Early activation of ankle muscles following unexpected light touch displacement at the fingertip during treadmill walking

By

TANIA SHIVA

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

In

Rehabilitation Science-Physical Therapy

Faculty of Rehabilitation Medicine

University of Alberta

ABSTRACT

Lightly touching a stable surface has been shown to reduce sway in people standing with their eyes closed. Recently, it was shown that if this surface is unexpectedly moved, some people will react with a sway in the opposite direction, consistent with a balance correction. However, this balance correction is only seen following the first trial and in only about 60% of participants. One possible reason for the inconsistent expression of these responses might be that the touch-related feedback is not interpreted as a critically relevant input when standing on a stable surface. To increase the relevance of the touch-related feedback, participants were asked to walk on a treadmill with their eyes closed, a task that cannot be performed without provision of a spatial reference such as with touch. It was hypothesized that unexpected displacement of the touch reference would evoke responses more consistently across participants and with repeated touch displacements when touch is critically relevant to the performance of the task, such as when walking on a treadmill without vision. Twenty participants received 10 unexpected touch displacements delivered at right heel strike while walking on treadmill with eyes closed. Ten participants received forward touch displacements, while the other 10 received backwards displacements. All 20 participants responded to the touch displacements with activation of muscles at the ankle, suggestive of a corrective response. In particular, all participants responded to multiple trials of the disturbance. This is in contrast to what was seen during standing where participants reacted to the initial disturbance, but did not respond to any subsequent trials. However, the number of participants that reacted to the initial disturbance during walking was not different than what was seen during standing. These results suggest that sensory information related to the touch reference can be incorporated into the control of balance and stability during walking. However, the inconsistency in the expression of the evoked responses suggests that the contribution of this feedback is modulated within the context of the ongoing task and the other available sensory feedback, despite the critical importance of the touch reference to maintaining position on the treadmill.

ACKNOWLEDGEMENT

This thesis has become possible because of immense support and guidance both professionally and personally from a lot of people. Foremost, I would like to acknowledge the extensive training and mentoring I received from John Misiaszek and express my genuine gratitude for his guidance in my thesis. Thank you for helping me transform from a novice to a researcher. John has been the cornerstone of my thesis, as he has always shown confidence in my work. His composure, patience, determination and willingness to endure has made me progress in my professional life as a student. Thank you for giving me an opportunity to conduct research under your excellent supervision.

Thank you to my committee members, Dr. Dave Collins and Dr. Jaynie Yang, for their important suggestions on my research project and thesis work.

I would like to acknowledge the valuable suggestions provided by my colleagues; Juan Forero in helping me understand the technical aspect of my research and Atif Khan for explaining me some concepts about the neural control of locomotion.

I am grateful to my friends William, Nikita, Sahil, Nooshin, Joyce, and Hema for always encouraging me in rough times. I would like to thank all the volunteers who had participated in my research study.

I am indebted to my loving family; grandparents who have always blessed me with good fortune. Their blessings have brought me this far in my life. Essentially, I wanted to thank Lord Krishna for always showing me the right path and taking good care of me in Canada.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

GENERAL INTRODUCTION

A common strategy employed by humans when balance becomes challenging is to grab an external support with their hands. This could be a nearby rock when scrambling up a hike, a safety rail when descending a steep set of stairs, or a mobility device when walking balance has become impaired by injury or disease. Usage of assistive devices like canes, crutches or walkers enable individuals with injury to maintain their balance and reduce the likelihood of falls while walking. The mechanical benefit of holding an assistive aid by grasping with hands provides stability by allowing some of the body's mass to be supported through the arms, thereby increasing the area of the base of support. In addition to the mechanical benefit offered by holding an aid, the contact of the hand to an external support also presents the potential for increased sensory feedback.

Our hands are endowed with a rich complement of somatosensory receptors, in particular in the glabrous skin related to touch. The sensory receptors in the glabrous skin respond to various stimuli like temperature, pressure, irritation, itch and pain. Specifically, the tactile cues related to touch respond to pressure, vibration and texture of an object that is contacted (McGlone & Reilly, 2010). About, 17000 mechanoreceptors innervate the glabrous skin (Johansson & Vallbo, 1979), critical in providing tactile information about the external world (Johansson & Vallbo, 1983). Low-threshold mechanoreceptors (LTMR's) comprising of Pacinian corpuscles, Meissner's corpuscles, Merkel's disks and Ruffini endings, respond to different stimuli when grasping an object. Although proprioceptive cues from muscles and joints are also important, the focus of this thesis will be cutaneous cues that are argued to be important in providing an external spatial reference.

In the current literature, it has been consistently demonstrated that lightly touching (<1 N of vertical force) a stationary surface with a fingertip reduces postural sway in quiet standing with eyes closed (Jeka & Lackner, 1994). Lightly touching an external support does not provide mechanical stabilization (Holden, Ventura & Lackner, 1994; Kouzaki & Masani, 2008), but does provide additional sensory input from the skin to the nervous system which can be integrated within the balance control system and help maintain body stability. It has also been shown that standing body sway can be entrained to the movement of the fingertip light touch reference, if the movement of the light touch reference is imperceptible (Jeka, Schoner, Dijkstra, Ribeiro & Lackner, 1997). The entrainment of body sway with light touch movement suggests that shear forces might be important when lightly touching a stationary contact surface. When the tactile cues were blocked by tourniquet ischemia, in the absence of cutaneous cues light touch no longer reduced sway (Kouzaki & Masani, 2008). The purpose of the tourniquet ischemia is to partially block the sensory afferents in the hand while standing which eliminates the tactile feedback from the fingertip touch. These findings therefore suggest that light touch of the fingertip provides sensory cues that are integrated within our balance control system, contributing to the regulation of the postural sway and maintaining a stable body position while standing with eyes closed. The tactile cues from light touch are pronounced when visual cues are not available; but in the presence of vision light touch complements vision. These findings have therefore been argued to indicate that light touch cues can compensate for the loss of visual cues in maintaining balance.

Balance control can be broadly categorized as either proactive or reactive (Massion, 1992, 1994). In proactive balance control, the available sensory information is utilized to anticipate the motor commands which are required to maintain body stability ahead of expected or predicted demands of the task or threats to stability (Woollacott & Pei-Fang, 1997). In reactive balance control, unexpected threats to stability are counteracted by rapid corrective responses that are triggered by some sensory input that detects the threat (Nashner & Cordo, 1981). Therefore, the sensory inputs derived from contacting an external support could serve to provide additional information for proactive balance control, for example by providing an additional spatial reference (Johannsen, Wing & Hatzitaki, 2007). However, contact with the external support could also provide essential feedback relevant to reactive control, for example by detecting if the body is being displaced (falling) from the support. Alternatively, it could also be used when the external support itself has been compromised, and is the source of displacement. Then the threat to balance might be from the loss of support through the arms. If so, then an individual might interpret the light touch sensations from the fingertip in two possible ways: 1) that they have fallen backwards, relative to the touch reference; or 2) that the external support has moved relative to their position. In both cases, the feedback from the skin in contact with the support would be a desirable input to detect the threat, as this contact point would be the first indication of a potential problem. The glabrous skin provides information about the shear forces acting between the object that is being touched and the skin (Johansson & Vallbo, 1983). In particular, the fingers contain receptors that are well-suited for detecting slippage at the skin (Saddik, Orozco, Eid & Cha, 2011) and highly crucial to alter the muscle activity to prevent slippage of an object in our hand. Considering the importance of light touch, the cutaneous cues from the fingertip could provide a crucial feedback in detecting the loss of external support through the hands and trigger rapid balance reaction.

Recently, it was demonstrated that when subjects stand with their eyes closed, a sudden, unexpected rapid forward displacement of a fingertip light touch reference (away from the participant) evoked responses in the ankle muscles (Misiaszek, Forero, Hiob & Urbanczyk, 2016). Responses evoked in TA happened concomitantly with a forward sway of the body, suggesting an approach used by the participant to maintain fingertip contact with the touch plate. Participants have interpreted the touch plate displacement as if they were drifting (swaying) backward and hence evoked responses in TA to correct this by swaying forwards (Misiaszek et al., 2016). Likewise, participants interpreted backward touch plate displacements as if they were drifting forwards and corrected this by activating SOL, accompanied with backward sway of the body (Misiaszek et al., 2016). This indicates that the sensory feedback from a single fingertip can trigger a balance correction despite unaltered feedback from other balance-related sensory cues. The balance reaction to a rapid displacement of the fingertip light touch reference suggests that cutaneous inputs from the fingertip are critical in triggering balance corrections. In addition, forwards and backwards displacement of the touch plate leads to directionally specific responses in either TA or SOL, respectively. However, the occurrence of responses was not consistent across subjects with only 12 out of 20 participants demonstrating TA activation, with an onset latency of <120 ms following initial forward touch plate displacement (first trial). Only 1 out of 6 participants showed a response in SOL when initial backward displacement (first trial) was given at the touch plate. In the subsequent touch plate displacements (forwards and backwards) none of the participants produced responses in their ankle muscles (TA and SOL), instead activated their arm muscles (Misiaszek et al., 2016). These responses were termed as balance corrective responses because the touch plate displacement was unexpected and no disturbance to balance was actually induced (Misiaszek et al., 2016). The absence of ankle response in the subsequent trials suggests they had learned the displacement of the surface was not linked to a threat to balance. In the subsequent trials, activation of anterior deltoid (AD) was accompanied with elbow extension, suggesting use of an “arm-tracking” strategy to maintain contact with the touch plate. These findings suggest that there is considerable flexibility as to whether or not cutaneous feedback from the fingertip is used as an additional sensory reference for balance control and depends in part on the "weight” the participants give to the reference. Therefore, if the relevance of the touch reference was to increase, then it might be anticipated that more participants would respond to the touch displacement, and the evoked reaction might be expressed on repeated trials.

In this thesis, I have increased the relevance of the light touch reference for participants by asking them to walk on a motorized treadmill with their eyes closed, while touching a reference. Participants walking on a motorized treadmill with their eyes closed will drift towards the back of the treadmill without a spatial reference (Dickstein & Laufer, 2004; Durgin & Pelah, 1999; Paquet, Watt & Lefebvre, 2000). However, this backward drift is eliminated when participants are provided with a light touch spatial reference (Dickstein & Laufer, 2004). In this context, the cutaneous feedback from the fingertip is of critical importance as contact with the spatial reference is the only indicator of the position of the participant on the treadmill. As the participant's position moves relative to the spatial reference, shear forces at the fingertip will be generated by the movement. Our expectation is that if the light touch contact surface is unexpectedly displaced, this signal will be interpreted as though the participant has moved relative to the spatial reference and the corresponding correction will be activated. In other words, if the spatial reference is suddenly moved forward, relative to the position of the participant, this will be interpreted as the participant has drifted backward and we would then expect a correction that would restore the body forward. Therefore, we hypothesized that, 1) unexpected displacement of a light touch reference would evoke responses in the ankle muscles during walking with eyes closed with a greater frequency than was observed during standing; 2) the responses will be directionally specific, with activation of TA following forwards and SOL following backwards touch displacements; and 3) these responses will be of short latency (<200 ms) and suggestive of balance corrective responses.

CHAPTER 2

REVIEW OF LITERATURE

Although humans possess an innate ability to stand and walk, these activities are quite challenging and always require balance control. Maintaining balance is an integral ability of humans that allows us to achieve an erect posture and continue the act of walking while working through complex tasks of daily life. Our body is never completely still as internal disturbances arising from involuntary activities such as breathing, blinking of eyes, beating of heart, sneezing; and external disturbances, such as being pushed from behind or experiencing a sudden slip, generate forces that disrupt body equilibrium. Balance control can be broadly subdivided into static and dynamic equilibrium. Static balance control is achieved when the motion of the body is minimized and the center of mass (COM) is maintained within the base of support (BOS). In contrast, during dynamic balance control the body mass is moved in the performance of a task. During standing this might occur when a person leans towards a target or reaches to grasp an object that might require the COM to move outside the boundaries of the BOS. Dynamic balance control is most apparent during tasks such as walking or running, where the moving body means the COM is rarely within the BOS, yet the body remains in a state of stable, upright motion. The BOS is the region bound by the parts of the body in contact with a stabilizing surface; for example, the quadrilateral formed between the heels and the toes of the feet during erect standing (Horak & Macpherson, 1996). The BOS changes depending on the support surface that is contacting the body. For example, using a cane increases the area of the BOS to include the contact point of the cane with the ground. While sitting, the BOS is formed by the boundaries of the thighs, hips and pelvic regions in contact with the chair, including perhaps the seat back and armrests. Therefore, the BOS can change depending on the contact made between the body and the supporting external surface.

The biomechanical challenges of balance control in standing

In upright quiet standing, the body is not completely still and static equilibrium control tends to maintain stability as the body sways. In upright standing, the forces that act on our body are the force of gravity and force exerted by the support surface under our feet. The COM is defined as a point at which the entire body mass is concentrated and the resultant of all the extraneous forces act at this point in our body (Horak & Macpherson, 1996; Winter, 1990). The ability to maintain our body in an equilibrium state arises from the forces that act on the COM which must be equal and opposite to the force of gravity. Considering the segmented nature of the human body, the location of the COM is never fixed and changes with the positioning of our body segments. Thus, the COM may sometimes be positioned outside the BOS, creating a high demand for active control in order to maintain balance.

Bipedal upright stance is inherently unstable as it is maintained over a comparatively small BOS and the COM is maintained high above the ground (at approximately the second lumbar vertebra). On the contrary, in quadruped animals (such as cats and dogs) the boundary covered by the four feet forms a relatively wide BOS and the COM is relatively closer to the ground, thus providing more stability. When the BOS is larger, the COM can move within a large area and thereby maintain mechanical stability. During erect standing, the center of pressure (COP) is defined as a point at which the average net ground reaction force emerges from the supporting surface (Horak & Macpherson, 1996). While standing, the force of gravity acts vertically downwards, whereas the ground reaction force originating from the COP acts vertically upwards on our body. The COP and COM are two different entities, COP is related to the force and body acceleration, and in contrast COM is determined by the body position in space. Both horizontal and vertical forces are to be considered when determining the COM position for our body (Horak & Macpherson, 1996). The head, arms and trunk contribute two thirds of the body mass. Whenever the COM is not directly aligned with the supporting skeletal structure, gravitational acceleration results in the conversion of a large amount of potential energy into kinetic energy, destabilizing the upper body (Grey, 2001). Thus, standing is a challenging mechanical task requiring active balance control to maintain stability. Considering the challenge of standing, maintaining body stability during walking can be more demanding as the BOS keeps changing.

The biomechanical challenges of balance control in walking

Human locomotion is a complex and demanding task that involves rhythmic, synchronous arm and leg movements in an alternating fashion to propel the body towards an intended destination. Maintaining balance during walking is quite challenging as the COM is located outside the BOS over 80% of the time. The muscles of our trunk and extremities must work in a coordinated fashion to create a state of equilibrium as we experience forces in an ever-changing environment and can encounter unexpected disturbances, such as receiving a sudden push, pull or a slipping on ice. The challenge in locomotion is the need to establish a new BOS on an uncertain support surface with each step and for periods of time the BOS is very small (less than a single foot). The gait cycle is often described in broad terms as being divided into a stance phase, when the foot is in contact with ground, and a swing phase when the foot is being transported to a new point of ground contact. Heel strike is a crucial point in the gait cycle as the body weight is transferred to the foot of the leading lower extremity. When heel strike happens, the foot has to conform to the uneven terrain (such as sand, grass, pebbles, ice, snow or concrete) and quickly absorb various forces to maintain the COM in proper position and continue the act of walking. Therefore, the challenge of heel strike is the uncertainty of transferring body weight from one leg to the other when the stability of the footing is unknown. If foot placement is poor then the subsequent stance phase and weight support can be compromised, potentially leading to a fall.

The challenge of walking is further increased in the swing phase because the BOS is reduced as the swing leg does not contact the ground. At this point, the demand of locomotion becomes tremendous as a single leg (stance leg) bears the entire body weight to maintain body equilibrium. During single leg stance, the COM moves beyond the medial border of the foot that is bearing the body weight, and consequently the gravitational torque acts on the ankle joint, causing the body to incline antero-laterally in the direction of the swinging lower extremity (Grey, 2001). There is an additional threat to our balance during the swing phase because of the potential of the swing foot to strike an obstacle, or for an external force to the swinging leg or body to cause the swing trajectory of the foot to be deviated, i.e. leading to a misplaced step, a trip or a stumble. Locomotion presents a more challenging mechanical problem than standing, requiring balance control of the body while continuing the act of rhythmically moving through an uncertain environment toward a destination.

Balance control strategies

Two-thirds of our body weight is located in the highest two-thirds of our stature, making us unsteady and increasing the critical demands on our balance and postural control systems

(Winter, Patla & Frank, 1990). Our body is guarded from falling by the interaction between the upper body (torso, shoulder, elbows and hands) and the lower body (hip, knee and ankle) and the musculature surrounding these joints, ensuring body stability. A myriad of strategies is used by humans to correctly alter the position of the COM while standing. Humans have different ways to react against any external disturbance or force that tends to disrupt the equilibrium position. Studies have reported reactions to standing surface translations to incorporate the use of an ankle strategy, in which an individual tends to sway antero-posteriorly to perturbations given at the ankle, and tend to rotate about their ankles to alter the location of the COM (Horak, 1987), thereby maintaining balance. Another commonly used strategy is a hip strategy which involves flexion and extension movements at the hip joint to maintain COM positioning. Hip flexors, extensors and abductors have been reported to stabilize the upper body mass over the lower body in the sagittal and frontal planes (Patla, 2003) when using a hip strategy. Change-in-support strategies, such as reaching for a handrail, or taking a step to prevent loss of balance are also often used to maintain balance (Maki and McIlroy, 2007). Moreover, the simple act of moving your arm away from your body to counterbalance some of the body mass is another commonly used strategy. Each of these strategies can be considered “reactive” responses to unexpected perturbations. Hence, a variety of different “reactive” strategies are used to maintain the COM position and contribute to motor coordination necessary to maintain erect stance and control balance during standing.

To ensure a steady, stable and safe gait pattern, that propels the body forward and maintains a continued stepping pattern, balance control is needed. The ability to counteract the forces of gravity and hold a stable posture requires adequate balance control by our body (Winter, 1991). When encountering unexpected disturbances during walking, comparable strategies to what are described in standing likely contribute to maintenance of balance. For example, torques applied at the ankles or hips of the stance leg, similar to the ankle or hip strategies during standing, can adjust the motion or position of the COM over the foot. Alternatively, an individual can maintain balance by adapting the trajectory of the swinging leg to adjust the next placement of the foot, thereby adjusting the position of the BOS beneath the COM, in a manner comparable to a stepping strategy in standing (Horak, 1987). The ability to adapt the motion of the COM or the positioning of the BOS requires that the nervous system integrates various sensory information to maintain stability during walking. This integration of sensory information can be achieved either proactively, to avoid or prevent destabilizing events from occurring, or reactively, to correct for unexpected events after they occur.

Neural concepts of proactive and reactive balance control

To maintain stability while walking, reactive, predictive and anticipatory strategies can successfully help in maintaining the COM location and motion in a varying environment and altering support surface (Patla, 2003). The COM is kept within the postural limits of stability to ensure dynamic equilibrium during walking that involves the acceleration and deceleration of the COM (Patla, 1993). Patla (2003) argued that the first interaction of maintaining balance control is often predictive in nature, due to awareness about the disturbance; however the second interaction involves a reactive component (unexpected disturbance) to balance that is manifested through the available sensory information. The proactive balance strategy involves anticipated and predicted postural adjustments prior to possible expected balance threats, such as walking on a slippery surface (for example, on an icy sidewalk). Proactive control relies on prior experience in order to prevent loss of balance during normal walking (Tang, Woollacott & Chong, 1998).

Consequently, this pre-planning for the execution of movements involves higher executive functions, including cognitive processing, memory, judgement and planning, to maintain balance during locomotion. Therefore, the ability to maintain the stable movement of the COM over a continuously changing BOS can be made possible using proactive balance control strategies that involve prior experience with the event.

