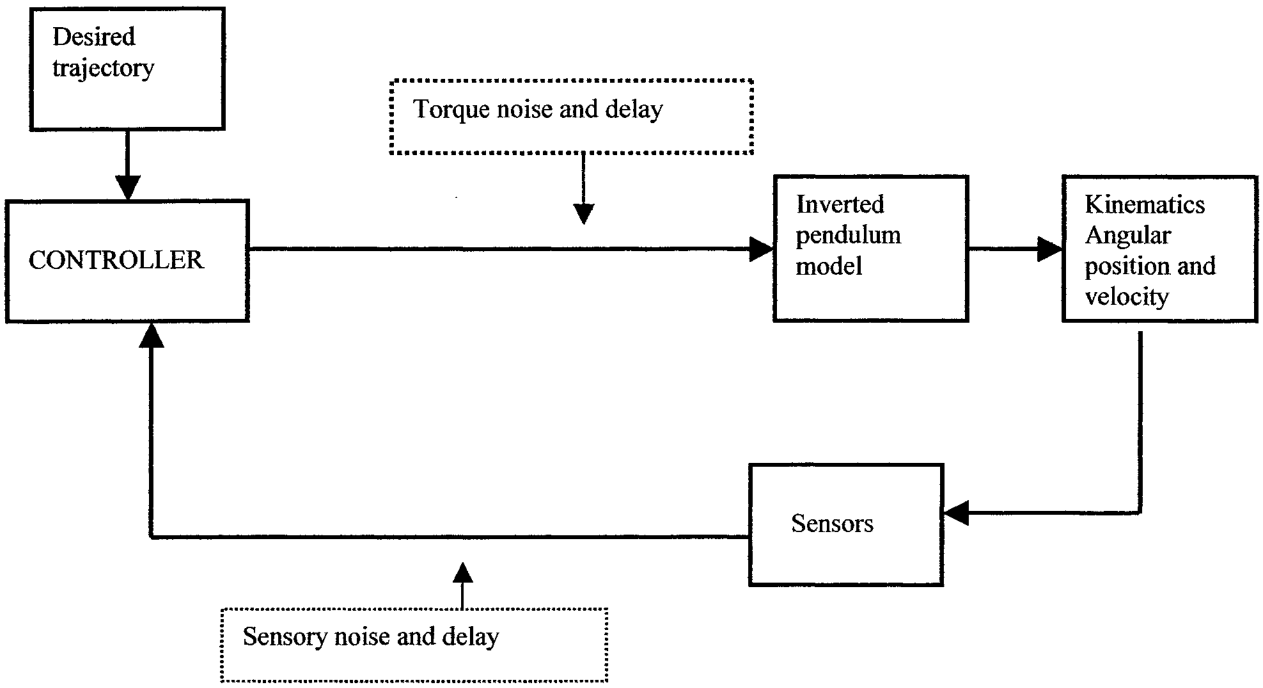

Desired trajectory
Torque noise and delay
CONTROLLER
Inverted pendulum model
Kinematics Angular position and velocity
Sensors
Sensory noise and delay

Figure 2

Fig. 3 **A** Stability boundaries for platform acceleration ($\ddot{x}_p = 0$). The two stability boundaries represent the maximum COM velocity that can be reduced to zero relative to the BOS and the minimum COM velocity that can carry the COM inside the BOS while maintaining the COP at the either one of the BOS extremes, heel or toe. COM position normalized to foot length is plotted on the x axis, and COM velocity normalized to height is plotted on the y axis. The two extremes of the BOS, the toe and heel correspond to 0 and -1 positions on the x axis, respectively. Outside of these boundaries, on the right side of the right boundary the subject will certainly fall backwards and on the left side of the left boundary the subject will fall forward.

B Three-dimensional side view of stability space and the two stability boundaries planes. Platform acceleration is illustrated on the z axis, COM position normalized to foot length on the x axis and COM velocity normalized to height on the y axis. The system is stable as long as the COM position-velocity trajectory is between the two planes.