Reactive balance control strategies occur in response to unanticipated balance perturbations in an attempt to regain postural stability (Patla, 1993, 1995). Examples of reactive postural corrections from daily life during walking includes, getting pushed or pulled from behind while walking, loss of balance on a slippery surface, tripping on uneven ground, change of support surface (such as sand, wood or marble), or missing a step while going downstairs (Winter et al., 1990). In such unanticipated situations, our tendency is to regain the lost balance and achieve stability through incorporating a variety of different strategies. The expression of these strategies are particular to each individual, and can range from generating forces to act through the existing BOS, grasping a nearby hand rail, adapting a step trajectory to broaden the subsequent BOS or raising the arms to redistribute the location of the COM. Therefore, the reactive balance control strategy can be crucial in counteracting the unexpected perturbations encountered in daily life by accomplishing body stability.

The central nervous system (CNS) counteracts an unexpected disturbance by generating muscular corrective actions to regain balance control. For example, unexpected displacement of a force platform under the feet results in motor responses in leg muscles during standing (Manchester, Woollacott, Zederbauer-Hylton & Marin, 1989). Specifically, activation of leg muscles occurred in a distal to proximal temporal sequence. Furthermore, there was directional specificity of these responses as anterior platform translations caused posterior sway and a resultant increased activation of tibialis anterior, quadriceps and abdominal muscles; whereas, posterior platform translations induced an anterior sway generating responses in gastrocnemius, biceps femoris and paraspinal muscles. Similar findings have been reported during walking. For example, Nashner (1980) showed that a sudden forward translation of a support surface at the instant of heel strike during walking caused increased TA activation. In contrast, backward platform translations caused increased gastrocnemius activation. These authors suggested that such alterations in ankle muscle activity based on the direction of support surface displacement were reactive responses generated by the CNS. Similarly, unexpected rapid treadmill deceleration resulted in bilateral TA activation and ipsilateral gastrocnemius muscle activation (Berger, Dietz & Quintern, 1984). Therefore, considering the methods of inducing balance perturbations in the aforementioned studies, these muscle activation patterns would be a result of reactive balance control strategies that counteract unexpected perturbations in both standing and walking.

Sensory contribution to balance control

Our body equilibrium can be disturbed from forces that are self-induced (voluntary movements) or unanticipated, such as a sudden displacement of the support surface. The movements under voluntary control require postural adjustments using a feedforward control strategy to combat any anticipatory disturbances to body equilibrium. Massion (1992) suggested anticipatory postural adjustments are a requirement of voluntary movements as the associated displacement of the limbs creates a disturbance in the position and motion of the COM that must be controlled to maintain balance and equilibrium of the body. These postural adjustments happen prior to the onset of the voluntary movement and use a feedforward control to stabilize and counteract the predicted or anticipated effects of the planned movements. Maintaining equilibrium following an unanticipated event requires feedback control, where corrections are made after the disturbance has occurred. Many of the examples described in the previous sections, such as translation of support surface, a push to the body, or a slip on some ice, are examples of unexpected events that would destabilize balance and require feedback control. Sensory information is vital to both feedforward and feedback control; however, the focus of this thesis is feedback control in relation to postural adaptations in response to an unexpected sensory disturbance. Therefore, this literature review will focus on the contribution of sensory systems to feedback control of balance during walking.

Sensory systems form an integral part of our postural control system. The visual, vestibular and somatosensory systems each hold a strong influence in our balance control (Mohapatra & Aruin, 2013; Winter, 1995). In the elderly and individuals with balance impairments, a decline in the functioning of these systems predisposes an individual to a greater risk of falls (Baker & Harvey, 1985). The availability of afferent inputs from the visual, vestibular and somatosensory systems is responsible in maintaining body stability during normal standing (Mauritz & Dietz, 1980). If sensory cues from any one of the sensory systems are missing, the remaining cues compensate in order to achieve a stable posture and maintain our balance control. For instance, in the absence of vision, individuals tend to rely more on their vestibular and somatosensory system to maintain their postural stability (Pereira, 1990; Rosen, 1997). Overall, these systems deliver the sensory information that is crucial in maintaining balance control and posture. Misiaszek (2006) described a finite state control model (If-Then rules) to argue that the nervous system combats a variety of situations by integrating sensory information from the available systems (visual, vestibular and somatosensory) and generating a specific motor action. Moreover, according to the finite state model, the sensory information provided in the balance control system can be added, removed or scaled depending on the task requirements. However, when the sensory systems are impaired as a consequence of a disability, or have suppressed activity in challenging environments, such as walking in the dark, the available sensory cues can compensate. While the main focus of this thesis is to emphasize the role of cutaneous sensory feedback in maintaining balance control during locomotion, to better lay the groundwork for the importance of sensory feedback in walking, a brief description about the visual, vestibular, and the somatosensory system is presented in the upcoming section of this literature review.

Visual system

Vision has a stabilizing influence on our posture in normal conditions (Dichgans & Brandt, 1978). However, standing with eyes closed is challenging and results in a 50% increase in postural sway, compared to standing with the eyes open (Diener & Dichgans, 1988). The moving room paradigm is a commonly used technique to evaluate the role of visual information in controlling posture and sway of an individual. In a moving room paradigm, the individual stands on a stable reference point and the surrounding environment (for example, the walls of the room or a virtual display of the walls) moves relative to a fixed reference point (Brandt, Dichgans & Koenig, 1973; Lee & Lishman, 1975; Stoffregen, 1985; Warren, Kay & Yilmaz, 1996). When the visual field is stationary relative to the surrounding environment, postural stability is achieved. However, postural sway is induced (Brandt et al., 1973) in the same direction as the visual field motion to restore balance (Lee & Aronson, 1974). Similarly, results of another study showed increased COP fluctuations in ageing adults with impaired balance control when the visual surround was moved, in comparison to both young and healthy ageing participants (Sundermier, Woollacott, Jensen & Moore, 1996). These authors argue that an increased reliance on vision for stability of posture could potentially have a destabilizing influence on the body when the visual surround moves unexpectedly. This could be attributed to somatosensory deficits in the ageing individuals that made them a susceptible candidate to lose their balance with much ease. Thus, this can potentially impact the individuals who rely on visual cues as a main source of sensory information in maintaining their balance control. Consequently, ageing individuals with balance problems are at risk of falls due to disequilibrium in their balance, when the visual surround moves. This is especially evident in unexpected situations where surrounding environment is moving, for example; standing beside a moving train, riding an escalator, crossing a road with traffic moving in same or in the opposite direction, driving on crowded streets and walking across a busy grocery store (Sundermier et al., 1996). In summary, the evidence suggests that the visual system works as an integral part of the postural control system and maintains upright stance through various postural adjustments. The postural adjustments occur in phase with the spatiotemporal aspects of the visual field in our surrounding environment. Therefore, the availability of vision serves to maintain stability of posture during standing.

While walking, vision helps to encounter obstacles on the way by ensuring proper feet placement and spatially orienting an individual to the surrounding environment. This further serves to maintain stability during locomotion by providing advance visual cues about the intended destination. In the absence of vision, the risks of slipping or running into obstacles that might interfere with maintaining balance and could ultimately lead to a fall increases. Vision allows us to alter our walking speed to maintain an optimal pace for encountering obstacles that arise while walking through uneven terrain that might require a detour. An important role of vision is to spatially orient an individual in the surrounding environment against any external threat by adjusting the posture to prevent disequilibrium. Prokop, Schubert & Berger (1997) have studied how optic flow changes can affect human locomotion. Optic flow refers to the pattern of motion perceived by the moving observer. During locomotion, discrepancies between the direction perceived from optic flow and from the target guide the observer (Williams, Bruce, Wendy, Andrew & Stephanie, 2001). In this study, participants walked on a treadmill in front of a big spherical screen that displayed various visual patterns (Prokop et al., 1997). The findings indicated that optic flow tends to regulate the walking velocity of the participants due to alterations in the stride length over a period of time. The ability to steer our walking in a particular direction using optic flow which is the relative motion happening between the eyes and the surrounding environment has been demonstrated (Warren et al., 2001). It was suggested that optic flow is an important component of accurate visual control of locomotion (Warren et al., 2001). Vision takes a proactive action against any external disturbance that tends to disrupt the stability of our body. Although, feedforward strategy is important for responding proactively in advance of the event, the visual feedback plays a larger role by fine-tuning (Marigold, 2008) of the already available information from the feedforward control. Therefore, it can be expected that optic flow (feedback) modulates human locomotion and affects balance control for the body. Overall, it implies that the visual system provides information via the feedforward and feedback (optic flow) control systems to maintain and shape body stability while walking.

Light touch and vision both serves to shape the postural control system by providing stability during standing. As noted above, standing with the eyes closed results in an increase in sway during standing. However, contacting a stationary touch reference using a fingertip is seen to attenuate this increase in postural sway even when the touch contact is below 1N force; thus not providing additional mechanical support to the body (Holden et al., 1994). When the touch reference is oscillated, body sway is seen to match the frequency of the touch plate sway (Jeka et al., 1997, 1998). This oscillation of the touch reference can be considered similar to the dynamic environment that was seen with the moving room paradigm. These findings suggest that somatosensory stimuli (touch) and visual cues holds similar influence on our postural control system during upright stance. In this thesis, occluding vision is a major challenge to participants walking on a treadmill with their eyes closed. The sole purpose of removing the visual cues in my thesis is to increase the reliance on other senses, in particular, light touch of the index finger. Thus, walking with eyes closed can be a challenging situation that can lead to alterations in gait patterns and being more cautious (Hallemans, Beccu, Van Loock, Ortibus, Truijen and Aerts, 2009) as the relevance of sensory cues from the light touch of the fingertip is increased.

Vestibular system

The combined signals from the visual, vestibular, and somatosensory systems, along with cortical and cerebellar inputs reaching the vestibular nuclei in the brainstem, ultimately elicit motor responses for maintaining upright balance (Cullen, 2012). The anatomy of the vestibular system includes two vestibular receptors: 1) the semicircular canals, that respond to angular movements of the head; and 2) the macular otoliths (the utricle and the saccule) that respond to linear movements (due to gravity and translational movements) of the head. The information from these vestibular receptors is then carried via the afferent fibers of the vestibular component of the vestibulocochlear nerve (8th cranial nerve) to the vestibular nuclei in the brain stem.

Further, the information from the vestibular nuclei then travels via the projection neurons to signal for controlling eye movements (gaze stabilization), self-motion and maintenance of posture and balance. Thus, the central nervous system receives information from the aforementioned circuit which then indicates the position of the head for maintaining postural orientation relative to gravity by counteracting the external forces (Cullen, 2012).

The vestibular system is responsible for orienting an individual to the surrounding environment by stabilizing their head and generating appropriate postural responses that are essential to maintain body balance (Macpherson & Inglis, 1993; Takahashi, Hoshikawa, Tsujita & Akiyama, 1988). Galvanic vestibular stimulation (GVS) has been used to look at the function of the vestibular system during standing. For example, Nashner & Wolfson (1974) showed that GVS generated short-latency responses (~100 ms) in the gastrosoleus muscles (GS). The GVS response evoked in GS was dependent on the functional relevance of the vestibular system to the task such that when subjects stood on a firm surface, the response had little consequence. However, if subjects stood on a sway-referenced platform, which increases the critical importance of the vestibular system to balance control, the GVS evoked responses were markedly increased and caused destabilizing sway. Thus, it was suggested that the vestibular system is critically important in augmenting postural control when other sensory cues have been eliminated or suppressed. Moreover, the rapid response onset following GVS is interpreted by subjects as an actual unexpected head movement that could be considered a potential threat for our body (Fitzpatrick & Day, 2004). Therefore, the vestibular system enables a protective mechanism by activating a rapid reaction to potential threats to stability detected by unexpected movements of the head.

During walking the head moves in an anticipated and predictable way as the body is moved over the ground. Therefore, there might be an interaction between the expected and unexpected signals from the vestibular system during walking. To further understand the vestibular system, GVS has been applied during walking with eyes closed (EC). In a control trial without GVS, individuals were able to walk with their eyes closed (EC) to reach a target that they had previously been shown. However, these individuals were seen to deviate towards the anodal current in their walking trajectory when GVS was applied (Fitzpatrick, Wardman & Taylor, 1999). It was suggested that the anodal current decreases the input from the vestibular organs of that side, thus causing participants to interpret the signal as a difference in the speed of linear motion on either side of the head, such as would occur during a turn. The subjects then change their walking trajectory to counteract this effect, thereby deviating from the straight path. With the eyes closed vestibular and somatosensory feedback are suggested to maintain body stability and walking trajectory without GVS application. GVS is seen to affect the walking trajectory in the EC condition because the availability of somatosensory feedback alone is not sufficient to maintain the walking trajectory. Therefore, galvanic stimulation is seen to integrate both the somatosensory cues and the vestibular cues in standing and walking.

Individuals with impaired functioning of their vestibular system have impaired balance control, because they are unable to detect their head movement in relation to the movement of the rest of their body. As an alternative, individuals with impaired vestibular functioning compensate by using other sensory modalities, such as visual or somatosensory cues (Pozzo, Berthoz, Lefort & Vitte, 1991). For instance, individuals with bilateral vestibular loss showed a reduction in their postural sway when given an external stationary touch reference as a means of contact (Lackner, Dizio, Jeka, Horak, Krebs & Rabin, 1999). Furthermore, the authors showed that provision of light touch resulted in sway reduction in individuals with vestibular loss and without vision. The vestibular loss individuals cannot maintain standing without vision for more than 10 seconds without falling over when not provided the touch contact. Furthermore, children with loss of their vestibular function were asked to stand on a foam surface with their eyes closed (Enbom, Magnusson & Pyykko, 1991). In these children, vestibular cues were absent, closing their eyes eliminated the visual cues, and standing on the foam surface underneath the feet caused decreased awareness of the surface and hence lowered the feedback from the somatosensory cues. This ultimately resulted in a fall due to the combined sensory impairment created by these conditions. However, if one of the sensory inputs is available, balance can still be maintained and the chances of falling can be reduced. Summing up, the vestibular system holds a strong impact in maintaining the balance control during standing and walking.

Somatosensory system

The somatosensory system includes tactile (i.e. touch, tickle, pressure and vibration), proprioceptive (i.e. kinesthesia, joint position sense, resistance), pain and temperature sensations (Riemann & Lephart, 2002). Although the visual and vestibular systems contribute considerably to maintaining balance, the somatosensory system also offers a significant role in balance control through proprioceptive and tactile (touch) feedback. Somatosensory information is derived from a variety of mechanoreceptors in the skin, pressure receptors, muscle spindles, Golgi tendon organs and articular receptors each providing critical information important for maintaining body orientation and equilibrium (Horak & Macpherson, 1996). The Somatosensory receptors are widely distributed throughout the entire body, whereas the visual and vestibular receptors are located only in the head. The visual and vestibular receptor functions to maintain head orientation by deriving information about body configuration from the somatosensory receptors in limbs and trunk (Horak & Macpherson, 1996). In contrast, the widespread coverage of the body provided by the somatosensory system provides a rich sensory field for the detection of instability and threats to balance. Therefore, somatosensory feedback likely plays an important role in the control and regulation of balance.

The role of muscle mechanoreceptors in balance control, including muscle spindles and Golgi tendon organs (GTO's) are crucial in providing information about the postural control system. The muscle spindle and GTO's continuously provide feedback to the CNS about the status of each muscle. The muscle spindle signal changes in muscle length or its rate of change in length that occurs with rotation about joints that makes muscle spindles well suited for detecting joint angle. Muscle spindle afferents other than being sensitive to changes in muscle length also responds to velocity and acceleration of the perturbation (Prochazka, 1996). Therefore, unexpected changes in joint angle can be quickly detected by muscle spindles and reported by studies involving rotation or translation of the supporting platform (Nashner, 1977). Studies involving support surface translation in standing participants generated automatic postural reactions (APR's) which are considered to be compensatory muscle responses that control posture. The rapid onset of ankle muscle activity with platform rotations are likely triggered by muscle spindles which is mediated by stretch reflexes. The responses elicited in the leg muscles maintains the load carried by either leg and seem to be more complex responses than merely classified as muscle stretch reflex response (Nashner, 1977; Nashner, Woollacott & Tuma, 1979). The GTO's are suggested to signal the joint loading and the joint receptors provides information about the angular displacement following platform rotations (Dietz, 1992). The GTO's functions to play a protective mechanism in order to relax a muscle that is being overstretched. Additionally, when perturbations in the form of sudden treadmill acceleration or deceleration was given to walking participants, automatic functional responses were generated in the leg muscles to correct for imbalance and reduce sway (Dietz, Horstmann & Berger, 1989). Consequently, the muscle spindles afferents carry the information to the spinal cord and then the information is returned to the muscle fibres via the alpha motor neurons to contract and control the postural sway (Dietz et al., 1989). The EMG responses generated in the leg muscles (TA and gastrocnemius) are functionally relevant due to the stretch reflex activity and can be linked to controlling the COM, thereby regulating posture (Dietz et al., 1989). Summing up, the muscle spindles serve a protective role in balance control by reducing sway to externally induced perturbations.

Muscle spindles are sensitive to vibratory stimuli and when activated by vibration can induce a false sensation of a muscle being stretched. For instance, vibration of gastrocnemius and soleus muscles is interpreted by the CNS as though these muscles are being stretched, that is interpreted as though the participants are falling forwards. This resulted in a correction that caused subjects to sway or lean in response to the false signal of the vibrated muscle being lengthened (Lackner & Levine, 1979). This study demonstrated the role of muscle spindles for maintaining postural orientation by activating Ia afferents that caused leaning. Similarly, gastrocnemius muscle vibration in standing blindfolded individuals created an illusion that the muscle has been lengthened which was perceived as a forward postural sway. This was corrected by a slow backward lean, until tibialis anterior muscle pulled the body forward to prevent backward fall (Horak & Macpherson, 1996). In addition, people with an absence of large afferents serving muscle proprioceptors will experience poor balance control. Van Deursen & Simoneau (1999) showed loss of muscle spindle function and cutaneous mechanoreceptors in individuals with diabetic neuropathy, as they demonstrated reduced postural stability and imbalance. Furthermore, ischemia studies (Diener et al., 1984) have shown that temporary loss of large diameter afferents, serving muscle proprioceptors, leads to poor balance control and disrupted balance corrective reactions. Therefore, muscle spindles and other proprioceptive feedback is critically important in the regulation of balance. In this thesis, the focus of the contribution of the somatosensory system in balance control is with the tactile feedback. However, it is important to acknowledge that the displacements of the touch reference introduced as the sensory stimulus could potentially also activate muscle spindles. Given the importance of muscle spindles to detecting muscle length changes, this potential contributing signal cannot be exclusively ruled out.

Sensations from the skin have also been implicated in proprioception. For example, Collins and Prochazka (1996) demonstrated that stretching the skin spanning finger joints was perceived as movement of the fingers. Studies have demonstrated that stretching of the skin around other joints more related to maintaining balance and it is reasonable to suggest that movement related to skin stretch is integrated into the balance control system and could provide sensory feedback. However, in this thesis my focus is on the role of cutaneous feedback as it relates to light touch. Light touch is seen to be incorporated in our balance control system and functions to control the posture and will be discussed in greater detail in subsequent sections of this literature review.

Somatosensory feedback from the hands is a potentially rich source of sensory information for balance control when the hands are used to assist with support. For instance**,** using assistive devices like canes, crutches or walkers; or grasping a rail, a friend’s arm or a tree by the side of a trail can help to maintain balance while standing and walking. The sensory feedback from the hands then becomes available as the hands represent an additional contact point with the support surface, increasing the BOS. The benefit of engaging the hands in balance control is perhaps most pronounced in individuals with balance impairment. For example, Parkinson's patients that experience a slip while walking showed a smaller lateral excursion of the COM when using a cane than compared to individuals that did not use as cane (Boonsinsukh, Saengsirisuwan, Carlson-Kuhta & Horak, 2012). The difference between the cane users and non-users was most evident in the first trial, suggesting that mechanical benefit of the cane, which remained the same in the subsequent trials, was not the factor that produced this difference. Rather, it was suggested that the sensory feedback from the hands facilitated an improved balance response in these individuals.

Cutaneous feedback that might aid balance control is not restricted to only the hands, but can arise from receptors in the trunk, legs and feet as well to maintain trunk positioning while standing or walking (Horak & Macpherson, 1996). Studies have specifically argued that cutaneous signals from the feet provide crucial feedback for maintaining balance control as stability becomes impaired when cutaneous feedback is blocked with anesthetic or ischemia (Diener, Dichgans, Guschlabauer & Mau, 1984) or in individuals with sensory neuropathies (Simoneau, Ulbrecht, Derr & Cavanagh, 1995). Indeed, it has been demonstrated that augmenting cutaneous feedback from individuals with peripheral neuropathy can lead to functional improvements in balance (Inglis, Horak, Shupert & Jones-Rycewicz, 1994). Therefore, although my thesis focuses on the contribution of cutaneous feedback from the hands in the regulation of balance, cutaneous feedback from other regions of the body is known to also be important in balance regulation. It is likely that some of the principles that arise from my thesis work will also apply to these other sources of cutaneous feedback.

Light touch and balance control in standing

The role of light touch on balance control during standing was first demonstrated by investigating the impact of light touch on sway (Holden, Ventura & Lackner, 1987). In this study, participants stood on a force platform and maintained light touch with a stationary touch reference using their index finger. When these participants were standing without vision (eyes closed), an increase in postural sway was noticed. However, provision of a light touch reference attenuated the body sway and was thought to stabilize the body in the eyes closed condition, similar to having complete sight. A long list of studies since has shown that the provision of light touch with just the index finger reduces postural sway in healthy individuals (Holden et al., 1994; Jeka & Lackner, 1994, 1995; Kouzaki & Masani, 2008; Lackner, Rabin & Dizio, 2001; Rabin, Dizio, Ventura & Lackner, 2008). Thus, light touch can provide sensory cues that can be integrated into balance control during standing.

The role of light touch in providing increased stability is not likely to be attributed to supplementary mechanical support when contacting an external touch reference. Holden et al. (1994) showed that light touch contact below 1N force is capable of reducing sway, despite not providing additional mechanical support to the body. Kouzaki & Masani (2008) showed that application of tourniquet ischemia in the arm abolished the stabilizing effect of light touch from the index finger, irrespective of any mechanical support. Moreover, Rogers, Wardmann, Lord & Fitzpatrick (2001) demonstrated that passive light touch of the shoulder, which was incapable of providing any mechanical support, also reduced sway during eyes closed standing. Taken together these results suggest that sensory feedback related to the light touch was the important factor in the regulation of sway that was observed.

The ability of light touch to stabilize sway also extends to populations with impaired balance control. For example, light touch of a stationary surface is shown to enhance the postural stability in participants with impaired balance due to diabetic neuropathy that reduced somatosensory feedback from their feet (Dickstein, Shupert & Horak, 2001). The findings from this study showed that light touch stabilized balance (reduction in sway fluctuations) in individuals with somatosensory loss, similar to healthy individuals with intact sensations. Kanekar, Lee & Aruin (2007) showed the crucial role of light touch cues in maintaining postural control in individuals suffering with multiple sclerosis. In this study the impairments to balance control resulting from the multiple sclerosis were further challenged by asking the subjects to stand with their eyes closed and with a reduced BOS. The provision of light touch significantly improved balance in these conditions despite the diffuse nature of the neural deficit caused by the multiple sclerosis. Thus, using light touch cues further confirms the importance in improving postural control and can be used as a rehabilitation strategy to augment balance control in standing.

Light touch and balance control in walking

Dickstein & Laufer (2004) demonstrated the importance of lightly touching a stationary touch surface while walking on a treadmill with eyes closed to provide a somatosensory anchor. When subjects walked on a motorized treadmill without vision, they inevitably drifted backward and were unable to maintain a stable gait. However, when they were provided a light touch spatial reference, the subjects walked with near normal movements and stability (Dickstein &

Laufer, 2004). More recently, Forero & Misiaszek (2013) demonstrated that light touch during treadmill walking facilitated balance reactions produced when subjects with eyes closed were pulled at the waist. These authors argued that the additional sensory feedback from the finger replaced the visual reference that was lost with the eyes being closed and was used to scale the size of the balance response produced by the waist pull. The importance of using light touch during walking by using an assistive device, such as a cane, was shown by Boonsinsukh, Panichareon, & Phansuwan-Pujito (2009). The somatosensory information available by using a cane (average touch force of 2.3 N) in stroke participants improved lateral stability by facilitating activation of muscles on the affected lower limb in the stance phase of walking (Boonsinsukh et al., 2009). Therefore, the tactile cues from the hand seems to play an important role in balance regulation during walking, as revealed in the aforementioned studies that specifically showed the influence of using light touch during walking.

Cutaneous mechanoreceptors

The hands can sense light cutaneous contact when touching or grasping, and the nervous system then integrates this information in order to generate appropriate postural responses. Human skin can be categorized as either being glabrous or hairy. The hairy skin regulates our body temperature, in addition to joint proprioception, kinesthesia and motor control functions performed by the receptors that are present in the hairy skin (Edin, 1992). The focus of this thesis will be on the receptors located within the glabrous skin because light touch of the fingertip involves only the glabrous skin. There are numerous mechanoreceptor units in the glabrous skin that are highly sensitive to tactile cues (Knibestol & Vallbo, 1970). These mechanoreceptor afferents innervate the volar aspect of our hands. Evidence suggests that approximately 17,000 mechanoreceptor units are critical in providing tactile information about the external world (Johansson & Vallbo, 1979; Johansson & Vallbo, 1983). Approximately 44% of these receptor units are categorized as slow adapting (SA) receptors, and 56% are categorized as fast adapting (FA) receptors. These subtypes can also be differentiated by the size of their receptive field, which can be either small with clearly defined borders (FA I and SA I receptors), or larger with equivocal borders (FAII and SAII receptors). A receptive field is defined as a region of skin in which mechanoreceptor units can be stimulated, either by using von Frey hairs or blunt probes (Johansson, 1978). These afferents have been classified into their adaptation pattern and characteristics of their receptive field, and therefore can be either slow- and fast-adapting type I or II afferents (SA-I, SA-II, FA-I and FA-II). These afferents have corresponding end-organs, such as the Merkel's disc, Ruffini endings, Meissner corpuscles and Pacinian corpuscles respectively.

Functional significance of mechanoreceptors

SA and FA receptor subtypes are classified according to their ability to respond to sustained skin indentation. For instance, the FA units respond to the onset of a stimulus (e.g. skin indentation), but then rapidly adapt and cease firing until perhaps the stimulus removed; whereas the SA units respond to the onset of the stimulus, but then sustain firing for the duration of the stimulus. The functional significance of these receptor units is important as they can provide accurate spatial information from the hand while touching an object. Cutaneous mechanoreceptors of the human hands have been previously studied in detail using percutaneous microelectrode recordings from the peripheral nerves in humans (Vallbo & Hagbarth, 1968). The neural activity recorded from the volar aspect of the distal phalanx of the index finger, showed an increased firing of the FA receptors occurred when touching a rough surface of a matchbox, in comparison to the smooth surface of the matchbox (Vallbo & Hagbarth, 1968). This suggests that surface texture variation is responsible for specific mechanoreceptor units firing, and the contact between the glabrous skin of the fingertip and an external contact surface leads to their activation. In contrast, SA I afferent units are sensitive to edge detection and object contours while touching, hence indicating their ability to contrast between object shape and edges (Johansson & Vallbo, 1983). The spatial acuity of our hands is highest distally at the fingertips and reducing proximally from metacarpophalangeal, intercarpal and wrist joints. The density of the FA I and SA I receptors are 140 units/cm^2 and 70 units/cm^2 at the fingertips, respectively, further suggesting the crucial role played by these receptors when an object is touched using the tips of the index finger and thumb. In particular, the most distal aspect of the distal phalanx is shown to possess a higher density of receptors and demonstrates more precise spatial resolution, than more proximal surfaces of the fingers (Hill, 1974). Furthermore, motion of the hands and finger joints activates certain afferents that are directly involved in proprioception. Due to their high rate of sensitivity, about 100% of the FA II receptors fire in response to joint movements, in comparison to 57%, 66% and 94% of FA I, SA I units and SA II receptor units respectively (Johansson & Vallbo, 1983). Overall, different mechanoreceptor types are suited for a particular function when an object is touched using the hands or fingertips. Altogether, the CNS receives combined information about the object or surface including the shape and texture. In addition, if the contact surface or the finger move relative to each other, then information about touch dynamics, including direction and speed is readily encoded by the touch mechanoreceptors in the skin of the fingers or hand.

Unexpected slip detection by SA I and SA II receptors

When an external surface that is being touched moves unexpectedly, the glabrous skin provides spatiotemporal tactile cues related to the mechanical events at the interface between the skin and contract surface (Srinivasan, Whitehouse & LaMotte, 1990). If an unexpected slip happens, the skin region in contact with the external touch surface either moves in the direction of the movement or remains stationary, activating specific mechanoreceptors that innervate that area (Srinivasan et al., 1990). Several studies revealed that FA receptors are strongly associated with slip detection of objects held in the hands (Johnson, Yoshioka & Vega-Bermudez, 2000; Srinivasan et al., 1990). In addition, when the hands are contacting an object that is pulled away, the skin gets stretched with activation of SA II receptor units that respond specifically to changes in the lateral skin tension, with differential sensitivity to the direction and magnitude of the pull (Johansson, 1978). Moreover, anesthetizing the fingertip leads to increased occurrence of slippage of a grasped object, suggesting that cutaneous mechanoreceptors play an important role in detecting the relative movement between an object and the skin (Johansson & Westling, 1984). Furthermore, stroking the skin produces a subtle difference in the sensitivity of proprioceptive cues that convey joint movement (Stephen & Darian-Smith, 1984; Loomis & Lederman, 1986). The mechanoreceptors in the finger pads are ideally suited for detecting the tangential scanning motions that function for fine motor and fine spatial resolution (Darien-Smith & Kenins, 1980; Johansson & Vallbo, 1979). A precision grip prevents sliding of the object between the fingertip and the thumb to maintain stability of the grip. The ability to control these grip forces arises from the shear force between the object and the skin, which then activates the specific tactile units in the glabrous skin of our hands (Johansson & Vallbo, 1983).

Therefore, now we are able to understand specific mechanoreceptor activation in providing feedback cues to the CNS following unexpected slip of an object from the hands.

Cutaneous reflex studies during locomotion

Cutaneous reflexes have been extensively studied in humans and are functionally relevant to generate a protective mechanism that provides stability of posture during walking. Cutaneous reflexes can be described as complex responses which are generated after electrically stimulating the nerves and the response can be further subdivided into early, middle and late latency. For instance, tibial nerve stimulation results in a smooth swing phase and subsequent weight transference to initiate the stance phase of the gait cycle. This co-ordinated motion happens without any dragging or falling of the swing leg, and is often referred to as a stumbling corrective response (Zehr, Komiyama & Stein, 1997). The stumbling corrective responses that result from electrical stimulation are functionally very similar to the corrective stumbling responses that occur when objects placed in the swing path of the foot cause a physical stumble (Shillings, Wezel & Duysens, 1996). Therefore, the responses that arise from electrical stimulation of cutaneous nerves likely reflect functionally relevant motor responses important for the control of balance and walking.

Dietz (2002) argued that the coordinated movements of the upper and lower extremities during walking were actively controlled by the nervous system and were important for maintaining stability of the moving body. Interlimb reflexes are argued to be functionally relevant in coordinating the movements between arms and legs during locomotion (Haridas & Zehr, 2003). Delwaide & Crenna (1984) were the first to demonstrate that electrical stimulation of cutaneous afferents in the fingers produced interlimb facilitation of motoneurons of the ankle muscle soleus. More recently, Haridas & Zehr (2003) showed that interlimb reflexes following stimulation of cutaneous nerves of the hand were modulated during walking, suggesting the interlimb reflexes evoked in the ankle muscles were functionally relevant. Lamont & Zehr (2007) demonstrated that interlimb reflexes in the arm, following stimulation of cutaneous nerves in the foot, were facilitated when subjects were lightly touching a handrail. Therefore, the implication is that interlimb cutaneous reflexes may be important for coordinating the actions of the arms and legs during walking, particularly for the maintenance of balance and stability. Moreover, Forero & Misiaszek (2015) demonstrated that interlimb reflexes in ankle muscles from median nerve stimulation, but not radial nerve stimulation, were facilitated when subjects with eyes closed lightly touched a stable reference during treadmill walking. This indicates that the interlimb reflexes associated with the median nerve were specifically upregulated because the afferent information in the median nerve was functionally relevant (i.e. providing a light touch feedback cue) to maintaining balance during the treadmill walking task. Taken together, these studies indicate that cutaneous interlimb reflex connections might be functionally relevant in the coordination of the arms and legs and important for maintaining balance while walking.

Central Pattern Generators in locomotion

The rhythmic placement of the feet and formation of the new BOS is achieved through the neural control of locomotion, in which central pattern generators (CPGs) form one part of the control. CPGs refer to a network of neurons (Pearson, 1993) that are present in the spinal cord and are functionally relevant in generating rhythmic movements. Grillner (1985) suggests that CPGs possess the capacity to generate movement patterns during locomotion that are self-sufficient in mammals. CPGs are particularly involved in generating the basic spatiotemporal patterns that are a typical feature of rhythmic locomotion (Arshavsky, Deliagina & Orlovsky, 1997). MacKay-Lyons (2002) argues that despite an inability to provide direct evidence, it is most likely that similar spinal neuronal networks capable of eliciting locomotion are also present in humans.

Misiaszek (2006) suggested a finite state control model for balance control during walking that incorporated the timing and rhythmicity of CPGs to help determine and execute appropriate corrective responses. It was argued that the timing of CPGs is important in regulating timing of muscle activation, in addition to activation of specific rules governing the emergence of balance reactions. Furthermore, the rules in the finite state control system were argued to adapt according to the anticipated demands imposed on the system. According to the model provided by Misiaszek (2006), sensory feedback is important at three levels: 1) selection or weighting of rules; 2) generating a balance corrective response; or 3) counteracting any mechanical disturbances by generating a specific motor output. Misiaszek (2006) specifically suggests that selection of balance reactions is in part regulated by the predictable pattern of neural activity (and therefore anticipated pattern of sensory feedback) that is regulated and controlled by the CPG. This rhythmic pattern of neural activity will impact the integration of sensory feedback that can be crucial in predicting events in advance, or adapting the walking pattern to maintain the locomotor rhythm and timing, while also conveying information about body biomechanics (Misiaszek, 2006). For example, studies have shown a phase-dependant reflex reversal (Yang & Stein, 1990) and a context-dependant modulation of reflexes (Haridas, Zehr & Misiaszek, 2006) that maintains the alternating pattern of walking. Yang & Stein (1990) showed reflex responses to be elicited during walking when the tibial nerve was electrically simulated. Following tibial nerve stimulation, excitation of the TA muscle was evident during the swing phase, whereas there was inhibition during swing to stance transition. The reflex reversal response is seen to maintain lower extremity trajectory and continue the act of smooth and co-ordinated locomotion in humans (Yang & Stein, 1990). It is further argued that the patterned out of the CPG could be responsible for controlling the switch in reflex output to meet the needs of the alternating walking pattern. Furthermore, Haridas et al. (2006) showed electrical stimulation given to nerves in the foot under a variety of situations (such as arms crossed with or without perturbations) were regulated differentially across the step cycle depending upon the level of threat to balance. The responses evoked by the stimulation of this sensory region of the foot are argued to be important for shaping foot placement on the ground in different terrains (Kostov, Hansen, Haugland & Sinkjaer, 1999). Due to the established phase and context dependency of reflexes that are modulated by the CPGs, it may be that sensory information relevant to balance control, such as the light touch disturbances introduced in this thesis, are modified or influenced by the activation of the CPG that generates the rhythmic alternating walking pattern.

Influence of descending control

Misiaszek (2006) suggested that descending control can modify the rules and weighting of specific sensory inputs in his finite state model to ultimately generate corrective responses that were tailored to demands of the task. The supraspinal selection of rule sets varies according to task requirements under different situations. Having prior knowledge about an event can influence the rule sets in advance and results in generation of appropriate responses in an efficient manner. However, unexpected events such as slips induced during locomotion can result in a robust reactive response in contrast to subsequent exposures which were proactively controlled by an individual (Marigold, Bethune & Patla, 2003). This implies that an unexpected slip happening for the first time can result in a different response and lead to advance preparation to prevent future slips. Prochazka (1989) referred to this “setting” or “tuning” of the sensory-motor responses based upon the predicted or known demands of the task as postural set. For example, when participants receive unexpected perturbations at the torso while walking on a treadmill, the amplitude of corrective responses were increased when subjects walked with their arms crossed, in comparison to walking normally with arms at the side (Misiaszek & Krauss, 2005). Thus, the evidence suggests that the corrective responses generated by participants depend on a rule based selection system that in itself is dependent on the task requirements.

The postural set or tuning of the sensory weighting likely involves several supraspinal nervous system structured. For example, a region of the brainstem known as the mesencephalic locomotor region (MLR) is argued to be important in activating the spinal the CPG for locomotion (See review by Grey, 2001). Stimulation of the MLR region of the brainstem in decerebrate cats results in increased activity of the vestibulospinal tract, along with other descending pathways (reticulospinal and rubrospinal tracts), that causes the “spinal stepping mechanism to be switched on” (Shik, Severin & Orlovski, 1966). Therefore, the activation of this brainstem region and the associated descending tracts is likely involved in regulating and tuning the sensory weighting important for balance control during walking. The cerebellum receives information about the different phases of gait via efferent fibers of motor neurons in the spinal cord, and further via afferent signals through the ventral spinocerebellar and spinoreticulocerebellar tracts (Rovainen, 1979). Removal of the cerebellum in cats showed disequilibrium in walking, such as legs colliding with each other (Shik & Orlovsky, 1976). The cerebellum then controls the activity of the motor neurons for the entire step cycle via vestibulospinal, rubrospinal and reticulospinal tracts and the signals convey information that adjust the step cycle of locomotion (Grillner, 1985). Therefore, the cerebellum and its associated descending tracts is involved in adapting and regulating the timing and pattern of the step cycle, which then also likely will influence and regulate the integration of balance control during walking.

Evidence has emphasized the cerebral cortex (specifically the frontal lobe) to be responsible for maintaining balance and locomotor control (Nutt, Marsden & Thompson, 1993). The setting of sensory weight or selection of the finite rules is related to the cortex, as there is a cognitive element of adjusting the control of balance and control of locomotion based upon the context or the environment (Misiaszek, 2006). Walking on uneven surfaces is quite challenging and skillful as the feet must be able to establish firm contact with the ground under varied environmental situations. The predictive events encountered during walking such as crossing over obstacles or climbing a ladder can be accomplished through the motor cortex and the corticospinal tract. Previously, proactive control is argued to involve cognitive control (Maki & McIlroy, 2007) when placing feet on the ground during walking. The proactive elements of control help us to adjust to changes encountered in the surrounding environment when placing feet over ground. For example, adapting gait to maintain a wide BOS, or taking a longer stride, or even walking on ice requires cortical inputs to presumably adjust and adapt certain control elements of the "automated" system, i.e. sensory weighting and preselecting the finite rules will likely incorporate specific changes to the finite state rules to accommodate for the adapted gait pattern.

Summary

Locomotion can be quite demanding when the eyes are closed as there are biomechanical challenges encountered in everyday life. Previously, it was demonstrated that an unexpected slip of a spatial reference from the hand triggers balance correction during standing. Misiaszek et al. (2016) showed ankle muscle activation following unexpected slip of the touch reference in standing. Later, the challenge was increased by asking participants to stand on an unstable surface, such as foam (Misiaszek & Vander Muelen, 2017) that would increase the relevance of light touch to maintain balance. Using a foam surface and giving unexpected displacements at the touch reference resulted in a more consistent expression of balance corrections, compared to standing on a firm surface (Misiaszek & Vander Muelen, 2017). Furthermore, it was previously demonstrated that light touch provides an essential spatial reference for treadmill walking in the absence of vision (Dickstein & Laufer, 2004). In this thesis, it is hypothesized that unexpected displacement of a light touch reference would evoke short-latency (<200 ms) responses in the ankle muscles during treadmill walking in the absence of vision. Walking on a treadmill without visual feedback would increase the importance of using light touch cues as a spatial reference, resulting in responses to be expressed more frequently than what was observed previously during standing (Misiaszek et al., 2016).