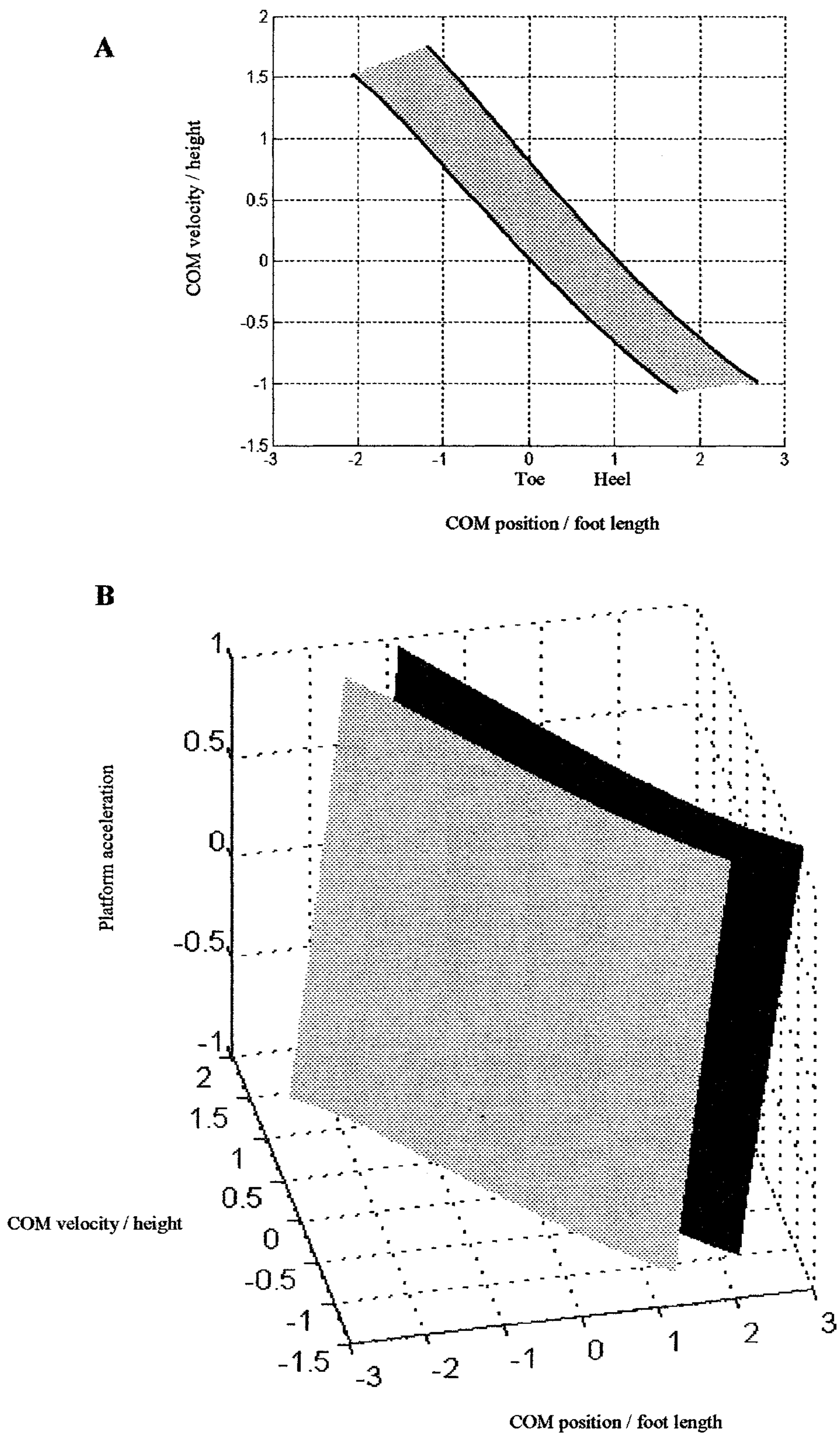
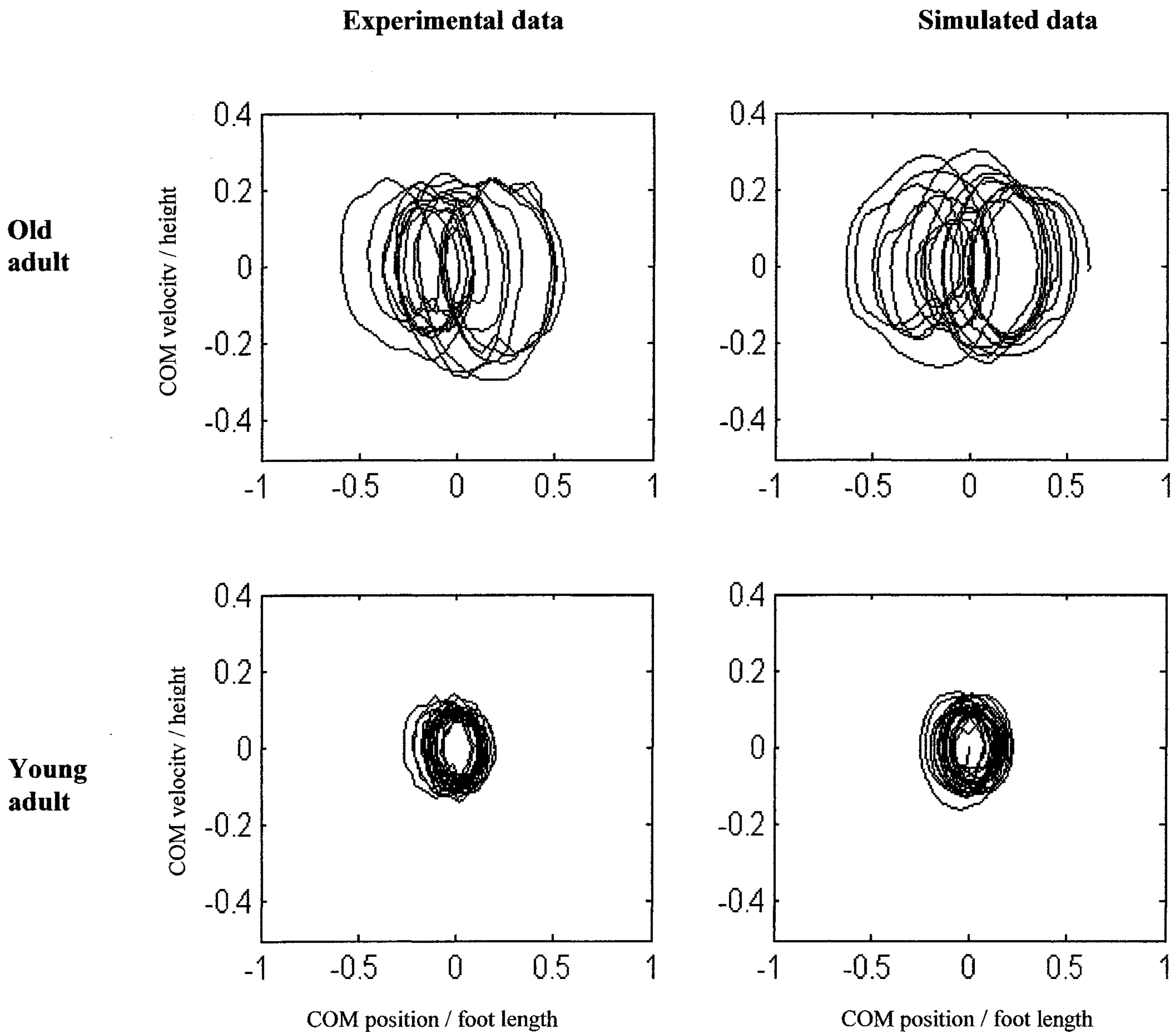