CHAPTER 3

METHODOLOGY

Participants

Twenty participants (age 18-35), 14 females and 6 males volunteered to participate in this study. Subjects r0eported no history of neurological, musculoskeletal, metabolic or cardiovascular disease, and had not experienced musculoskeletal injury, back pain, or concussion in the past 6 months. All participants provided written informed consent, and the project was approved by the University of Alberta Research Ethics Board.

Protocol

Participants walked on a motorized treadmill, at a self-selected speed (range: 0.9 to 1.2 m/s) that was maintained for all conditions thereafter. Because some of the trials involved walking with eyes closed (EC) without touching, participants were trained for a minute prior to walking with EC. During this training period gentle cueing (a hand placed in the small of the back) was provided to ensure that participants do not drift towards the back or on either sides of the treadmill. For some conditions, instructions were given to the participants to lightly touch (<1 N of vertical load) their right index finger on a horizontal stationary plate placed in front of them (Fig.1). For each participant, data were collected for three conditions: 1) walking with their eyes open (EO) and arms swinging normally; 2) walking with their EC with the arms swinging normally; 3) walking with their EC while lightly touching (<1 N) the stationary touch plate, which was unexpectedly displaced in either a forwards or a backwards direction. The order of presentation of the three conditions was kept constant for each participant. The eyes open not touching (NT), eyes closed (NT), and initial 1 minute of eyes closed lightly touching conditions were performed in part to create the deception that the touch plate remains stable throughout the experiment. For the first two conditions we recorded 1 minute of walking, but for the third condition we recorded 8-9 minutes of walking.

The direction of the touch plate displacement (forward or backward) was randomized between participants such that 10 participants received forward displacements and another 10 received backward displacements. Each participant received 10 such displacements of the touch plate that were given at the right heel strike. Participants were not informed about the timing of displacement (heel strike) and the displacement direction (forwards or backwards), but we assume they became aware by the 10th trial. Between these displacements, the touch plate was repositioned slowly (5 seconds) to the initial reference point, while the participant continued to maintain contact with the touch plate. The next displacement was delivered between 5 and 10 steps after the touch plate had been repositioned to the original position. Typically, this resulted in the delivery of a displacement once every 35 to 45 s.

Set-up and apparatus

Our primary goal was to observe participant's reactions to a sudden, unexpected displacement of a touch plate while walking. The touch plate consisted of a 3.75 cm× 7.5 cm brushed aluminium plate, mounted on a steel rod that allowed for the height of the touch plate to be adjusted. The right index finger was held vertical on the center of the touch plate, and the forearm was held approximately horizontal by maintaining the right wrist in a neutral position. The elbow was flexed at 90^o and a neutral position was maintained at the shoulder. In order to generate a linear displacement of the plate, the touch plate was mounted on a square rail acme screw drive positioning stage (Lintec 130 Series), driven by a computer-controlled two-phase stepper motor (Applied Motion Products 5023-124 2-phase hybrid step motor). The onset of the displacements was manually triggered by a researcher. The touch plate was displaced by 12.5 mm, with a peak velocity of 124.5 mm/sec. The entire touch plate apparatus was mounted on top of an AMTI MC3A-100 6 component force plate to allow for the vertical component of the touch force to be measured. The touch force was monitored online and auditory feedback was provided if the force exceeded 1N. Participants were instructed to place the tip of the distal phalanx of their right index finger vertically on a raised dimple in the centre of the plate. The use of a raised dimple on the touch plate was necessary as pilot testing revealed that participants were unable to maintain their position on the treadmill with a smooth contact surface and would seek to contact the edges of the touch plate as a reference. As a consequence, they were instructed to curl the remaining fingers inside the palm, to avoid any contact with the touch plate. All participants were instructed to use their right hand to contact the touch plate, regardless of their hand dominance as the role of cutaneous feedback does not differ between hands in this context. In all conditions the left arm was free to swing naturally. Visual input was removed by asking the participants to wear a pair of darkened goggles for all the testing conditions except the eyes open condition. In addition, to mask any auditory cues that might be present during the operation of the motor, the participants were equipped with a pair of over-the-ear headphones and received white noise throughout the experiment. For safety of the participants, a spotter was present throughout the experiment.

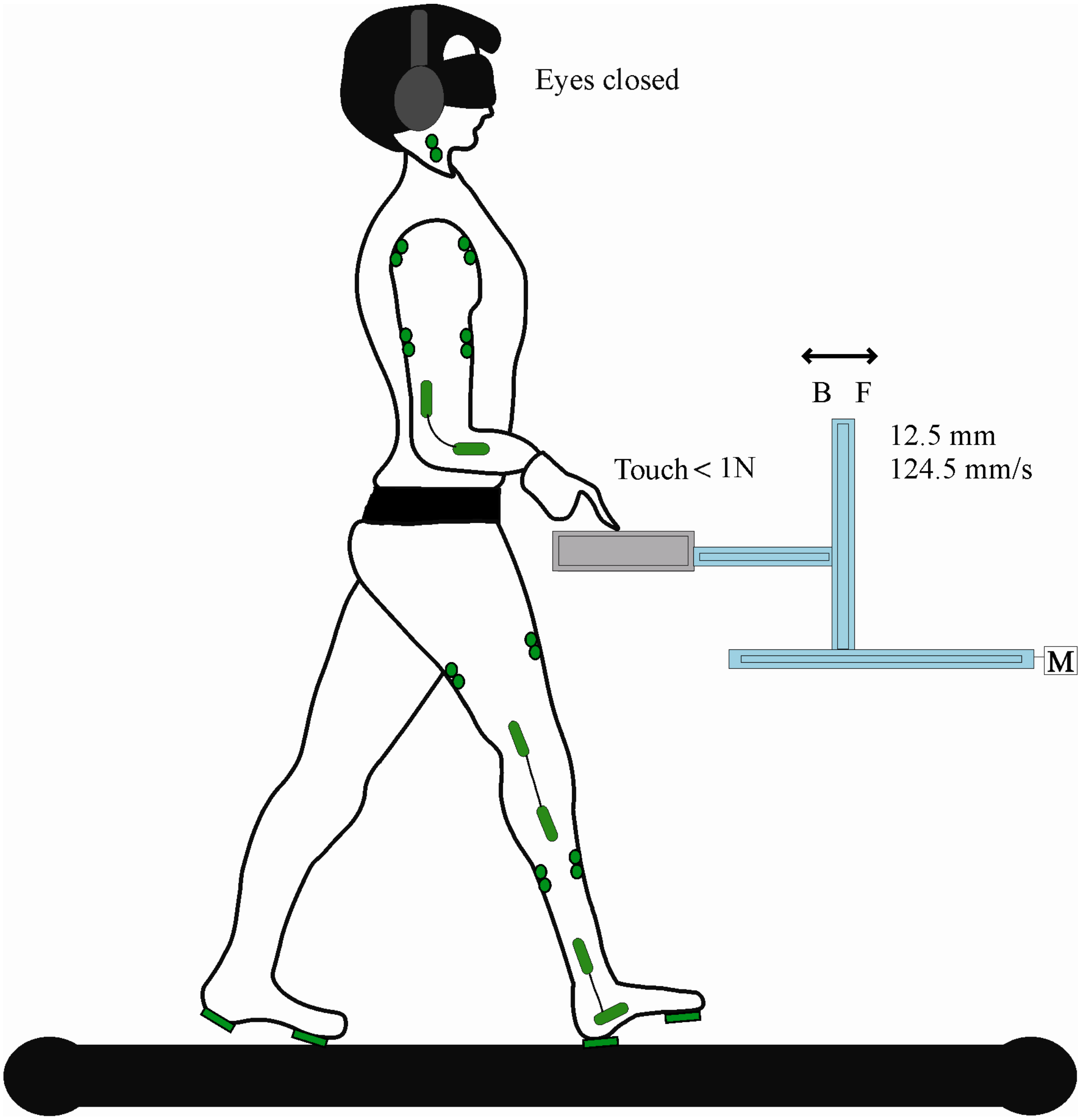


Figure 1: Schematic representation of the experimental set-up. Subjects walked on a motorized treadmill, either with their eyes open (EO) or eyes closed (EC). Subjects walked with their arms swinging freely, or lightly touching their right index finger (< 1 N) on the touch plate. Unexpected displacements were delivered at the right heel strike, either in the forwards or in backwards direction.

Recording and data acquisition

Electromyographic (EMG) activity was recorded from the sternocleidomastoid (SCM), anterior deltoid (AD), posterior deltoid (PD), biceps brachii (BB) and triceps brachii (TB) muscles of the right arm; and tibialis anterior (TA), soleus (SOL), vastus lateralis (VL) and biceps femoris (BF) of the right leg. EMG activity was recorded using pairs of Ag/AgCl electrodes (Neuroplus A10040) placed on the skin over the bellies of the intended muscles, parallel to the predicted orientation of the muscle fibers, with an inter-electrode distance of about 2 cm. Ground electrodes were placed over the olecranon process of the right arm and on the anterior tibia of the right leg. Before the electrodes were applied, the skin over the muscle belly was shaved with a razor and cleaned with alcohol. The electrode site was then tested (Grass F-EZM5 impedance meter) to ensure an impedance of less than 20 kΩ. The EMG signals were variably amplified and band-pass filtered (30 Hz-1 kHz with a 60 Hz notch filter, Grass P511 amplifiers) prior to digitization.

Electrogoniometers (Biometrics, Newport, UK) were placed across the right ankle, knee and elbow joints. Force-sensitive resistors (Interlink electronics) were placed on the insoles of both shoes under the heel and the head of the first metatarsal to record the foot contact data bilaterally. All other analog signals were digitized at 4000 Hz (PCI-MIO-16E-4, National Instruments) and stored on a hard drive in a computer using a custom data acquisition routine (LabVIEW v. 8.2, National Instruments) for later analysis.

Data analysis

Data analysis was performed post-hoc using custom written LabVIEW v. 8.2 routines. The EMG signals were digitally full-wave rectified and low-pass filtered (50 Hz, 4^{th} order zero-lag Butterworth filter). The mechanical signals were low-pass filtered (20 Hz, 2nd order zero-lag Butterworth filter). For the purpose of analysis, perturbed steps and control steps were extracted from the continuous data feed. For each step an 1800 ms trace was extracted and aligned at the right heel strike, taking a period of 200 ms prior to the right heel strike. Perturbed steps are those in which touch displacement occurred within ±100 ms of the right heel strike. For each perturbed step the five steps preceding the perturbation were extracted as the control steps. From these five control steps average control traces were calculated to construct a 95% confidence interval band. The average control traces were then subtracted from the perturbed traces to create subtracted traces for each individual touch plate displacement. A response in a particular muscle, or a disturbance in a goniometer trace, was identified when the subtracted trace exceeded the 95% confidence band for the average control trace for more than 25 ms continuously. The onset latency of a response was identified as the time when the subtracted trace began to deviate from the zero level. We selected the onset latency from within the confidence interval band because an active muscle will have a larger 95% confidence interval band and hence greater variability (Misiaszek 2003). The response amplitude was measured from each individual subtracted trace and calculated as the mean amplitude over the 100 ms window (see figure.2).

The background EMG was calculated for the first 50 ms before the initial displacement was given at the touch plate. The background activity was normalized (% Max EMG) and calculated for all trials, but analyzed only for those trials in which participants generated a response. For analysis of bilateral foot data, the step cycle, stance and swing durations for each participant were measured. The steps in which touch plate displacement was given were collected as perturbed steps, and the steps immediately preceding the perturbed steps were collected as control steps for each trial in all participants. The stance duration was calculated from heel strike of one foot till the same foot leaves the ground. The swing duration was calculated from the time foot leaves the ground, until it contacts the ground again. The step cycle duration was calculated from heel strike of one foot to the heel strike of the same foot again. The vertical touch force was monitored throughout the experiment for each participant and maintained below 1 N. The vertical touch force was measured for each trial, for each participant. The sample data from one participant showing the first trial response is shown in Figure 2. In this figure, A) shows the full unsubtracted traces, and B) an individual subtracted trace showing a TA response, and C) shows the right foot data.

A post-experiment questionnaire was provided to 15 participants to record their subjective feeling, immediately after the 10th trial was over. The questionnaire consisted of a series of questions evaluating if participants became aware of the touch displacement, or if some other disturbance (e.g. a change in treadmill speed) had occurred. It also asked participants to estimate the number of any such disturbances experienced. This questionnaire has not been tested for validity or reliability.

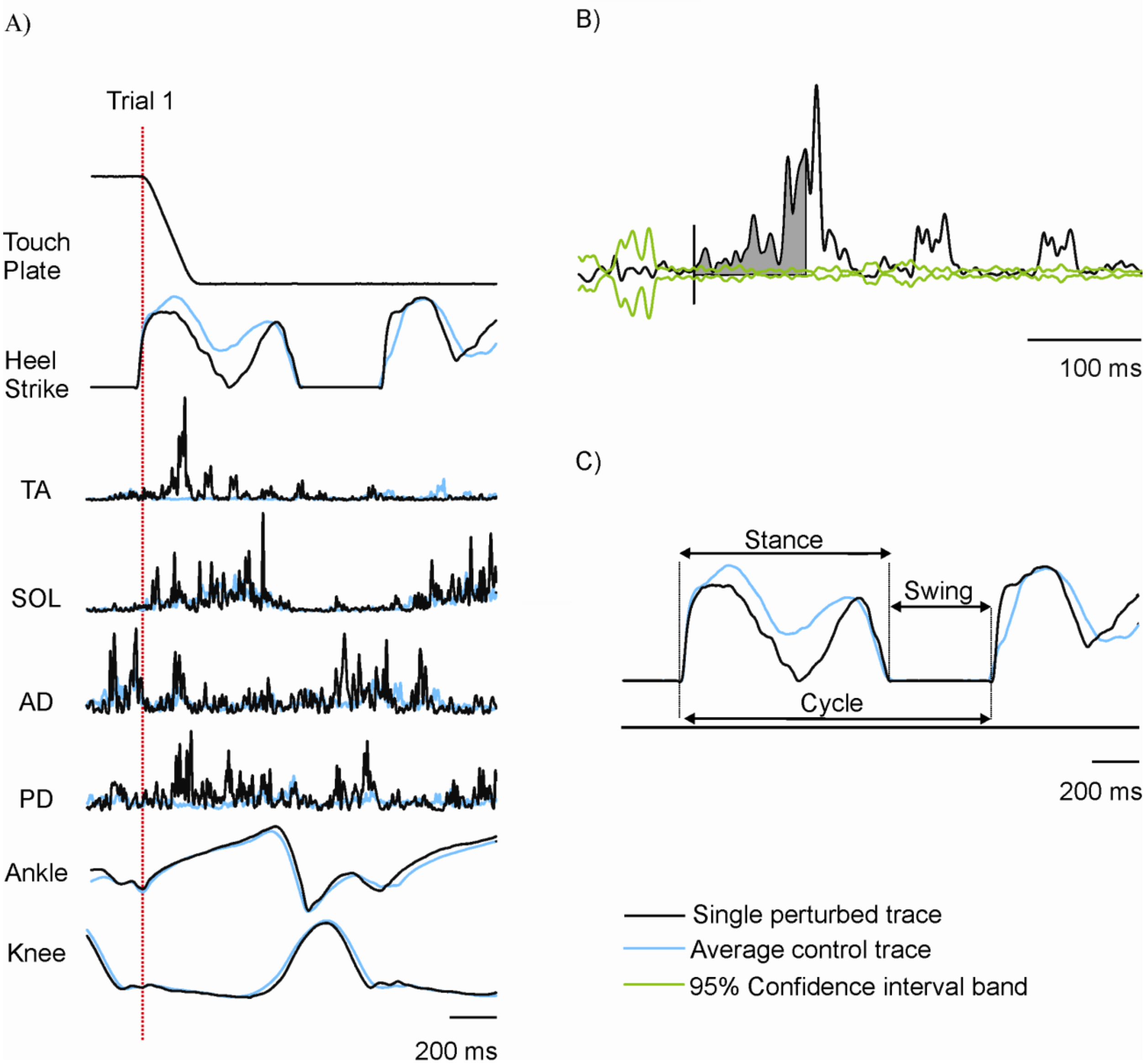


Figure 2: Sample data from one participant when forward displacement was given at the touch plate and resulted in early activation of TA on the first trial generating a corrective reaction. The vertical dashed red line denotes the onset of the touch plate displacement that is targeted at the right heel strike. A) First trial response displaying complete data traces (unsubtracted), B) Subtracted trace of TA showing the first trial response, C) Right foot sensor data.

Statistics

The frequency of responses expressed across subjects following the first trial during walking was compared to the first trial frequency during standing using a Fisher's exact test. In addition, the trial 2-10 frequency response was also compared between walking and standing. The data reported in Misiaszek et al. (2016) was used as a reference for the standing data. Paired t-tests were used to compare the onset latency and amplitude of evoked responses for the first response to that of the last response. Paired t-tests were also used to compare the background EMG and touch force for the first response to that of the last response. The time when the muscle showed a response for the first time is considered a "first response", and when the same muscle showed a response for the last time is considered a "last response". Stance, swing and step cycle duration parameters were compared using one-way repeated measures analysis of variance (ANOVA). In each of these parameters, a comparison between average control steps, trial 1 and trial 10 steps were analyzed using a one-way repeated measures analysis of variance (ANOVA). If ANOVA showed a significant difference between the above mentioned comparisons, a bonferroni post-hoc comparison test was conducted to identify which factor was different from another. All comparisons were performed using a statistical significance level of 0.05.

CHAPTER 4

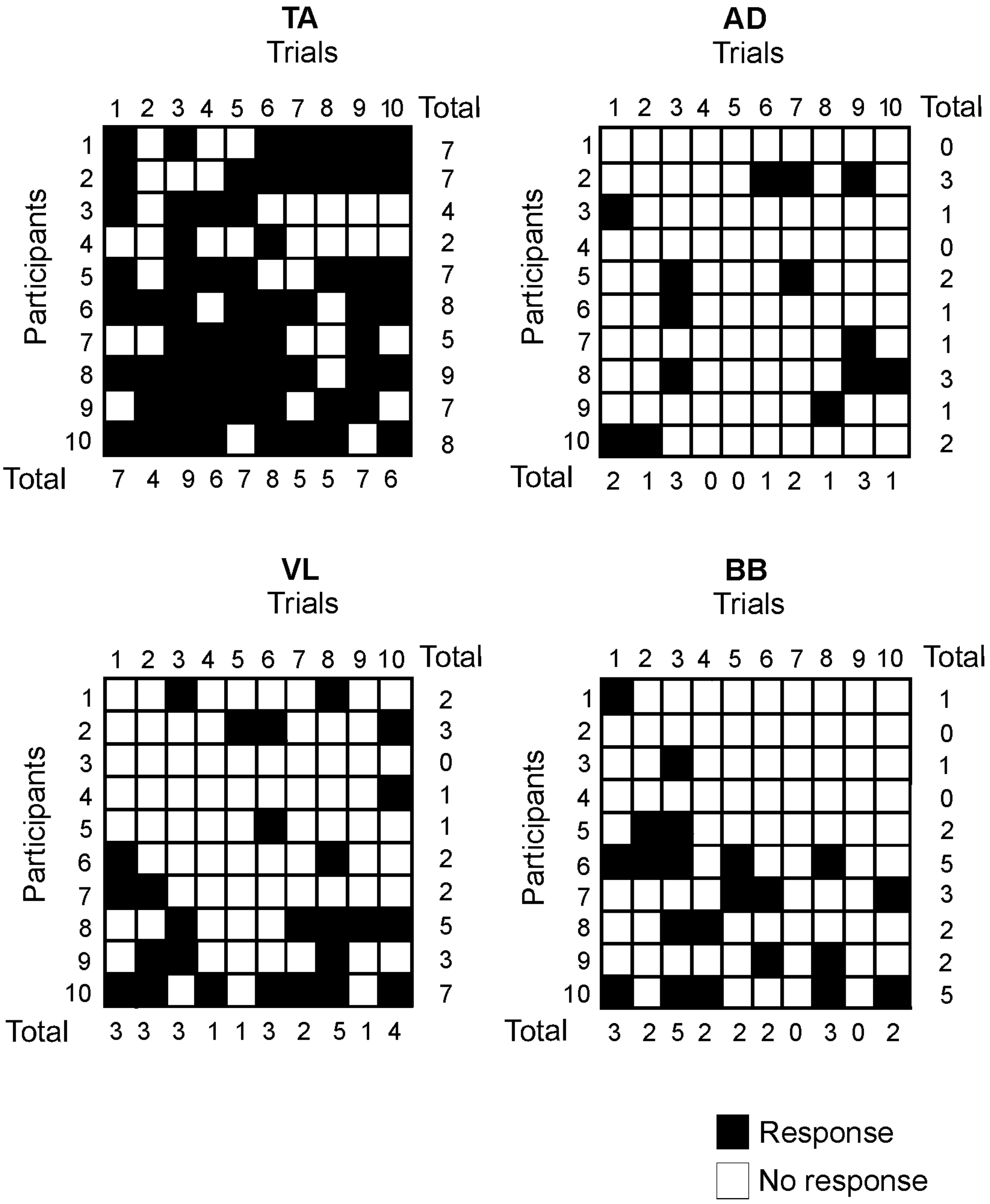
RESULTS

Unexpected displacement of a touch plate evoked short-latency responses (<200 ms) in all 20 participants. All participants that received forward touch displacements reacted with activation of TA, expressed in 64/100 total trials. Similarly, backward displacements of the touch plate evoked responses in SOL in all participants, with responses expressed in 64/100 trials. It was rare to observe responses in SOL following forward displacements, or responses in TA following backward displacements. Responses in other leg muscles (VL and BF) were rare with fewer than 30 responses observed. Responses in the arm muscles were also observed, but were generally rare, with the exception of responses in PD following backward displacements where all participants produced responses in at least 2 trials and responses were expressed in 56/100 total trials. The occurrence of responses is depicted in Figure 3 for forward displacements and in Figure 4 for backward displacements. A summary of response frequencies for all muscles recorded is provided in Table 1. The remainder of the Results will focus on the description and comparison of responses evoked in TA to forward displacements, and SOL and PD to backward displacements given the rarity with which responses were observed in the other muscles recorded.

Response frequencies across trials

As shown in Figure 3, the first forward touch displacement evoked responses in TA in 7 out of 10 participants during treadmill walking. This is not significantly different (Fisher's Exact Test = 0.7) from the 12 out of 20 first trial responses observed in TA during standing (Misiaszek et al., 2016). In contrast, in trials 2-10 responses were evoked in TA for 59 out of 90 trials, which is significantly different (Fisher's Exact Test <0.001) from the 0 responses observed from 180 trials during standing. First trial responses in AD during treadmill walking occurred in 2 out of 10 participants, which is not significantly different (Fisher's Exact Test = 0.24) from the 10 out of 20 participants that responded to the first trial with AD during standing (Misiaszek et al., 2016). Responses in AD were rarely observed in trials 2-10 during treadmill walking with only 12 of 90 trials exhibiting a response. This is significantly less than (Fisher's Exact Test < 0.001) the 133 responses observed in 180 trials during standing.

Figure 4 depicts the occurrence of responses evoked following backward touch displacements. First trial responses were observed in SOL in 3 out of 10 participants during walking, which is not different from the 1 out of 5 responses observed during standing (Fisher's Exact Test = 1). Responses were evoked in 61 out of the 90 subsequent trials (trials 2-10) in SOL, with all participants responding in at least 4 of the remaining 9 trials which is significantly different from the 0 responses observed in 40 subsequent trials during standing (Fisher's Exact Test <0.001). Responses were observed in PD in 4 out of 10 participants during walking, which is not different from the 1 out of 5 participants that responded during standing (Fisher's Exact Test = 0.60). PD responded frequently in trials 2-10 with all 10 participants responding in at least 2 of the remaining 9 trials, for a total of 52 out of 90 trials. This was not different from the 26 responses observed in 40 subsequent trials during standing (Fisher's Exact Test = 0.56). [Trial 2-10 data were not reported for backward displacements during standing in Misiaszek et al. (2016), but were available via personal communication.]



TA

Trials

Participants	1	2	3	4	5	6	7	8	9	10	Total
1	■	□	■	□	□	■	■	■	■	■	7
2	■	□	□	□	■	■	■	■	■	■	7
3	■	□	■	■	■	□	□	□	□	□	4
4	□	□	■	□	□	■	□	□	□	□	2
5	■	□	■	■	■	□	□	■	■	■	7
6	■	■	■	□	■	■	■	□	■	■	8
7	□	□	■	■	■	■	□	□	■	□	5
8	■	■	■	■	■	■	■	□	■	■	9
9	□	■	■	■	■	■	□	■	■	□	7
10	■	■	■	■	□	■	■	■	□	■	8
Total	7	4	9	6	7	8	5	5	7	6	

AD

Trials

Participants	1	2	3	4	5	6	7	8	9	10	Total
1	□	□	□	□	□	□	□	□	□	□	0
2	□	□	□	□	□	■	■	□	■	□	3
3	■	□	□	□	□	□	□	□	□	□	1
4	□	□	□	□	□	□	□	□	□	□	0
5	□	□	■	□	□	□	■	□	□	□	2
6	□	□	■	□	□	□	□	□	□	□	1
7	□	□	□	□	□	□	□	□	■	□	1
8	□	□	■	□	□	□	□	□	■	■	3
9	□	□	□	□	□	□	□	■	□	□	1
10	■	■	□	□	□	□	□	□	□	□	2
Total	2	1	3	0	0	1	2	1	3	1	

VL

Trials

Participants	1	2	3	4	5	6	7	8	9	10	Total
1	□	□	■	□	□	□	□	■	□	□	2
2	□	□	□	□	■	■	□	□	□	■	3
3	□	□	□	□	□	□	□	□	□	□	0
4	□	□	□	□	□	□	□	□	□	■	1
5	□	□	□	□	□	■	□	□	□	□	1
6	■	□	□	□	□	□	□	■	□	□	2
7	■	■	□	□	□	□	□	□	□	□	2
8	□	□	■	□	□	□	■	■	■	■	5
9	□	■	■	□	□	□	□	■	□	□	3
10	■	■	□	■	□	■	■	■	□	■	7
Total	3	3	3	1	1	3	2	5	1	4	

BB

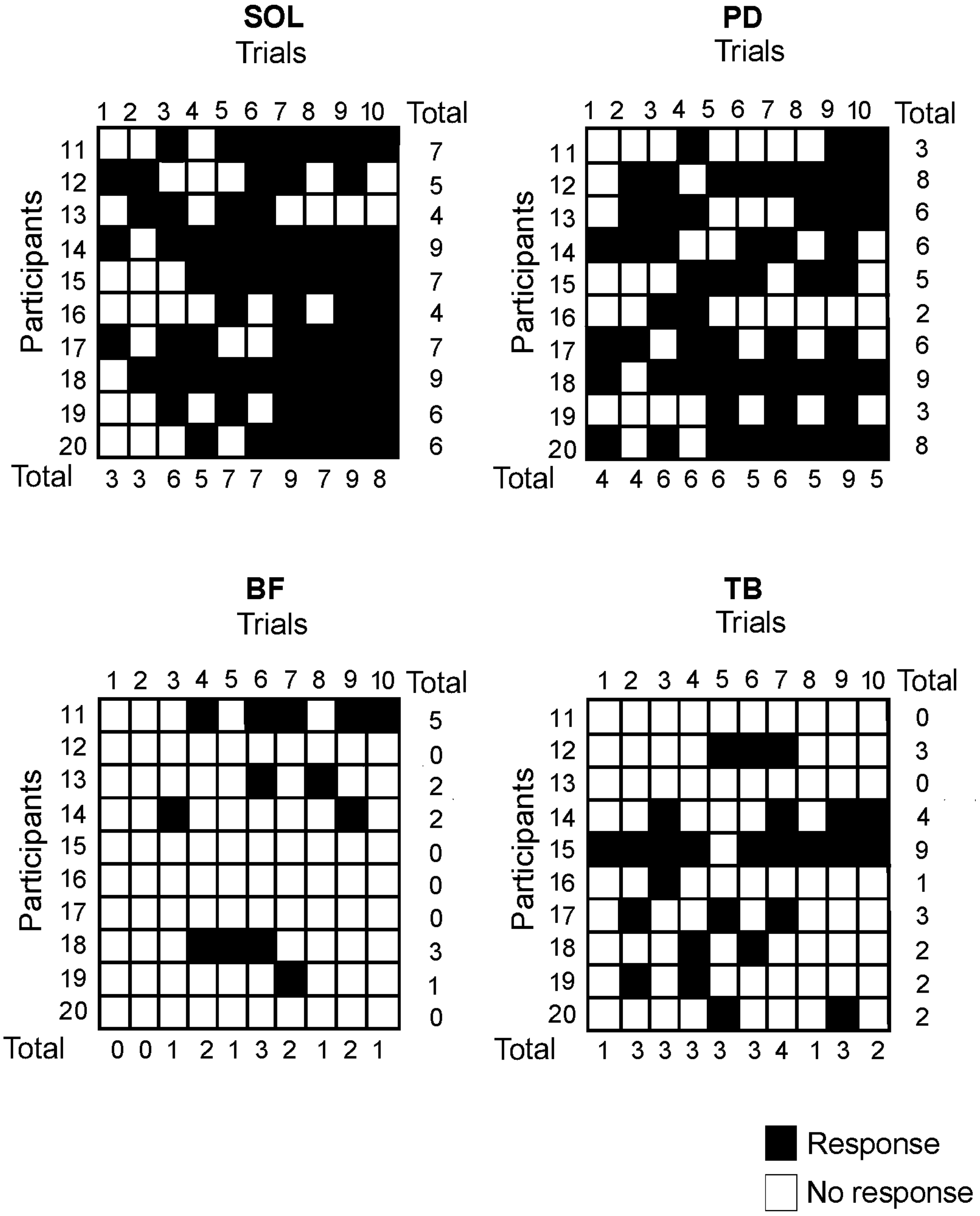
Trials

Participants	1	2	3	4	5	6	7	8	9	10	Total
1	■	□	□	□	□	□	□	□	□	□	1
2	□	□	□	□	□	□	□	□	□	□	0
3	□	□	■	□	□	□	□	□	□	□	1
4	□	□	□	□	□	□	□	□	□	□	0
5	□	■	■	□	□	□	□	□	□	□	2
6	■	■	■	□	■	□	□	■	□	□	5
7	□	□	□	□	■	■	□	□	□	■	3
8	□	□	■	■	□	□	□	□	□	□	2
9	□	□	□	□	□	■	□	■	□	□	2
10	■	□	■	■	□	□	□	■	□	■	5
Total	3	2	5	2	2	2	0	3	0	2	

■ Response

□ No response

Figure 3: Grid indicating the presence of detectable EMG responses in TA, VL, AD, and BB following forward touch plate displacements across all participants (rows) and trials (columns). The darkened cells indicate trials for which a response was present.



SOL

Trials

Participants	1	2	3	4	5	6	7	8	9	10	Total
11	□	□	■	□	■	■	■	■	■	■	7
12	■	■	□	□	□	■	■	□	■	□	5
13	□	■	■	□	■	■	□	□	□	□	4
14	■	□	■	■	■	■	■	■	■	■	9
15	□	□	□	■	■	■	■	■	■	■	7
16	□	□	□	□	■	□	■	□	■	■	4
17	■	□	■	■	□	□	■	■	■	■	7
18	□	■	■	■	■	■	■	■	■	■	9
19	□	□	■	□	■	□	■	■	■	■	6
20	□	□	□	■	□	■	■	■	■	■	6
Total	3	3	6	5	7	7	9	7	9	8	

PD

Trials

Participants	1	2	3	4	5	6	7	8	9	10	Total
11	□	□	□	■	□	□	□	□	■	■	3
12	□	■	■	□	■	■	■	■	■	■	8
13	□	■	■	■	□	□	□	■	■	■	6
14	■	■	■	□	□	■	■	□	■	□	6
15	□	□	□	■	■	■	□	■	■	□	5
16	□	□	■	■	□	□	□	□	□	□	2
17	■	■	□	■	■	□	■	□	■	□	6
18	■	□	■	■	■	■	■	■	■	■	9
19	□	□	□	□	■	□	■	□	■	□	3
20	■	□	■	□	■	■	■	■	■	■	8
Total	4	4	6	6	6	5	6	5	9	5	

BF

Trials

Participants	1	2	3	4	5	6	7	8	9	10	Total
11	□	□	□	■	□	■	■	□	■	■	5
12	□	□	□	□	□	□	□	□	□	□	0
13	□	□	□	□	□	■	□	■	□	□	2
14	□	□	■	□	□	□	□	□	■	□	2
15	□	□	□	□	□	□	□	□	□	□	0
16	□	□	□	□	□	□	□	□	□	□	0
17	□	□	□	□	□	□	□	□	□	□	0
18	□	□	□	■	■	■	□	□	□	□	3
19	□	□	□	□	□	□	■	□	□	□	1
20	□	□	□	□	□	□	□	□	□	□	0
Total	0	0	1	2	1	3	2	1	2	1	

TB

Trials

Participants	1	2	3	4	5	6	7	8	9	10	Total
11	□	□	□	□	□	□	□	□	□	□	0
12	□	□	□	□	■	■	■	□	□	□	3
13	□	□	□	□	□	□	□	□	□	□	0
14	□	□	■	□	□	□	■	□	■	■	4
15	■	■	■	■	□	■	■	■	■	■	9
16	□	□	■	□	□	□	□	□	□	□	1
17	□	■	□	□	■	□	■	□	□	□	3
18	□	□	□	■	□	■	□	□	□	□	2
19	□	■	□	■	□	□	□	□	□	□	2
20	□	□	□	□	■	□	□	□	■	□	2
Total	1	3	3	3	3	3	4	1	3	2	

■ Response
□ No response

Figure 4: Grid indicating the presence of detectable EMG responses in SOL, BF, PD, and TB following backward touch plate displacements across all participants (rows) and trials (columns). The darkened cells indicate trials for which a response was present.

EMG response characteristics

Figure 5 depicts TA responses evoked following forward touch displacements for one participant. This participant responded with the first trial and in 6 of the subsequent 9 trials. The onset latency of the responses in this participant varied between 99.50 ms and 179.25ms, however there did not appear to be a progressive or systematic change in either the onset latency or appearance of the responses with repeated exposures. The average onset latency across all 64 trials for which a response in TA was evoked was 142.57 (±36.63) ms, with onset latencies ranging between 67 ms and 197.75 ms. The average latency of the first response observed in a participant was 132.67 (±39.38) ms, which was not significantly different from the average last response latency of 135.15 (±43.75) ms (paired $t_{(9)}$ = 0.14, p=0.88; Figure 6A). Response amplitudes did not systematically vary across trials with an average amplitude of the first response observed in a participant of 42.0 (±25.13) %MVC, compared with an average amplitude of the last response observed of 34.4 (±29.75) %MVC (paired $t_{(8)}$=0.57, p=0.59, Figure 7A).

The average response latency in SOL across all 64 responses to backward touch displacements was 123.7 (±34.13) ms, with onset latencies ranging between 52.25 ms and 194.75 ms. The average latency of the first response observed in a participant was 125.7 (±46.66) ms, which was not significantly different from the average last response latency of 128.4 (±40.62) ms (paired $t_{(9)}$=0.23, p=0.82; Figure 6B). The average amplitude of the first response was 55.1 (±37.83) %MVC, which was not significantly different from the average amplitude of the last response of 39.0 (±35.26) %MVC (paired $t_{(9)}$=1.58, p=0.15, Figure 7B). The average response latency in PD across all 54 responses to backward touch displacements was 120.2 (±38.79) ms, with onset latencies ranging between 49.25 ms and 193.25 ms. The average latency of the first response observed in a participant was 110.7 (±44.80) ms, which was not significantly different from the average last response latency of 120.5 (±45.67) ms (paired $t_{(9)}$=0.53, p=0.60; Figure 6B). The average amplitude of the first response was 8.7 (±13.14) %MVC, which was not significantly different from the average amplitude of the last response of 14.2 (±25.90) %MVC (paired $t_{(9)}$=1.33, p=0.22).

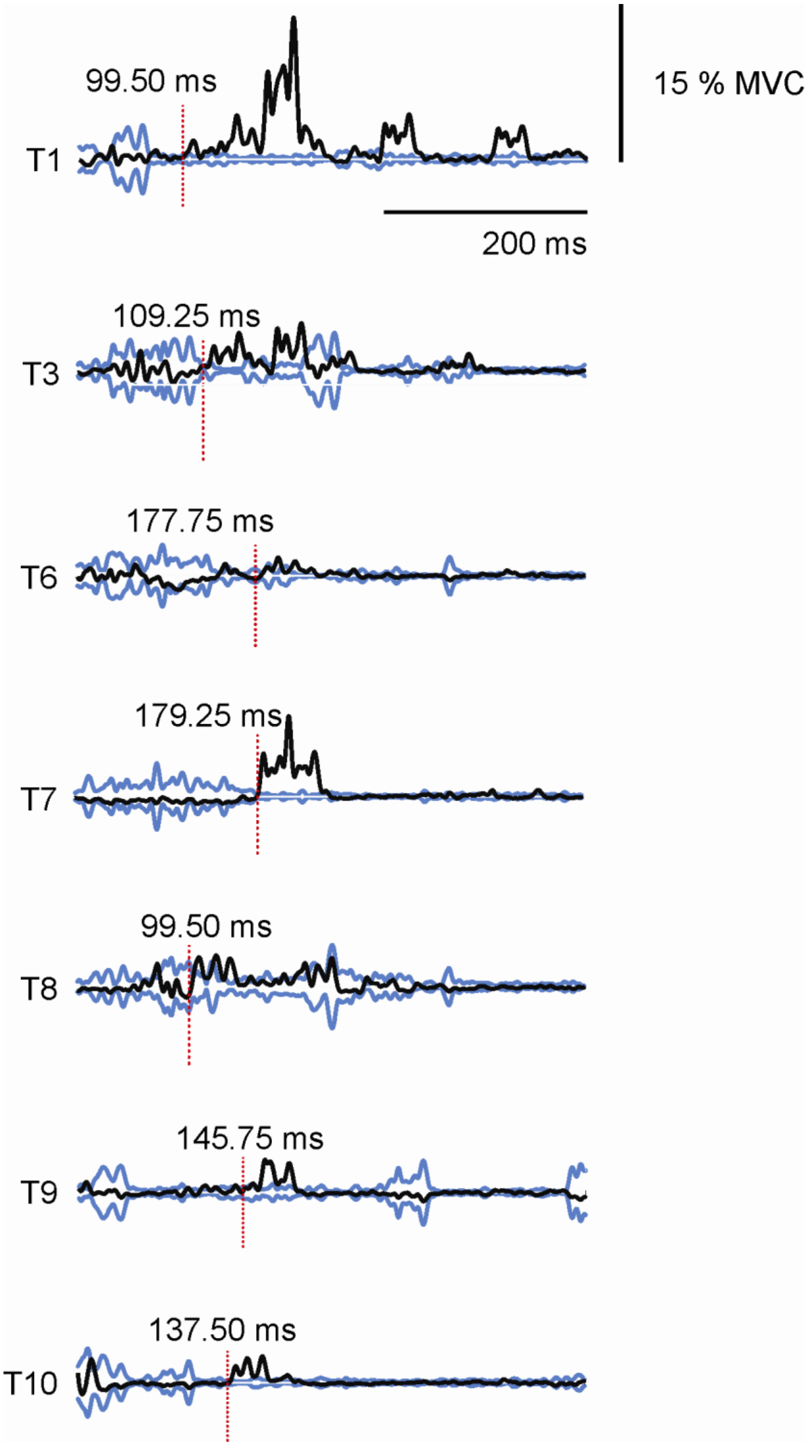


Figure 5: Sample data from one participant showing TA response in repeated exposures to forward displacement of the touch plate. The vertical red line indicates the onset latency of the response in TA. The black line represents the subtracted trace for the trials that showed a significant response to the forward touch plate displacements, and the blue line represents the 95% confidence interval band.