A
COM velocity / height
2
1.5
1
0.5
0
-0.5
-1
-1.5
-3
-2
-1
0
1
2
3
Toe
Heel
COM position / foot length
B
Platform acceleration
1
0.5
0
-0.5
-1
COM velocity / height
2
1.5
1
0.5
0
-0.5
-1
-1.5
-3
-2
-1
0
1
2
3
COM position / foot length

Figure 3

Fig. 4 Center of mass position-velocity trajectories for an old (top panels) and young (bottom panels) adult. Data from experimental (left panels) and simulation (right panels) trials are presented. COM velocity is normalized to height and COM position is normalized to foot length.



Experimental data
Simulated data
Old adult
Young adult
COM velocity / height
COM position / foot length
0.4
0.2
0
-0.2
-0.4
-1
-0.5
0
0.5
1

Figure 4

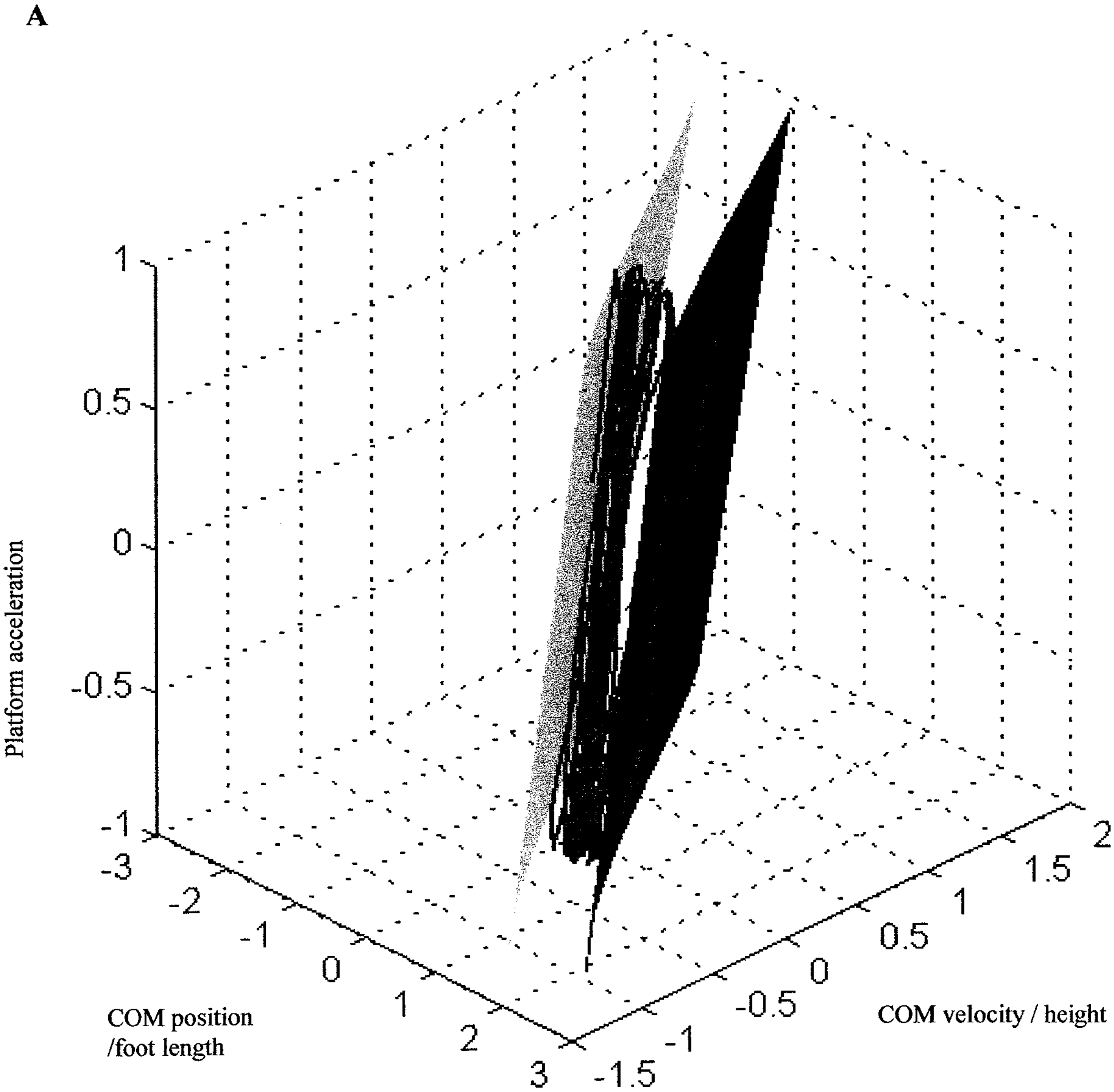
Fig. 5 Normalized COM position on the x axis, normalized COM velocity on the y axis and platform acceleration on the z axis. Stability border planes illustrated as two vertical walls.

A Example of COM trajectories inside the 3D stability space. Simulated data from an old adult. The crossings of the stability plane (light grey trace crossing black boundary) indicate two steps.

B Example of COM trajectories inside the 3D stability space. Simulated data from a young adult.

C Example of COM trajectories inside the 3D stability space. Experimental data from an old adult. The crossings of the stability plane indicate external support.