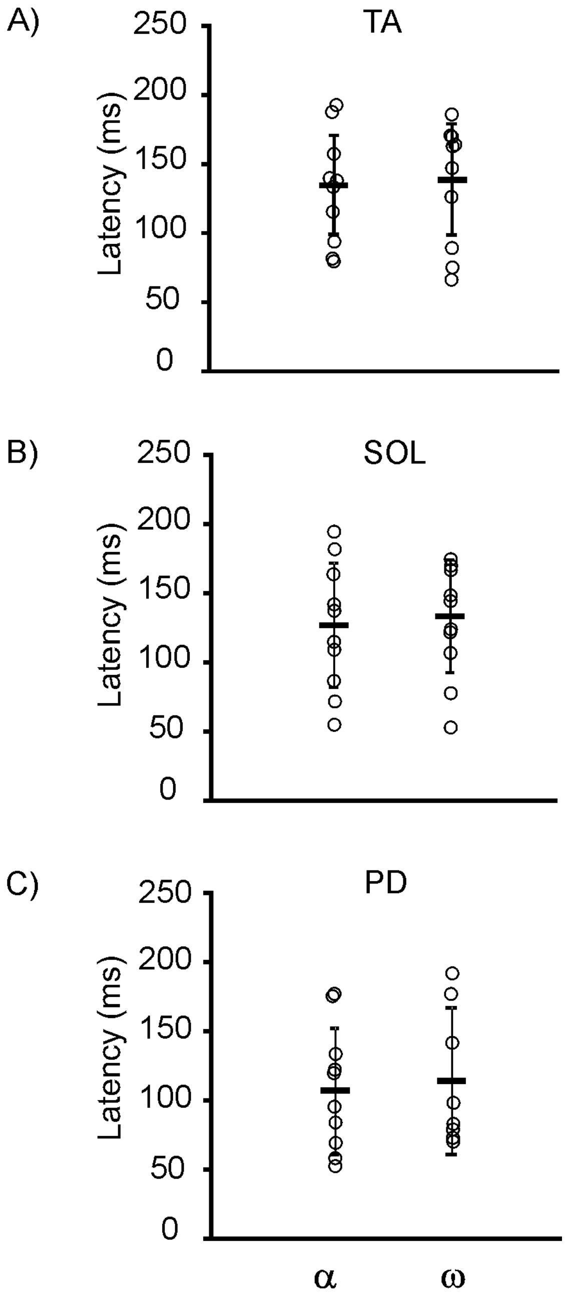


Figure 6: Response onset latencies for the first (α) and the last (ω) demonstrated responses following touch plate displacement. A) Responses in TA following forward touch plate displacement. B) Responses in SOL following backward touch plate displacement. C) Responses in PD following backward touch plate displacement. The thick horizontal bars represent the mean with standard deviations.

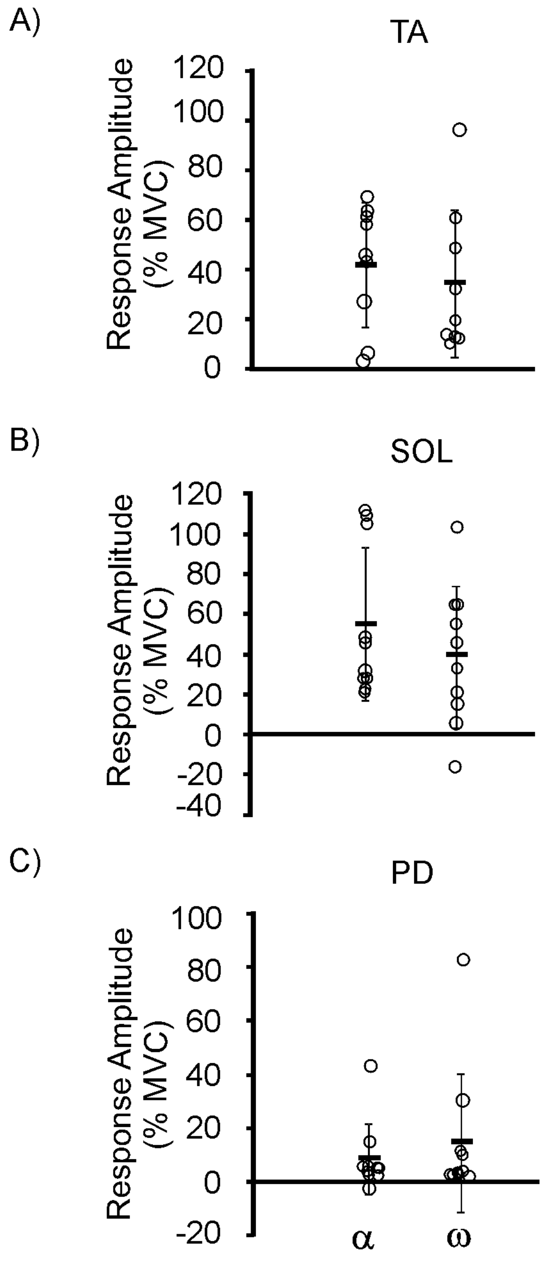


Figure 7 : Response EMG amplitudes (% MVC) for the first (α) and the last (ω) demonstrated responses following touch plate displacement. A) Responses in TA following forward touch plate displacement. B) Responses in SOL following backward touch plate displacement. C) Responses in PD following backward touch plate displacement. The thick horizontal bars represent the mean with standard deviations.

Effects on the step cycle

Unexpected displacement of the light touch reference produced subtle changes in the ongoing stepping pattern of the participants. Figure 2A depicts the force sensitive resistor traces, along with ankle and knee goniometer traces, for 1 trial from 1 participant. This example data suggests that any behavioral effects of the touch displacement are quite small. Indeed, none of the participants lost their balance, stumbled or produced any other overt behavior that would suggest the touch displacement presented a significant challenge to their continued walking. Nevertheless, displacement of the touch reference did result in significant changes to the stepping patterns.

Figure 8 depicts average step cycle, stance and swing durations across participants that received forward touch displacements. One-way repeated measures ANOVAs comparing control, trial 1 and trial 10 steps revealed main effect of trial on the duration of all three measures for the right leg (step cycle: $F_{(2,18)}=10.49$, $p<0.001$; stance: $F_{(2,18)}=8.49$, $p<0.01$; swing: $F_{(2,18)}=9.78$. $p<0.01$). Bonferroni post-hoc comparisons identified that the step cycle duration following the first touch displacement (1103.0 ± 120.17 ms) was significantly ($t_{(9)}=4.04$, $p<0.01$) shorter than the control steps (1169.1 ± 112.52 ms). Following the 10th touch displacement the step cycle duration was 1169.9 (± 127.20) ms, which was not different from the control steps ($t_{(9)}=0.06$, $p=0.95$). Stance durations following the first trial (677.4 ± 87.76 ms) were shorter, but not significantly ($t_{(9)}=1.19$, $p=0.26$) different from control (690.4 ± 78.78ms). In contrast, the stance durations following trial 10 were 720.6 (± 89.71) ms, significantly longer than the control stance durations ($t_{(9)}=2.99$, $p=0.015$). First trial swing durations (425.6 ± 49.78 ms) were significantly reduced ($t_{(9)}=3.78$, $p<0.01$) compared to control (478.6 ± 70.44 ms). The trial 10 swing duration (449.3 ± 49.40 ms) was shorter than control, but not significantly at the adjusted alpha of 0.017 ($t_{(9)}$=2.58, p=0.03). No main effects of trial on the step cycle, stance or swing durations of the left leg (Figure 7B) were identified (step cycle: $F_{(2,18)}$=0.18, p=0.84; stance: $F_{(2,18)}$=0.73, p=0.50; swing: $F_{(2,18)}$=0.22, p=0.81). Backward touch displacements did not result in any differences in the step parameters of either the right (step cycle: $F_{(2,18)}$=1.67, p=0.21; stance: $F_{(2,18)}$=2.35, p=0.12; swing: $F_{(2,18)}$=0.15, p=0.86) or left leg (step cycle: $F_{(2,18)}$=0.87, p=0.43; stance: $F_{(2,18)}$=1.95, p=0.17; swing: $F_{(2,18)}$=0.33, p=0.71).

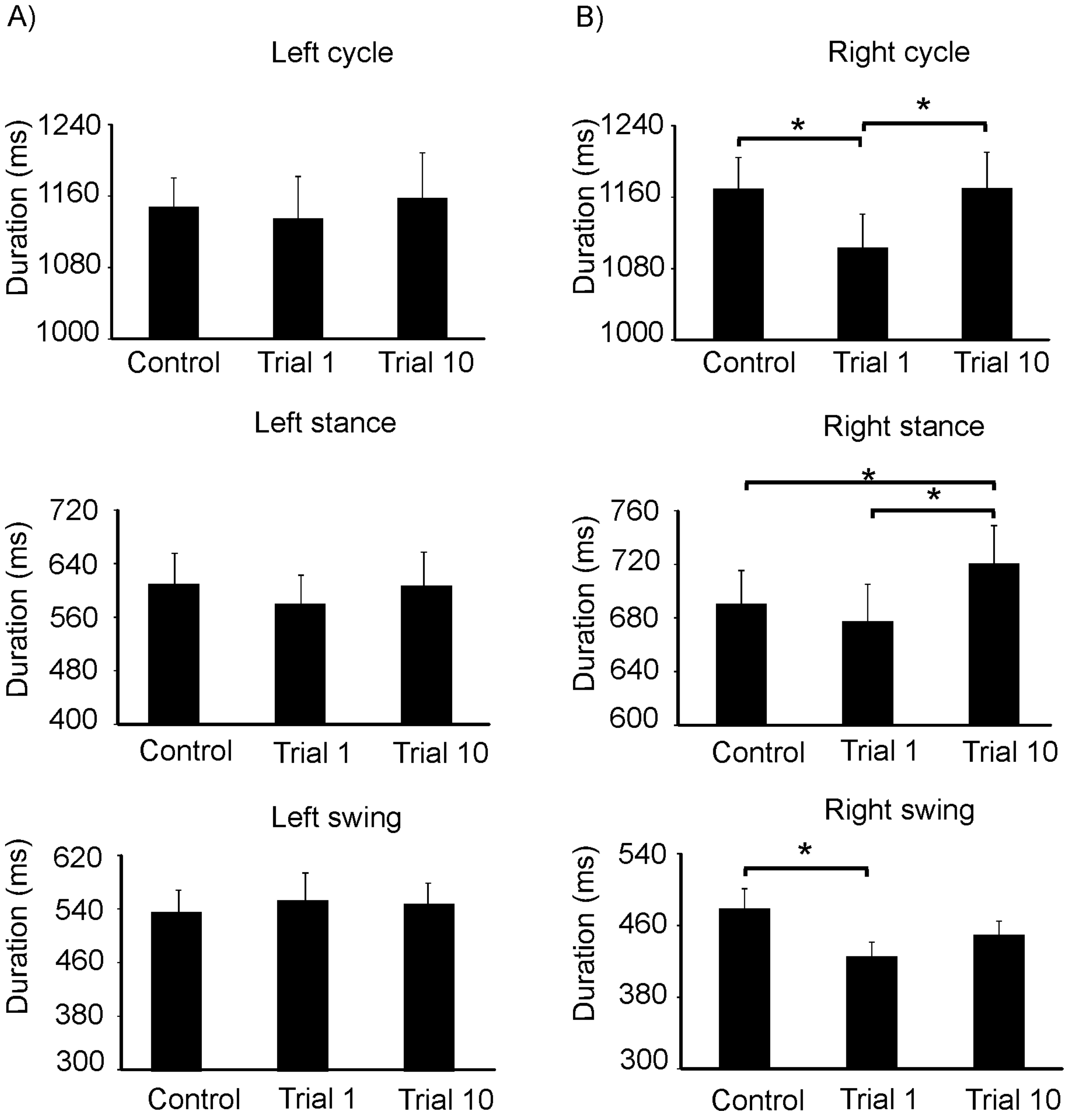


Figure 8: Average duration of the step cycle, stance phase and swing phase following forward touch plate displacements applied at right heel-strike: A) Left foot step cycle data, beginning from left toe-off, and B) right foot step cycle data, beginning at right heel-strike for control, trial 1 and trial 10 steps. Error bars represent the standard deviations. The asterisks indicate significant differences identified by post hoc Bonferroni adjusted paired t-tests (p<0.05).

Background EMG and touch force

Forward touch displacements did not result in systematic changes in the background EMG of any muscle recorded. Background activity in TA tended to be larger in trial 10 (24.3 ± 13.78 %MVC) than in trial 1 (18.6 ± 5.01 %MVC), but this was not significantly different ($t_{(8)}$=1.53, p=0.17). Similarly, backward touch displacements did not result in systematic changes in the background EMG of any muscle recorded. Background activity in SOL tended to be smaller in trial 10 (15.4 ± 12.89 %MVC) than in trial 1 (20.5 ± 12.52 %MVC), but the difference was not significant ($t_{(9)}$=1.02, p=0.34). The vertical touch force applied by participants that received forward touch displacements was stable throughout the testing. The first trial touch force (0.76 ± 0.49 N) and the trial 10 touch force (0.75 ± 0.31 N) were not different ($t_{(9)}$=0.14, p=0.89). The touch force applied by participants that received backward touch displacements tended to decrease with repeated touch displacements [trial 1: 0.67 ± 0.31 N; trial 10: 0.56 ± 0.32 N], however this difference did not reach significance ($t_{(9)}$=1.70, p=0.12).

Table 1: The mean background EMG (% MVC) for all the recorded muscles (TA, SOL, VL, BF, AD, PD, BB, TB), compared between the first trial and the tenth trial in both displacement directions.

	Mean ± SD			
Muscles	Trial 1	Trial 10	t-value	p-value
Forward displacement				
TA	18.59 ± 05.00	24.32 ± 13.78	1.52	0.16
SOL	10.81 ± 10.71	09.29 ± 06.92	0.58	0.57
VL	17.49 ± 12.13	22.92 ± 22.00	1.02	0.33
BF	16.62 ± 14.12	18.66 ± 12.05	0.69	0.50
AD	06.02 ± 05.03	05.69 ± 05.86	0.13	0.89
PD	08.64 ± 08.34	07.63 ± 04.84	0.34	0.74
BB	05.62 ± 03.85	04.55 ± 03.76	1.37	0.20
TB	14.36 ± 24.11	14.90 ± 24.14	0.32	0.75
Backward displacement				
TA	21.38 ± 13.79	22.18 ± 12.00	0.12	0.90
SOL	20.45 ± 12.51	15.42 ± 12.89	1.01	0.33
VL	19.15 ± 14.56	16.20 ± 15.92	0.51	0.62
BF	15.96 ± 10.37	12.99 ± 8.95	1.63	0.13
AD	10.03 ± 12.97	04.55 ± 03.76	1.37	0.20
PD	14.36 ± 24.11	12.20 ± 17.66	0.68	0.50
BB	06.08 ± 04.25	04.57 ± 03.08	1.36	0.20
TB	05.08 ± 02.60	03.42 ± 01.39	1.80	0.10

SD = Standard deviation

Psychophysical outcomes

Fifteen participants (7 that received forwards touch displacements) completed the post-experiment questionnaire (appendix A4). Question 1 asked participants if they became aware that disturbances were being applied during the testing trial. Questions 2 to 4 asked participants to detail characteristics of any perturbations they experienced, including to estimate the number and source of any disturbances. The salient data are summarized in Table 2. Of the 15 participants that responded to the questionnaire, all but 1 reported detecting the presence of perturbations. Of the 14 that indicated they detected perturbations, 9 underestimated the total number of disturbances applied, 3 indicated the correct number, and 2 overestimated the number of perturbations. A total of 12 participants reported detecting the touch plate move, however only 5 of the participants identified the disturbances as being isolated to the touch plate. Nine participants indicated they felt that the treadmill belt speed had been disturbed, including 2 participants that identified the disturbances as being isolated to the treadmill speed. Three participants reported being pushed or pulled during the testing. Seven participants reported a combination of disturbance sources. Participants that reported multiple sources of stimuli indicated that the touch plate disturbances occurred later in the trial. From these data it is apparent that the displacement of the touch plate was often misattributed to a gait disturbance or not perceived against the regular oscillation of the finger against the touch plate during walking. Table 3 presents a sample of the written comments provided in response to Question 1 of the questionnaire which highlight the perception of the disturbances as experienced by the participants.

Table 2: The summary of psychophysical data obtained from the post-experiment questionnaire responses, indicating the number of times participants experienced perception of; change in treadmill speed, push/pull at the waist, or rapid touch plate movement.

Participants		Perception	
	Treadmill	Push/Pull	Touch plate
Forward Displacement			
4	0	0	**4**
5	**6**	**4**	**4**
6	0	0	**10**
7	0	0	0
8	**4**	**3**	**3**
9	**8**	0	**8**
10	**4**	**2**	**1**
Backward displacement			
13	**7**	0	**4**
14	**3**	0	0
15	0	0	**10**
16	**4**	0	**5**
17	0	0	**7**
18	0	0	**9**
19	**1**	0	**1**
20	**5**	0	0

Table 3: The detailed explanation of the psychophysical responses, as identified by the participants in response to the last trial of the experiment.

During the last trial we added one or more disturbances to test your balance. Did you become aware of the disturbance(s)?

Yes No

If yes, when did you become aware of what was happening? How did you figure it out?

Participant	Responses made by the participants	Frequency
5	It felt like a quick stop or start (of the treadmill)	6 Treadmill, 4 Pushes, 4 Touch plate
6	I felt it (the touch plate) move beneath my finger and my finger slipped off	10 Touch plate
8	I felt jolted several times and at one point Tania had to reposition my finger	4 Treadmill, 3 Pushes, 3 Touch plate
9	The tip I was touching gave a jerk and it seemed to change the speed (of the treadmill)	8 Treadmill, 8 Touch plate-same event
13	I felt bumps with my legs and through hands that was touching the plate	7 Treadmill, 4 Touch plate
14	I would feel that the speed would change	3 Treadmill
15	I lost balance and started walking funny. I sensed since the first disturbance and trying to compensate but it was difficult	10 Touch plate
16	I felt like there were pulses from the treadmill belt or the bar that I was touching with my finger	4 Treadmill, 5 Touch plate
17	I felt the tip where I the finger was moved back and forward and Vibrates sometimes.	7 Touch plate
18	I felt the metal plate to bounce back once in a while	10 Touch plate
20	I figured it out when small breaks (brakes) were applied to ongoing treadmill	5 Treadmill

CHAPTER 5

DISCUSSION AND CONCLUSION

The aim of this study was to determine whether unexpected displacement of a light touch reference would evoke short-latency (<200 ms) responses in the ankle muscles during treadmill walking in the absence of vision. It was further hypothesized that the challenge of walking on a treadmill without visual feedback would increase the importance of the light touch cues as a spatial reference, which would result in these responses being expressed more frequently than what was observed previously during standing. This second hypothesis is only partially supported. The number of participants that responded to the first unexpected displacement of the touch plate during walking was comparable to that observed during standing (Misiaszek et al., 2016). However, the persistent expression of responses on subsequent exposures to the touch plate displacement during treadmill walking was dramatically different from standing wherein responses were only ever observed in the ankle muscles with the first trial (Misiaszek et al., 2016).

First trial responses

Unexpected displacement of a light touch reference evokes postural responses in the ankle muscles of participants standing on a firm surface in approximately 60% of forward touch displacements, and 20% of backward touch displacements (Misiaszek et al., 2016). It was hypothesized that increasing the relevance of the touch reference, in this case by asking participants to walk on a treadmill without visual feedback, would increase the occurrence of responses in the first trial as it was previously demonstrated that light touch provides an essential spatial reference in the absence of vision (Dickstein & Laufer, 2004). However, this did not occur as responses were only evoked in 70% and 30% of first trials for forward and backward touch displacements, respectively. Similarly, it was recently shown that increasing the challenge to standing balance did not affect the frequency with which first trial responses were observed following touch displacement (Misiaszek & Vander Meulen, 2017). In that study, participants stood on foam without visual feedback. Provision of light touch stabilized their sway to match the eyes open condition, indicating that the light touch mimicked the spatial feedback provided by vision. Nevertheless, only 60% of participants responded to the first forward displacement of the touch reference with activation of TA. Together, these results suggest that the incorporation of tactile feedback for the control of stability may depend in part on the individual differences in the interpretation of the feedback. That is, if participants believe the touch reference is stable then presumably displacement of the touch plate is interpreted as displacement of the body relative to the touch plate and a postural response is generated. In contrast, some participants might anticipate that the touch plate could move and interpret the detected slip at the finger for what it is and respond with a different strategy, or not at all.