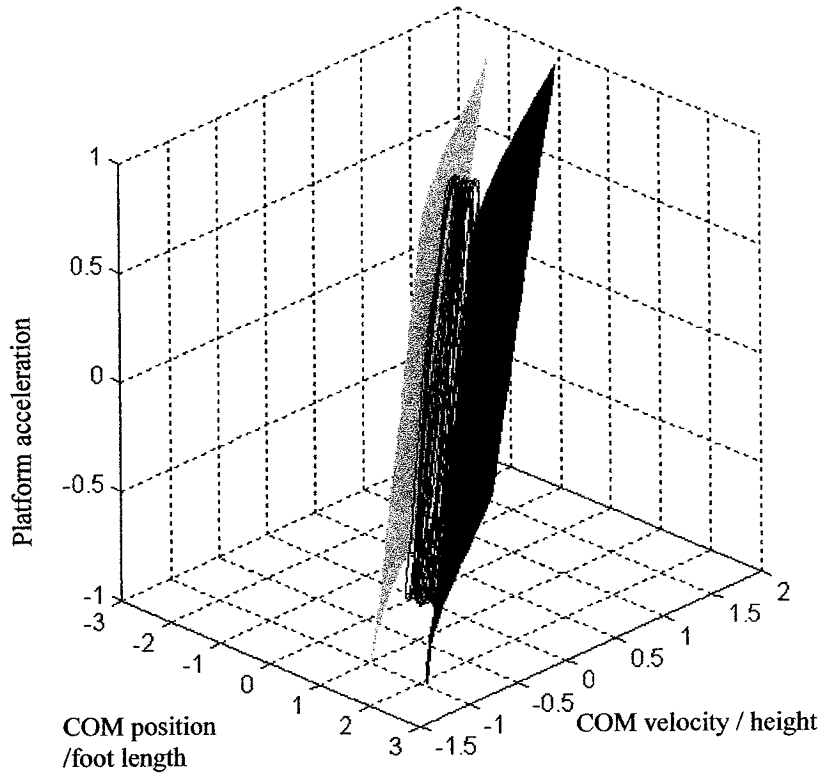
A



Platform acceleration
1
0.5
0
-0.5
-1
-3
-2
-1
0
1
2
3
COM position
/foot length
-1.5
-1
-0.5
0
0.5
1
1.5
2
COM velocity / height

Figure 5 A

B



C

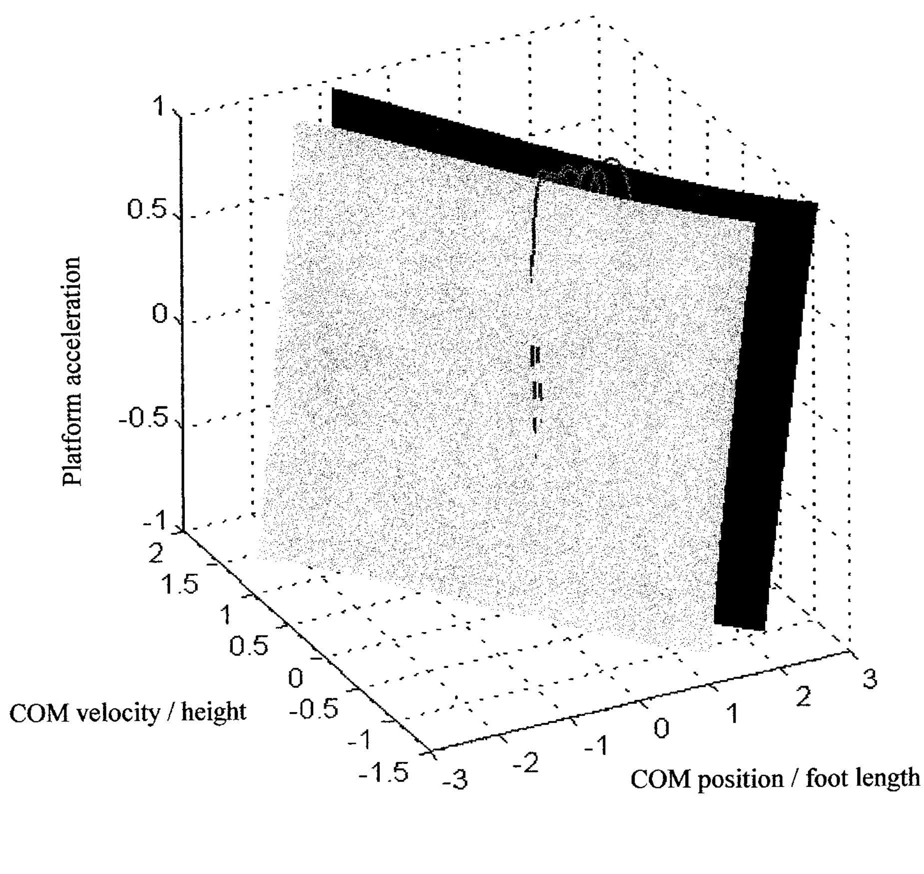


Figure 5 B, C

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CHAPTER 6 GENERAL DISCUSSION

6.1 MAJOR FINDINGS AND THEIR SIGNIFICANCE

The results from these experiments clearly show that the ability to compensate for an impending and highly predictable perturbation decreases with age. This was particularly evident under conditions of externally-triggered perturbations, where the predictability of the perturbation came only from the inferred knowledge of perturbation type and magnitude over repeated cycles at a constant frequency. In this situation, the old adults responded using reactive postural adjustments independent of the frequency of platform oscillation, the direction of perturbation and without adapting postural responses over multiple trials.

Old subjects displayed greater displacement of the COP than young adults and no significant scaling of COM displacement was evident with increases in platform frequency. Greater phase lags between platform-COP and platform-COM signals in the old adults compared to those in young adults illustrate a behaviour driven mainly by platform movement. Compared to young adults, postural muscles were activated consistently later in the oscillation cycle in both transition and steady state periods by the old adults for both directions of platform movement. In young adults, earlier postural muscle activity was recorded in the transition period and values remained stable during the steady state period at every frequency. No shift in postural muscle onset latency was noted during the transition period in the old adults. Moreover, old adults did not reach the same values of anticipatory or early postural muscles onset latencies as the young adults even after 10, 30 or 40 cycles in the steady state periods at 0.25, 0.5 and 0.61 Hz respectively. Taken together these results suggest that older adults used reactive postural control mechanisms.

In response to perturbations of uncertain occurrence, young adults make short-term anticipatory adjustments to reduce the likelihood of balance loss based on conditions last experienced. Over a longer term, young adults adapt to acquire an "optimal" movement strategy that decreases the overall likelihood of balance loss with a net result of reduced reliance on reactive responses to maintain balance in an uncertain environment (Pavol and Pai, 2002). Based on our results, this is not the case for the old adults.

The continuous use of a reactive mechanism in steady state periods, where the perturbations are highly predictable, may be a consequence of an improper reactive response in the transition period, when the occurrence of perturbation is unpredictable. Before a switch to the anticipatory mechanism is possible, a certain level of postural stability may be required. The role of the reactive mechanism inside the transition period, as well as throughout the stable state, could be to achieve this stability. It is possible that because of a lack of the ability to initially successfully integrate the multiple sensory sources and generate appropriate responses, old adults never achieved a level of stability which would permit a subsequent switch to anticipatory mechanisms.

The ability to compensate for predictable perturbations improves in old adults if the perturbations are self triggered. For the old adults who clearly struggled to maintain their balance during the externally-triggered perturbations, the self-triggered perturbations provided the opportunity to access a safer mechanism of control. The knowledge of timing and magnitude of perturbations allowed better prediction and use of anticipatory mechanisms. Self-triggering of perturbations with the hand-held device allowed the old subjects to better stabilize the body before changing oscillation frequency and facilitated earlier activation of postural muscles. This stabilization was translated into a closer coupling of the COP A/P displacement to the platform movement as illustrated by the decrease in phase lags between the two variables. Self-triggered perturbations also elicited fewer steps during both transition and steady state periods. Specifically, the number of steps taken by each subject decreased and no external support was required to maintain balance. Although the old adults were able to somewhat limit the COP A/P movement following self-triggered perturbations, the maximum range of COP A/P movement was similar to that recorded in the young adults following externally-triggered perturbations. Moreover, for an increased percentage of time, old adults' COP A/P was located in less safe regions at the boundaries of the base of support, when compared to young adults, especially during transition periods as platform oscillation frequencies increased.

In self-triggered perturbations, old adults reacted primarily to the slowing down and not in response to the change in direction of the platform. In a sinusoidal continuous translation, the decrease in platform speed is the first indication of an upcoming perturbation and reversal in the direction of platform movement. Only in self-triggered perturbations were old adults able to make use of this information potentially by decreasing the threshold for detecting the change in platform speed. Earlier detection would permit earlier postural muscle activity limiting the amount of destabilization triggered by the perturbation.

Stimulation of cutaneous mechanoreceptors from foot plantar surface boundaries improved the old adults' ability to compensate for predictable continuous perturbations. In old adults, mechanical stimulation of foot plantar surface boundaries improved the ability to control feet-in-place reactions, decreased the center of pressure excursion and the percentage of time the COP was located near the boundaries of the base of support. The additional sensory stimulation resulted in earlier postural muscle activity in response to unpredictable, externally-triggered perturbations. The progressive shift towards earlier postural muscle onset latencies indicates an increased ability of old adults to adapt and incorporate anticipatory postural control mechanisms. This is of particular importance since, without sensory stimulation similar responses were not observed in old adults. More subtle effects of the sensory stimulation were observed in the postural responses to self-triggered perturbations, indicating that the effects of predictability and sensory stimulation are not additive. However, even in highly predictable self-triggered perturbations, stimulation of mechanoreceptors from foot plantar surface boundaries facilitated anticipatory postural activity. Effects of mechanical stimulation of cutaneous afferents from feet plantar surface boundaries were present despite available visual, vestibular and proprioceptive information, indicating that the cutaneous mechanoreceptors provide distinctive information not substituted by other inputs.