The first trial responses that were observed in this study are likely postural responses associated with a perceived balance disturbance. During standing, whether on a firm (Misiaszek et al., 2016) or foam (Misiaszek & Vander Meulen, 2017) surface, the first trial responses in TA or SOL typically generate an anterior-posterior sway observed in the center of pressure. In the present study, forward touch displacements at right heel-strike resulted in a significant reduction in the right step cycle duration, suggesting that the evoked response was functionally related to stabilizing gait. The first trial backward touch displacements did not generate a similar adaptation to the step cycle, perhaps because only 3 participants responded to the backward touch displacement with a response in SOL. The most compelling evidence suggesting that the touch plate displacements were perceived as balance disturbances is the frequency with which participants reported believing the treadmill belt had changed speeds, or that the participant had received a pull at the waist. Although it is clear that the reported perceptions of the participants (Table 2) do not directly match the occurrence of responses in TA and SOL (Figure 3 and 4), the misinterpretation of the sensation from the fingertip indicates that in some participants the touch reference is expected to be stable. It is therefore reasonable to suggest that the sensorimotor set (Prochazka, 1989), or motor system bias, would also be influenced by this expectation and the slip detected at the fingertip would trigger a correction to a presumptive “fall”, or misstep.

Are the first trial responses observed here startle responses? In daily life the first exposure to a balance threat is often the only exposure that an individual will experience. Despite this, the postural reaction generated must be sufficient to prevent a fall, or at least minimize the consequences of an impending fall. Due to the unexpected nature of balance disturbances they are often startling experiences, resulting in exaggerated responses (Allum, Tang, Carpenter, Nijhuis & Bloem, 2011). It was recently argued that postural reactions do indeed include a startle component (Campbell, Squair, Chua, Inglis & Carpenter 2013). However, a common feature of first trial postural responses is habituation of the responses with repeated exposure to identical disturbances (Siegmund, Blouin & Inglis, 2008; Allum et al., 2011; Campbell et al., 2013). Moreover, startle typically evokes responses in SCM, including when the startle is induced by a balance disturbance (Oude Nijhuis, Allum, Valls-sole, Overeem & Bloem, 2010; Campbell et al., 2013). The responses in the present study did not include responses in SCM and did not tend to habituate with repeated exposure to the touch plate displacement, suggesting that responses observed in this study unlikely to be accounted for by startle alone. Furthermore, the startle component to first trial responses is argued to amplify an underlying postural response (Campbell et al., 2013). The postural responses observed in this study were initiated by the displacement of the touch plate, regardless of whether a startle component was present or not.

Trials 2-10

The most striking outcome of this study was the persistent expression of responses in the ankle muscles with repeated exposure to the touch plate displacements. This is in direct contrast to the absence of any responses observed by Misiaszek et al. (2016) when standing on a firm surface. During standing, the evoked responses had onset latencies of about 100 ms (Misiaszek et al., 2016). The responses observed here during walking were typically slower, with onset latencies of about 130 ms. Therefore, it is possible the responses evoked during walking represent different motor responses and the continued expression observed here is unrelated to increasing the balance threat by walking on a treadmill with eyes closed. However, Misiaszek & Vander Meulen (2017) recently demonstrated comparable continued expression of ankle muscle responses to touch plate displacements when standing on an unstable foam surface, suggesting that increase threat to balance contributes to a more persistent expression of ankle muscle responses. The longer latency responses observed presently during walking might be a consequence of the increase variability introduced into both the stimulus signal and analysis methods by walking. That is, the finger lightly touching the touch plate will tend to oscillate on the surface as the body rhythmically oscillates on the treadmill. The onset of the touch plate disturbance would then potentially be masked in part by this background level of activity (or noise) in the touch receptors. Furthermore, the methods used to identify a response in the EMG traces utilize a 95% confidence constructed from the control steps preceding the perturbation.

The variability around these control steps will be larger than would occur during standing because of the higher activity during walking. This makes it less likely that the single trace analyzed here will exceed the 95% confidence band until the signal is sufficiently large to overcome the inherently larger band adding an element of Type II error to the analyzed approach and contributing to an apparent delay in onset latency. Therefore, the delay in the responses during walking is not likely reflective of differences in the mediating neural pathways, but in technical aspects of the execution of the study.

Another important difference between the responses observed on subsequent trials during walking and those during standing is the lack of the emergence of an obvious "arm-tracking" behavior in the present study. During standing, whether on a firm surface (Misiaszek et al., 2016) or unstable foam surface (Misiaszek & Vander Meulen, 2017), subsequent exposures of the touch plate displacement result in the extinction of a postural sway response and the appearance of a distinct "arm-tracking" response wherein, following forward displacements, AD is activated and the elbow is extended. This did not occur in the present study, in particular for forward touch displacements where AD was rarely activated. Although backward touch displacements generated frequent responses in PD with subsequent trials during walking, this was not accompanied by any observable elbow flexion behaviors. Therefore, the distinct "arm-tracking" behavior that emerged during standing did not occur during walking. This suggests that the responses observed with subsequent trials during walking continued to serve the same purpose as the responses to the first trial. However, this does not appear to be the case either as the step cycle was shorter following the first forward trial, as a result of a shorter swing phase, but not so for the tenth trial. On the contrary, the stance phase was prolonged following the tenth forward trial. Therefore, although responses in TA were more consistently expressed with repeated forward touch displacements during walking, it seems unlikely that the responses serve a consistent purpose with repeated trials. The functional relevance of the continued expression of the responses in the ankle muscles in trials 2-10 during treadmill walking is not easily delineated from the limited number of muscles recorded here and the minimal impact observed on the overall gait cycle. Nevertheless, it is apparent that the ankle muscles continued to be activated on subsequent trials and that these responses must be integrated within the ongoing task of treadmill locomotion.

Neural mechanisms

The displacement of the touch reference beneath the finger resulted in a slip of the touch plate relative to the finger. The displacement of the touch plate did not result in a demonstrable disturbance in the elbow goniometer trace, suggesting the touch plate disturbance did not result in a physical disturbance to the posture of the arm. Therefore, any responses to the displacement of the touch plate are unlikely to be related to muscle stretch reflexes or other proprioceptor-related feedback from the arm. Muscle receptors from the intrinsic muscles of the hands or wrist muscles cannot be ruled out (Marchand-Pauvert, Mazevet, Nielsen, Peterson & Pierrot-Deseilligny, 2000) as it is possible the shear forces at the finger provided a small tug at the finger, or the onset of touch plate movement initiated vibration. Nevertheless, tactile information from the fingertip is likely a strong candidate to detect the slip between the finger and the contact surface of the touch plate. Low-threshold mechanoreceptors of the skin are well suited for detecting slip with a contact surface. Srinivasan et al. (1990) demonstrated that slip stimuli at the finger pad specifically activate slowly adapting (SA) mechanoreceptors with a clear directional bias. Ruffini endings (SAII-type receptors) are known to be sensitive to skin stretch and have been argued to be important in the direction-specific detection of slip of grasped objects (Abraira & Ginty, 2013). Therefore, these receptors could also be important for signaling the direction-specific responses to the slip observed in this study. Other cutaneous receptors, including rapidly adapting type I mechanoreceptors (Meissner corpuscles) and Pacinian corpuscles are well-suited for detection of slip onset, but are less capable of coding the direction of slip (Srinivasan et al., 1990; Abraira & Ginty, 2013).

Electrical stimulation of the median nerve at the wrist will excite large diameter afferents, including those that serve the Merkel's, Ruffini endings, Meissner corpuscles and Pacinian corpuscles of the finger pad. Electrical stimulation of the median nerve leads to interlimb reflexes in the legs, indicating that the neural pathways necessary to link the cutaneous feedback from the fingertip with the ankle musculature are available (Delwaide & Crenna, 1984). Therefore, it is possible the activation of cutaneous mechanoreceptors at the fingertip can directly influence the activity of muscles at the ankles related to postural control. Zehr & Duysens (2004) argue that these interlimb connections might be particularly relevant in coordinating the actions of the arms and legs in response to unexpected disturbances, especially during rhythmic quadrupedal activities such as walking. This speculation was supported recently by the findings of Forero & Misiaszek (2015) who demonstrated that interlimb cutaneous reflexes in ankle muscles, arising from median nerve stimulation, were facilitated when fingertip touch was used to stabilize walking on a treadmill with eyes closed. As described earlier, the onset latencies of the responses are ambiguous as it is likely the 130 ms onset latency described following displacement of the touch plate overestimates the true onset latency. Nevertheless, the responses are sufficiently fast to suggest that spinal reflex circuitries could be involved. Median nerve interlimb reflexes have onset latencies typically ranging between 50 to 100 ms

(Kagamihara, Hayashi, Masakado & Kouno, 2003). Although longer loop neural circuitry, such as via the brainstem, cannot be specifically ruled out from contributing, these results combined suggest that activation of cutaneous mechanoreceptors with the slip of the touch plate beneath the finger initiate responses in interlimb cutaneous reflex pathways with direct activation of ankle muscles important for postural control during walking.

Functional considerations

It is well established that light touch influences standing balance. Sway is stabilized when lightly touching a stable reference (Holden et al., 1994; Jeka & Lackner, 1994), and becomes entrained to a contact surface that slowly oscillates (Jeka et al., 1998; Wing et al., 2011; Misiaszek et al., 2016). Moreover, rapid unexpected displacement of a light touch reference is capable of inducing a balance correction during standing, at least on the first trial (Misiaszek et al., 2016; Misiaszek & Vander Meulen, 2017). Similarly, light touch during walking has been shown to stabilize the position of the body on a moving treadmill (Dickstein & Laufer, 2004). In the present study, it was shown that rapid unexpected displacement of the touch reference is capable of inducing a response comparable to a balance response during treadmill walking. Together these results imply that the light touch sensory cues are incorporated in the balance control system to assist in regulating stability during both standing and walking.

Although light touch displacement evoked responses in the ankle muscles during treadmill walking, the impact on the walking cycle was relatively small. Indeed, none of the participants stumbled, tripped or otherwise had difficulty continuing to walk on the treadmill following the touch displacement. Presumably, this is because the displacement used (12.5 mm) was relatively small and the participants were able to maintain contact with the touch plate thereby continuing to provide a spatial reference. The size of the touch plate was known to the participants as they had opportunity to see it during the earlier conditions. Therefore, the relative threat posed by the perceived perturbation would have been readily accounted for. Despite this, the disturbance was not simply ignored and responses in the ankle muscles were evoked, that did have impact on the timing of the step cycle. This indicates that tactile feedback from the hands could provide the earliest cue indicating a potential threat to balance if the threat is initiated at the hands or if the hands are being used for additional support. For example, Forero and Misiaszek (2014) showed that when a set of handles that used to stabilize subjects walking on a treadmill are unexpectedly moved, rapid responses are triggered in the legs to restore balance. Tactile sensations from the hands would be the earliest sense to detect the disturbance and would provide a logical trigger for the responses observed. This could have important implications for understanding balance control for individuals that use mobility aids and assistive devices during walking where the threat to stability could be detected through the interface with the external support.

It is also important to note, however, that the touch plate displacement used in this study did not create an actual mechanical disturbance to the balance of the individual. Despite this, participants generated responses in the ankle muscles and adapted their step cycles. In other words, the participants reacted with a “false-positive” reaction that could itself be the cause of a potential catastrophic event. The “false-positive” nature of the evoked reactions is corroborated by the perception of some participants that the treadmill belt speed had been disturbed, or that they had been pulled at the waist. Previously reports have demonstrated similar “false-positive” or “sensory-illusion” events related to balance with vestibular (Day, Guerraz & Cole, 2002), visual (Van Asten, Gielen & Van Der Gon, 1988), and muscle mechanoreceptor inputs (Hayashi, Miyake, Jijiwa & Watanabe, 1981). The occurrences of these sorts of “false-positive” reactions are potentially destabilizing in themselves, and could pose a particular threat for individuals with compromised balance control. This threat could be further highlighted when the sensory signals themselves become less reliable, such as with aging. The difference between interpreting a slip at the finger as the body moving relative to a spatial reference (i.e. a fall) versus the movement of the object away from the body (i.e. a disturbance) could profoundly affect the consequences of that event.

Conclusion

Falls have always been a serious concern not only for the elderly population, but also in people having balance impairments. Contacting an external aid (such as cane, crutches or a walker) may serve to increase the sensory feedback available for balance control, in addition to the mechanical benefits afforded by the aid. To avoid falling, responses are generated in the muscles throughout the body to maintain the COM within the BOS. People can react to balance threats in a variety different ways, such as by taking a step or grasping a nearby handrail to prevent them from falling. In our study, participants reacted to an unexpected displacement of a light touch reference by activation of their ankle muscles, generating a balance correction. The sensory feedback from the hands, particularly cutaneous cues from the fingertip, is seen to provide spatial information about the body in space, particularly when visual information is absent with the eyes closed. Light touch is therefore seen to provide supplementary sensory inputs that help to maintain body stability. Furthermore, cutaneous feedback from a single fingertip is critically important as without contact with the spatial reference subjects are unable to maintain their walking position on a treadmill in the absence of vision. Previous evidence during standing with eyes closed (Misiaszek et al., 2016; Misiaszek & Vander Meulen, 2017) showed that rapid unexpected displacement of a light touch reference generated a balance correction on the unexpected first trial. However, a quick change in motor behavior was seen in the subsequent trials, as participants started using the cutaneous cues in an "arm-tracking" strategy. This is contrary to the present study in which balance reactions in ankle muscles were seen in repeated touch plate displacements. The demonstration of balance reactions with repeated exposures to touch plate displacements is a unique aspect of this study. To maintain contact with a positional reference when the eyes are closed, participants continued to rely on the touch reference despite eventually becoming aware that it might move.

Future directions

The main findings from this thesis are, 1) sensory feedback from a single fingertip is relevant in maintaining balance control while walking on a treadmill with eyes closed; 2) responses generated in the ankle muscles are frequently expressed across participants despite becoming aware of the repeated touch disturbance given at the fingertip. It might be important to replicate these findings in the elderly or people with balance disorders due to neurologic disease or impairment, to determine if the integration of sensory feedback from the fingers has similar effects on balance during walking. It is possible that in these populations the relevance of supplemental sensory feedback for balance control, such as from the hands, might be of greater importance. If so, then these disturbances at the finger might lead to greater challenges to stability during walking than what was seen presently for young, healthy adults. In addition, if sensory information from the hands is of greater importance to balance control during walking in at risk populations, then perhaps augmenting or facilitating sensory input from the hands would be a way to improve stability. For example, if the hands are being used to support balance, such as by using a walker or cane, then augmented sensory feedback from the hands might provide a richer sensory signal to be used in the balance control system. Similar approaches have been used to increase the sensory feedback from the feet to improve balance and stability.

In the current study, touch displacements were delivered at only the right heel strike. It is well documented that many reflexes, corrective reactions, and sensorimotor responses are modulated over the course of the step cycle. This modulation could be reflected by changes in response amplitude, or even reversal of sign (whereby a response that is facilitatory in one point in the step cycle becomes inhibitory in another point in the step cycle). It is therefore very likely the integration of sensory feedback from the hands will be regulated differently across the step cycle. Heel strike was chosen in this study as it represents a high risk point of the step cycle where a new base of support is being established and the mass of the body is being transferred from one leg to the other. However, other points in the step cycle might also be critical, such as during swing phase when trips are most likely to occur. A fuller description of how the sensory information from the hands is integrated in the neural control of walking balance will be important to fully understand the neural systems involved, and may be important in the future if technologies are developed that wish to integrate sensory information into powered assistive devices for walking.

Limitations

In this study, light touch displacements of 12.5 mm were used, consistent with what was used previously during standing (Misiaszek et al., 2016). However, during treadmill walking the body moves forwards and backwards with each step. Therefore, the hand position relative to the touch plate will also move forwards and backwards with each step. Consequently, the slip of the finger with the touch plate displacement of only 12.5 mm might have generated a smaller “signal” within the context of the ongoing background noise at the fingertip. Therefore, if anything, the approach used here would bias the results to fewer responses being generated and might contribute to why a difference in the number of first trial responders was not observed. However, the amplitude of 12.5 mm was used because a previous study of balance control during treadmill walking, that used pulls applied to the waist, demonstrated that those pulls resulted in displacement of the body center of mass of about 12.5 mm within the first 300 ms of the disturbance (Forero & Misiaszek, 2013). Light touch of a stable reference was demonstrated to facilitate the responses evoked by pulls at the waist and it was argued that detection of the slip of the finger could provide additional sensory input related to the effect. Therefore, the choice of the displacement magnitude has functional relevance.

The emphasis of this study was the contribution of tactile feedback from the finger to balance control during walking. Clearly, sensory input from the finger can impact muscle activity at the ankle and influence stability during walking. However, it was also clear that the impact on walking (i.e. the adaptation to the gait cycle) was only seen in the first trial and afterwards the participants adapted to the touch displacement in some way. This suggests that the interpretation of the touch displacement as a balance disturbance was corrected on subsequent trials, presumably because other sensory systems, including the proprioceptive and vestibular systems, would not have corroborated the “balance disturbance” detected at the finger. Therefore, although the relevance of light touch might have been augmented by asking the participants to walk on a motorized treadmill with their eyes closed, the conflict between the other sensory systems and the touch input would likely have allowed participants to learn the true nature of the disturbance at the finger.

Lastly, it is unclear why the psychophysical data and the physiological data (i.e. evoked responses and gait adaptations) are not in complete agreement. The participants tended to perceive a high number of balance disturbances and gait adaptations (i.e. "the treadmill belt speed changed") that were not reflected in the EMG or step cycle data. This mismatch might be reflective of different neural processes involved in the control of balance and walking, compared with the cognitive perception of sensory inputs. The inability of participants to accurately identify the nature of the disturbances, even when their gait and motor responses suggested a change in response, supports the argument that the motor reactions and integration of the touch sensory information into the control of walking is likely mediated through more rudimentary neural processes. The reason for the inaccurate cognitive perception of the sensory feedback during walking is an open question that might be important to study further and could have important implications for higher-order aspects of the control of walking, such as navigating a complex environment and proactive regulation that is seen in obstacle avoidance.

References

Abraira, V. E., & Ginty, D. D. (2013). The sensory neurons of touch. *Neuron, 79*, 618-639.

Allum, J., Tang, K., Carpenter, M. G., Nijhuis, L. O., & Bloem, B. R. (2011). Review of first trial responses in balance control: Influence of vestibular loss and Parkinson’s disease. *Human Movement Science, 30*, 279-295.

Arshavsky, Y. I., Deliagina, T. G., & Orlovsky, G. N. (1997). Pattern generation. *Current Opinion in Neurobiology, 7*, 781-789.

Baker, S. P., & Harvey, A. H. (1985). Fall injuries in the elderly. *Clinics in Geriatric Medicine, 1*, 501-512.

Bard, P. (1933). Studies on the cerebral cortex: I. localized control of placing and hopping reactions in the cat and their normal management by small cortical remnants. *Archives of Neurology & Psychiatry, 30*, 40-74.

Berger, W., Dietz, V., & Quintern, J. (1984). Corrective reactions to stumbling in man: Neuronal co-ordination of bilateral leg muscle activity during gait. *The Journal of Physiology, 357*, 109-125.

Boonsinsukh, R., Panichareon, L., & Phansuwan-Pujito, P. (2009). Light touch cue through a cane improves pelvic stability during walking in stroke. *Archives of Physical Medicine and Rehabilitation, 90*, 919-926.

Boonsinsukh, R., Saengsirisuwan, V., Carlson-Kuhta, P., & Horak, F. B. (2012). A cane improves postural recovery from an unpracticed slip during walking in people with Parkinson disease. *Physical Therapy, 92*, 1117-1129.

Brandt, T., Dichgans, J., & Koenig, E. (1973). Differential effects of central versus peripheral vision on egocentric and exocentric motion perception. *Experimental Brain Research, 16*, 476-491.

Campbell, A. D., Squair, J. W., Chua, R., Inglis, J. T., & Carpenter, M. G. (2013). First trial and StartReact effects induced by balance perturbations to upright stance. *Journal of Neurophysiology, 110*, 2236-2245.

Collins, D. F., & Prochazka, A. (1996). Movement illusions evoked by ensemble cutaneous input from the dorsum of the human hand. *The Journal of Physiology, 496*, 857-871.

Cullen, K. E. (2012). The vestibular system: Multimodal integration and encoding of self-motion for motor control. *Trends in Neurosciences, 35*, 185-196.