Decreases in sensory information affect the ability of older adults to compensate for predictable continuous perturbations and to use adaptive/anticipatory mechanisms. In general, sensory information about body orientation and motion is used to detect instability and to generate appropriate stabilizing responses, either by triggering and scaling anticipatory and adaptive reactions or by continuously updating ongoing reactive corrections (Maki and McIlroy 1996). A simple inverted pendulum model provided a good approximation of the experimental data, with correlation coefficients of 0.89 ± 0.03 and 0.83 ± 0.02 for the young and old individuals, respectively. Based on simulation parameters, the age-related difference in the control of standing balance on a continuous oscillating platform recorded in experimental data could be partially explained through increased levels of sensory noise and neural delays in old adults. Representative of the increased number of steps taken by old adults, the simulated COM trajectory of old adults crossed more often the regions of stability boundaries compared with the COM trajectory of young adults.

Insights on the anticipatory control mechanism

The use of appropriate compensatory reactions in response to a perturbation depends on the ability of the system to correctly detect the parameters of the perturbation and to generate appropriate stabilizing responses in a timely manner. In the presence of perturbations, anticipatory aspects of postural control prepare not only the motor system by pre-selecting postural strategies and muscle activation timing, but also the sensory system by priming it for signal detection and integration. Sensory information from different sources, each with its own reference frame, delay and level of noise, is integrated by the CNS. The ability of the system to choose, between all sources of sensory information, the one most accurate for a particular task and environment, and to extract the appropriate signal from the noise determines the appropriateness of response. Increased signal-to-noise ratio increases the chance of correct signal detection. As revealed by the simulation data, the sensory noise levels in older adults are higher. It is possible that a low signal-to-noise ratio prevents the older adults to detect a perturbation correctly and in a timely fashion. Therefore, in externally-triggered perturbations, older adults only elicit reactive responses.

In self-regulated postural perturbations, anticipation may have primed the CNS to attend to proprioceptive information: permitting the old adult to decrease the threshold for detecting changes in platform speed resulting in earlier postural muscle activity. Determining the fidelity of proprioceptive information related to position and velocity is difficult because of the interaction between distance and timing information. Velocity perception is more accurate when both distance and timing cues are available, indicating that all available cues are used to make judgements of movement velocity (Kerr and Worringham 2002). Therefore, self-triggered perturbations may have facilitated use of a better algorithm for extracting the relevant signal from the noise, improving the ability of older adults to activate postural muscle earlier and use anticipatory control strategies.

In the experiments with additional sensory stimulation from the boundaries of foot plantar surface, we demonstrated for the first time that cutaneous stimulation facilitates the use of anticipatory postural strategies in response to continuous perturbations to stance. In this situation the ability of older adults to activate their postural muscle earlier and use anticipatory control strategies may be based on an increased signal to noise ratio.

Age-related changes in postural control are multi-factorial. Although knowledge of type and timing of an upcoming perturbation along with available sensory information, in particular cutaneous sensation from the boundaries of plantar surface, seem to contribute a great extent to the postural reactions of older adults in response to continuous perturbations, age-related changes in postural control are likely a combination of these and other factors. This is evident since although the old adults' ability to compensate for a predictable perturbation improved under conditions of self-triggered perturbations or with cutaneous stimulation, their results remained different from young adults. When self-triggered perturbations and stimulation were combined, old adults stepped more, had increased COP excursions and later postural muscle onset latencies compared to young adults.

Clinical implications

The old adults' reliance on reactive postural mechanisms in response to externally triggered perturbations, even when these are predictable, has direct implications for falls caused by external factors. The reactive postural adjustments manage the regulation of posture on a crisis basis and, when all the components of the system work properly they are efficient in restoring balance. However, the use of a reactive mechanism in a response to a predictable perturbation does not take advantage of the redundancy in the system and can have negative consequences especially for old adults, since age-related changes in both reactive and anticipatory mechanisms have been identified. For example, a person standing on a bus that accelerates or decelerates as it is about to leave from or come to a stop sign, could theoretically predict the destabilization and activate appropriate anticipatory adjustments to prepare for and/or prevent destabilization of balance. This strategy would provide a degree of additional safety for postural control since, in the case of an inappropriate or ineffective anticipatory adjustment, a reactive postural adjustment could be used as a backup for additional control.

Providing increased warning of an impending perturbation and augmenting sensory information to allow for better/earlier detection of destabilization improves postural responses in old adults. Knowledge of perturbation timing allows anticipatory control to scale the appropriate motor output. This has potential implications for the design of rehabilitation programs aimed at improving balance. Programs that include self-triggered perturbations will allow the old adults to learn safer strategies in conditions were they feel more in control and the effects of anxiety and fear are reduced. Furthermore, the idea of interventions aimed at improving balance based on increased sensory information from feet soles has already been proposed and patents for possible footwear insoles already exist (Maki et al. 1999)

6.2 FUTURE RESERCH DIRECTIONS

Can old adults be trained to use anticipatory mechanisms and is that training transferable to other situations?

The use of anticipatory mechanisms has the potential of improving old adults' stability in response to continuous perturbations. It remains to be determined whether old adults can be trained to use anticipatory mechanisms and whether the training is transferable to other situations. Future research needs to confirm that old adults can in fact adapt and use anticipatory mechanisms of control in response to continuous platform perturbations with variable characteristics. Self-triggered continuous perturbations when the subjects have in fact the control of different magnitudes and frequencies of platform translation can be followed by perturbations where the subjects only think they have the control when in fact they do not. If old adults use anticipatory mechanism in preparation for specific characteristic of predicted perturbations, these postural adjustments are going to be inappropriate for the perturbations that are actually going to be triggered. These experiments would also provide insight into the modulation of central set in the older adult.

The benefits of balance training programs in an artificial laboratory environment are judged by their transferability to different situations, in particular to functional, daily activities that subjects encounter in the community. To increase the chances of transferring training effects to real life situations, the training programs have to be as realistic as possible. The continuous platform perturbations parameters can be set up to reproduce the motion of a bus or subway and train the postural balance of older adults in response to various accelerations and decelerations. Combining this with a virtual reality program that reproduces the visual environment normally encountered when on a bus or subway, would provide the subject with cues for predicting changes in perturbations and should open interesting opportunities for future studies.

Are the effects of cutaneous stimulation persistent over time?

The finding that the stimulation of mechanoreceptors from the boundaries of plantar foot surface improved the ability of healthy older adults to compensate for continuous perturbations highlights the potent influence of this sensory system. Further research is required to assess the generalizability of these findings to a broader range of test conditions and subjects characteristics. It is particular important to determine whether the beneficial effects of cutaneous stimulation are present over days, weeks and months of wearing a footwear insole or similar devices producing the stimulation.

Further development of the model

Our preliminary inverted pendulum model has generated good representation of experimental data and has identified age-related differences in sensory noise and delay. In the current model, the sensory noise and delay from all systems was represented as one parameter, when in fact multiple sensory systems provide information that contribute to the estimation of body position and velocity. We intend to further develop the model by incorporating multiple sensory channels representing the visual, vestibular and somatosensory system, each with its own gain, noise and delay and an integrator to represent the integrative function of the CNS. Furthermore, we intend to use the model to study and predict the postural responses to other continuous perturbations of the BOS, such as those created by a moving bus or subway train. These perturbations have different acceleration parameters and consequently different stability boundary planes. The model will be used to provide predictions about COM trajectories in different stability regions.

6.3 CONCLUSION

The present series of experiments used a continuously moving platform to create perturbations of standing balance of similar magnitude that could be compensated for using either reactive or anticipatory postural adjustments. The present results provide insight to how aging influences the use of reactive and anticipatory postural control strategies during continuous perturbations in an ecologically valid paradigm.

The ability to compensate for an impending and highly predictable perturbation decreases with age. In contrast to young adults who adapted and used anticipatory mechanisms, old adults relied on reactive postural mechanisms in response to predictable externally-triggered perturbations. Knowledge about timing and magnitude of upcoming perturbations under the self-triggered condition, improved the old adults' ability to compensate for predictable perturbations and use anticipatory mechanisms. The difficulty that older adults display with adopting anticipatory strategies may be related to impoverished sensory information from the feet. The present series of experiments demonstrated for the first time that cutaneous stimulation of the foot plantar surface boundaries increases stability and facilitates the use of anticipatory control strategies. These results support the importance of cutaneous mechanoreceptors from the boundaries of the foot plantar surface in the control of postural reactions evoked by unpredictable and predictable continuous perturbations and provide insights for the design of foot orthotics to improve balance control in older adults.

The age-related differences in the control of standing balance on a continuous oscillating platform recorded in the experimental data can be partially explained through increased levels of sensory noise and neural delays in the simulated data of old adults. Our results support the concept of a dynamic stability, according to which, in addition to the horizontal location of the COM with respect to the BOS, the magnitude and the direction of its corresponding velocity provide critical information pertaining to one's ability to control balance. Based on model work, we demonstrated that the acceleration parameters of a perturbation have to be taken into account when calculating stability limits. We derived for the first time the equations for calculating these stability limits related to continuous translations of the BOS.

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