Day, B. L., Guerraz, M., & Cole, J. (2002). Sensory interactions for human balance control revealed by galvanic vestibular stimulation. *Advances in experimental and medical biology 508*, 129-137.

Delwaide, P. J., & Crenna, P. (1984). Cutaneous nerve stimulation and motoneuronal excitability. II: Evidence for non-segmental influences. *Journal of Neurology, Neurosurgery & Psychiatry, 47*, 190-196.

Dichgans, J., & Brandt, T. (1978). Visual-vestibular interaction: Effects on self-motion perception and postural control. *Perception 8,* 755-804.

Dickstein, R., & Laufer, Y. (2004). Light touch and center of mass stability during treadmill locomotion. *Gait & Posture, 20*, 41-47.

Dickstein, R., Shupert, C. L., & Horak, F. B. (2001). Fingertip touch improves postural stability in patients with peripheral neuropathy. *Gait & Posture, 14*, 238-247.

Diener, H. C., Dichgans, J., Guschlbauer, B., & Mau, H. (1984). The significance of proprioception on postural stabilization as assessed by ischemia. *Brain Research, 296,* 103-109.

Diener, H., & Dichgans, J. (1988). On the role of vestibular, visual and somatosensory information for dynamic postural control in humans. *Progress in Brain Research, 76*, 253-262.

Dietz, V. (1992). Neuronal control of stance and gait. *Advances in Psychology, 87*, 483-499.

Dietz, V., Horstmann, G. A., & Berger, W. (1989). Significance of proprioceptive mechanisms in the regulation of stance. *Progress in Brain Research, 80*, 419-423.

Dietz, V. (2002). Do human bipeds use quadrupedal coordination? *Trends in Neurosciences, 25*, 462-467.

Durgin, F. H., & Pelah, A. (1999). Visuomotor adaptation without vision? *Experimental Brain Research, 127*, 12-18.

Edin, B. B. (1992a). Quantitative analysis of static strain sensitivity in human mechanoreceptors from hairy skin. *Journal of Neurophysiology, 67*, 1105-1113.

El Saddik, A., Orozco, M., Eid, M., & Cha, J. (2011). *Haptics technologies: Bringing touch to multimedia* Springer Science & Business Media.

Enbom, H., Magnusson, M., & Pyykko, I. (1991). Postural compensation in children with congenital or early acquired bilateral vestibular loss. *The Annals of Otology, Rhinology & Laryngology, 100*, 472-478.

Fitzpatrick, R. C., & Day, B. L. (2004). Probing the human vestibular system with galvanic stimulation. *Journal of Applied Physiology, 96*, 2301-2316.

Fitzpatrick, R. C., Wardman, D. L., & Taylor, J. L. (1999). Effects of galvanic vestibular stimulation during human walking. *The Journal of Physiology, 517*, 931-939.

Forero, J., & Misiaszek, J. E. (2013). The contribution of light touch sensory cues to corrective reactions during treadmill locomotion. *Experimental Brain Research, 226*, 575-584.

Forero, J., & Misiaszek, J. E. (2014). The effect of light touch on the amplitude of cutaneous reflexes in the arms during treadmill walking. *Experimental Brain Research, 232*, 2967-2976.

Forero, J., & Misiaszek, J. E. (2015). The amplitude of interlimb cutaneous reflexes in the leg is influenced by fingertip touch and vision during treadmill locomotion. *Experimental Brain Research, 233*, 1773-1782.

Forssberg, H. (1979). Stumbling corrective reaction: A phase-dependent compensatory reaction during locomotion. *Journal of Neurophysiology, 42*, 936-953.

Grillner, S. (1985). Neurobiological bases of rhythmic motor acts in vertebrates. *Science, 228*, 143-149.

Hallemans, A., Beccu, S., Van Loock, K., Ortibus, E., Truijen, S., & Aerts, P. (2009). Visual deprivation leads to gait adaptations that are age-and context-specific: I. step-time parameters. *Gait & Posture, 30*, 55-59.

Haridas, C., & Zehr, E. P. (2003). Coordinated interlimb compensatory responses to electrical stimulation of cutaneous nerves in the hand and foot during walking. *Journal of Neurophysiology, 90*, 2850-2861.

Haridas, C., Zehr, E. P., & Misiaszek, J. E. (2006). Context-dependent modulation of interlimb cutaneous reflexes in arm muscles as a function of stability threat during walking. *Journal of Neurophysiology, 96*, 3096-3103.

Hayashi, R., Miyake, A., Jijiwa, H., & Watanabe, S. (1981). Postural readjustment to body sway induced by vibration in man. *Experimental Brain Research, 43*, 217-225.

Hill, J. W. (1974). Limited field of view in reading letter shapes with the fingers. Geldard F.A. (Ed.), *Cutaneous Communication Systems and Device* (pp. 95-105), Published for the Psychonomic Society, Austin, Texas.

Holden, M., Ventura, J., & Lackner, J. R. (1994). Stabilization of posture by precision contact of the index finger. *Journal of Vestibular Research, 4*, 285-283.

Horak, F. B., & Macpherson, J. M. (1996). Postural equilibrium and orientation. L.B. Rowell, J.T. Shepherd (Eds.), *Handbook of physiology* (pp. 255-292). Published for the American Physiology Society by Oxford University Press, New York.

Horak, F. B. (1987). Clinical measurement of postural control in adults. *Physical Therapy, 67*, 1881-1885.

Inglis, J. T., Horak, F. B., Shupert, C. L., & Jones-Rycewicz, C. (1994). The importance of somatosensory information in triggering and scaling automatic postural responses in humans. *Experimental Brain Research, 101*, 159-164.

Jeka, J. J., Schoner, G., Dijkstra, T., Ribeiro, P., & Lackner, J. R. (1997). Coupling of fingertip somatosensory information to head and body sway. *Experimental Brain Research, 113*, 475-483.

Jeka, J. J., & Lackner, J. R. (1994). Fingertip contact influences human postural control. *Experimental Brain Research, 100*, 495-502.

Jeka, J. J., & Lackner, J. R. (1995). The role of haptic cues from rough and slippery surfaces in human postural control. *Experimental Brain Research, 103*, 267-276.

Johannsen, L., Wing, A. M., & Hatzitaki, V. (2007). Effects of maintaining touch contact on predictive and reactive balance. *Journal of Neurophysiology, 97*, 2686-2695.

Johansson, R. S., & Westling, G. (1984). Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. *Experimental Brain Research, 56*, 550-564.

Johansson, R. S. (1978). Tactile sensibility in the human hand: Receptive field characteristics of mechanoreceptive units in the glabrous skin area. *The Journal of Physiology, 281*, 101-125.

Johansson, R. S., & Vallbo, B. (1979). Tactile sensibility in the human hand: Relative and absolute densities of four types of mechanoreceptive units in glabrous skin. *The Journal of Physiology, 286*, 283-300.

Johansson, R. S., & Vallbo, K. B. (1983). Tactile sensory coding in the glabrous skin of the human hand. *Trends in Neurosciences, 6*, 27-32.

Johnson, K. O., Yoshioka, T., & Vega–Bermudez, F. (2000). Tactile functions of mechanoreceptive afferents innervating the hand. *Journal of Clinical Neurophysiology, 17*, 539-558.

Kagamihara, Y., Hayashi, A., Masakado, Y., & Kouno, Y. (2003). Long-loop reflex from arm afferents to remote muscles in normal man. *Experimental Brain Research, 151*, 136-144.

Kanekar, N., Lee, Y. J., & Aruin, A. S. (2013). Effect of light finger touch in balance control of individuals with multiple sclerosis. *Gait & Posture, 38*, 643-647.

Knibestol, M., & Vallbo, K. B. (1970a). Single unit analysis of mechanoreceptor activity from the human glabrous skin. *Acta Physiologica Scandinavica, 80*, 178-195.

Kostov, A., Hansen, M., Haugland, M., & Sinkjaer, T. (1999a). Adaptive restriction rules provide functional and safe stimulation pattern for foot drop correction. *Artificial Organs, 23*, 443-446.

Kouzaki, M., & Masani, K. (2008). Reduced postural sway during quiet standing by light touch is due to finger tactile feedback but not mechanical support. *Experimental Brain Research, 188*, 153-158.

Lackner, J. R., & Levine, M. S. (1979). Changes in apparent body orientation and sensory localization induced by vibration of postural muscles: vibratory myesthetic illusions. *Aviation, Space, and Environmental Medicine 50,* 346-354.

Lackner, J. R., Dizio, P., Jeka, J., Horak, F., Krebs, D., & Rabin, E. (1999a). Precision contact of the fingertip reduces postural sway of individuals with bilateral vestibular loss. *Experimental Brain Research, 126*, 459-466.

Lackner, J. R., Rabin, E., & Dizio, P. (2001). Stabilization of posture by precision touch of the index finger with rigid and flexible filaments. *Experimental Brain Research, 139*, 454-464.

Lamont, E. V., & Zehr, E. P. (2007). Earth-referenced handrail contact facilitates interlimb cutaneous reflexes during locomotion. *Journal of Neurophysiology, 98*, 433-442.

Lee, D. N., & Lishman, J. R. (1975). Visual proprioceptive control of stance. *Journal of Human Movement Studies, 1,* 87-95.

Lee, D. N., & Aronson, E. (1974). Visual proprioceptive control of standing in human infants. *Attention, Perception, & Psychophysics, 15*, 529-532.

Loomis, J. M. & Lederman, S. J. (1986). Tactual perception. K. R. Boff, L. Kaufman & J. P. Thomas (Eds.), *Handbook of perception and human performances* (pp. 1-41). Wiley, New York.

MacKay-Lyons, M. (2002a). Central pattern generation of locomotion: A review of the evidence. *Physical Therapy, 82*, 69-83.

Macpherson, J. M., & Inglis, J. T. (1993). Stance and balance following bilateral labyrinthectomy. *Progress in Brain Research, 97*, 219-228.

Maki, B. E., & McIlroy, W. E. (2007). Cognitive demands and cortical control of human balance-recovery reactions. *Journal of Neural Transmission, 114*, 1279-1296.

Manchester, D., Woollacott, M., Zederbauer-Hylton, N., & Marin, O. (1989). Visual, vestibular and somatosensory contributions to balance control in the older adult. *Journal of Gerontology, 44*, M118-M127.

Marchand-Pauvert, V., Mazevet, D., Nielsen, J., Petersen, N., & Pierrot-Deseilligny, E. (2000). Distribution of non-monosynaptic excitation to early and late recruited units in human forearm muscles. *Experimental Brain Research, 134*, 274-278.

Marigold, D. S. (2008). Role of peripheral visual cues in online visual guidance of locomotion. *Exercise and Sport Sciences Reviews, 36*, 145-151.

Marigold, D. S., Bethune, A. J., & Patla, A. E. (2003). Role of the unperturbed limb and arms in the reactive recovery response to an unexpected slip during locomotion. *Journal of Neurophysiology, 89*, 1727-1737.

Massion, J. (1992a). Movement, posture and equilibrium: Interaction and coordination. *Progress in Neurobiology, 38*, 35-56.

Massion, J. (1994). Postural control system. *Current Opinion in Neurobiology, 4*, 877-887.

Mauritz, K. H., & Dietz, V. (1980). Characteristics of postural instability induced by ischemic blocking of leg afferents. *Experimental Brain Research, 38*, 117-119.

McGlone, F., & Reilly, D. (2010). The cutaneous sensory system. *Neuroscience & Biobehavioral Reviews, 34*, 148-159.

Misiaszek, J. E., Forero, J., Hiob, E., & Urbanczyk, T. (2016). Automatic postural responses following rapid displacement of a light touch contact during standing. *Neuroscience, 316*, 1-12.

Misiaszek, J. E. (2006). Neural control of walking balance: if falling then react else continue. *Exercise and Sport Sciences Reviews, 34*, 128-134.

Misiaszek, J. E., & Krauss, E. M. (2005). Restricting arm use enhances compensatory reactions of leg muscles during walking. *Experimental Brain Research, 161*, 474-485.

Misiaszek, J. E., & Vander Meulen, J. (2017). Balance reactions to light touch displacements when standing on foam. *Neuroscience Letters, 639,* 13-17.

Mohapatra, S., & Aruin, A. S. (2013). Static and dynamic visual cues in feed-forward postural control. *Experimental Brain Research, 224*, 25-34.

Nashner, L. M., & Cordo, P. J. (1981). Relation of automatic postural responses and reaction-time voluntary movements of human leg muscles. *Experimental Brain Research, 43*, 395-405.

Nashner, L. M., Woollacott, M., & Tuma, G. (1979). Organization of rapid responses to postural and locomotor-like perturbations of standing man. *Experimental Brain Research, 36*, 463-476.

Nashner, L. M. (1980). Balance adjustments of humans perturbed while walking. *Journal of Neurophysiology, 44*, 650-664.

Nashner, L. M., & Wolfson, P. (1974). Influence of head position and proprioceptive cues on short latency postural reflexes evoked by galvanic stimulation of the human labyrinth. *Brain Research, 67*, 255-268.

Nashner, L. M. (1977a). Fixed patterns of rapid postural responses among leg muscles during stance. *Experimental Brain Research, 30*, 13-24.

Nijhuis, L. B. O., Allum, J. H., Valls-Sole, J., Overeem, S., & Bloem, B. R. (2010). First trial postural reactions to unexpected balance disturbances: a comparison with the acoustic startle reaction. *Journal of Neurophysiology, 104*, 2704-2712.

Nutt, J. G., Marsden, C. D., & Thompson, P. D. (1993). Human walking and higher-level gait disorders, particularly in the elderly. *Neurology, 43*, 268-279.

Paquet, N., Watt, D. G., & Lefebvre, L. (2000). Rhythmical eye-head-torso rotation alters fore-aft head stabilization during treadmill locomotion in humans. *Journal of Vestibular Research, 10*, 41-49.

Patla, A. E. (1995). A framework for understanding mobility problems in the elderly. Craik RL, Oatis CA (Eds.), *Gait Analysis: Theory and Application (pp.* 436-449). Mosby-Year Book, St. Louis.

Patla, A. E. (1993). Age-related changes in visually guided locomotion over different terrains: major issues. Stelmach GE, Homberg V (Eds.), *Sensorimotor impairment in the elderly* (pp. 231-252). Springer, Kluwer, Dordrecht.

Patla, A. E. (2003). Strategies for dynamic stability during adaptive human locomotion. *IEEE Engineering in Medicine and Biology Magazine: the quarterly magazine of the Engineering in Medicine and Biology Society, 22*, 48-52.

Pearson, K. G. (1993). Common principles of motor control in vertebrates and invertebrates. *Annual Review of Neuroscience, 16*, 265-297.

Pearson, K., G & Misiaszek, M. J. (2001). Locomotion. *Encyclopedia of Life Sciences* (pp. 1-7). John Wiley & Sons Ltd, University of Alberta, Edmonton.

Pereira, L. M. (1990). Spatial concepts and balance performance: motor learning in blind and visually impaired children. *Journal of Visual Impairment & Blindness, 84,* 109-117.

Pozzo, T., Berthoz, A., Lefort, L., & Vitte, E. (1991). Head stabilization during various locomotor tasks in humans. II. Patients with bilateral peripheral vestibular deficits. *Experimental Brain Research, 85*, 208-217.

Prochazka, A. (1989). Sensorimotor gain control: A basic strategy of motor systems? *Progress in Neurobiology, 33*, 281-307.

Prochazka, A. (1996). Proprioceptive feedback and movement regulation. L. Rowell, T. Sheperd (Eds.), Exercise Regulation and Integration of Multiple Systems, *Handbook of Physiology* (pp. 89-127) published for American Physiological Society, and New York.

Prokop, T., Schubert, M., & Berger, W. (1997). Visual influence on human locomotion modulation to changes in optic flow. *Experimental Brain Research, 114*, 63-70.

Rabin, E., Dizio, P., Ventura, J., & Lackner, J. R. (2008). Influences of arm proprioception and degrees of freedom on postural control with light touch feedback. *Journal of Neurophysiology, 99*, 595-604.

Riemann, B. L., & Lephart, S. M. (2002). The sensorimotor system, part I: The physiologic basis of functional joint stability. *Journal of Athletic Training, 37*, 71-79.

Rosen, S. (1997). Kinesiology and sensorimotor function. B. Blasch, W.R. Wiener, R.L. Welch (Eds.), *Foundations of Orientation and Mobility* (pp. 456-482). American Foundation for the Blind, New York.

Rovainen, C. M. (1979). Neurobiology of lampreys. *Physiological Reviews, 59*, 1007-1077.

Schillings, A. M., Van Wezel, B., & Duysens, J. (1996). Mechanically induced stumbling during human treadmill walking. *Journal of Neuroscience Methods, 67*, 11-17.

Shik, M. L., Severin, F. V., Orlovskii, G. N. (1966). Control of walking and running by means of electrical stimulation of mid-brain. *Biofizika* 11, 659-666.

Shik, M.L., Orlovsky, G.N. (1976) Neurophysiology of locomotor automatism. *Physiological Reviews* 56, 465-501.

Siegmund, G. P., Blouin, J., & Inglis, J. T. (2008). Does startle explain the exaggerated first response to a transient perturbation? *Exercise and Sport Sciences Reviews, 36,* 76-82.

Simoneau, G. G., Ulbrecht, J. S., Derr, J. A., & Cavanagh, P. R. (1995a). Role of somatosensory input in the control of human posture. *Gait & Posture, 3*, 115-122.

Srinivasan, M. A., Whitehouse, J. M., & LaMotte, R. H. (1990). Tactile detection of slip: Surface microgeometry and peripheral neural codes. *Journal of Neurophysiology, 63*, 1323-1332.

Stoffregen, T. A. (1985). Flow structure versus retinal location in the optical control of stance. *Journal of Experimental Psychology: Human Perception and Performance, 11*, 554-565.

Stephen, R. G., & Darian-Smith, I. (1984). Handbook of physiology: a critical, comprehensive presentation of physiological knowledge and concepts. J. M. Brookhart, V. B. Mountcastle & I. Darian-Smith (Eds.), *The nervous system: formerly section 1: Neurophysiology*. University of Michigan.

Sundermier, L., Woollacott, M. H., Jensen, J. L., & Moore, S. (1996). Postural sensitivity to visual flow in aging adults with and without balance problems. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 51*, M45-M52.

Takahashi, M., Hoshikawa, H., Tsujita, N., & Akiyama, I. (1988). Effect of labyrinthine dysfunction upon head oscillation and gaze during stepping and running. *Acta Oto-Laryngologica, 106*, 348-353.

Tang, P. F., Woollacott, M. H., & Chong, R. K. (1998). Control of reactive balance adjustments in perturbed human walking: Roles of proximal and distal postural muscle activity. *Experimental Brain Research, 119*, 141-152.

Vallbo, A. B., & Hagbarth, K. E. (1968). Activity from skin mechanoreceptors recorded percutaneously in awake human subjects. *Experimental Neurology, 21*, 270-289.

Van Asten, W. N., Gielen, C. C., & Van Der Gon, J. J. (1988). Postural movements induced by rotations of visual scenes. *Journal of the optical Society of America. A, Optics and image Science, 5*, 1781-1789.

Van Deursen, R. W., & Simoneau, G. G. (1999). Foot and ankle sensory neuropathy, proprioception, and postural stability. *The Journal of Orthopaedic & Sports Physical Therapy, 29*, 718-726.

Warren, W. H., Kay, B. A., & Yilmaz, E. H. (1996). Visual control of posture during walking: Functional specificity. *Journal of Experimental Psychology: Human Perception and Performance, 22*, 818-838.

Warren, W. H., Kay, B. A., Zosh, W. D., Duchon, A. P., & Sahuc, S. (2001a). Optic flow is used to control human walking. *Nature Neuroscience, 4*, 213-216.

Winter, D. A. (1991). The Biomechanics and motor control of human gait*:* Normal, elderly and pathological, *Waterloo Biomechanics*, Waterloo, Canada.

Winter, D. A. (1995). Human balance and posture control during standing and walking. *Gait & Posture, 3*, 193-214.

Winter, D. A., Patla, A. E., & Frank, J. S. (1990). Assessment of balance control in humans. *Medical Progress through Technology, 16*, 31-51.

Woollacott, M. H., & Pei-Fang, T. (1997a). Balance control during walking in the older adult: Research and its implications. *Physical Therapy, 77*, 646-660.

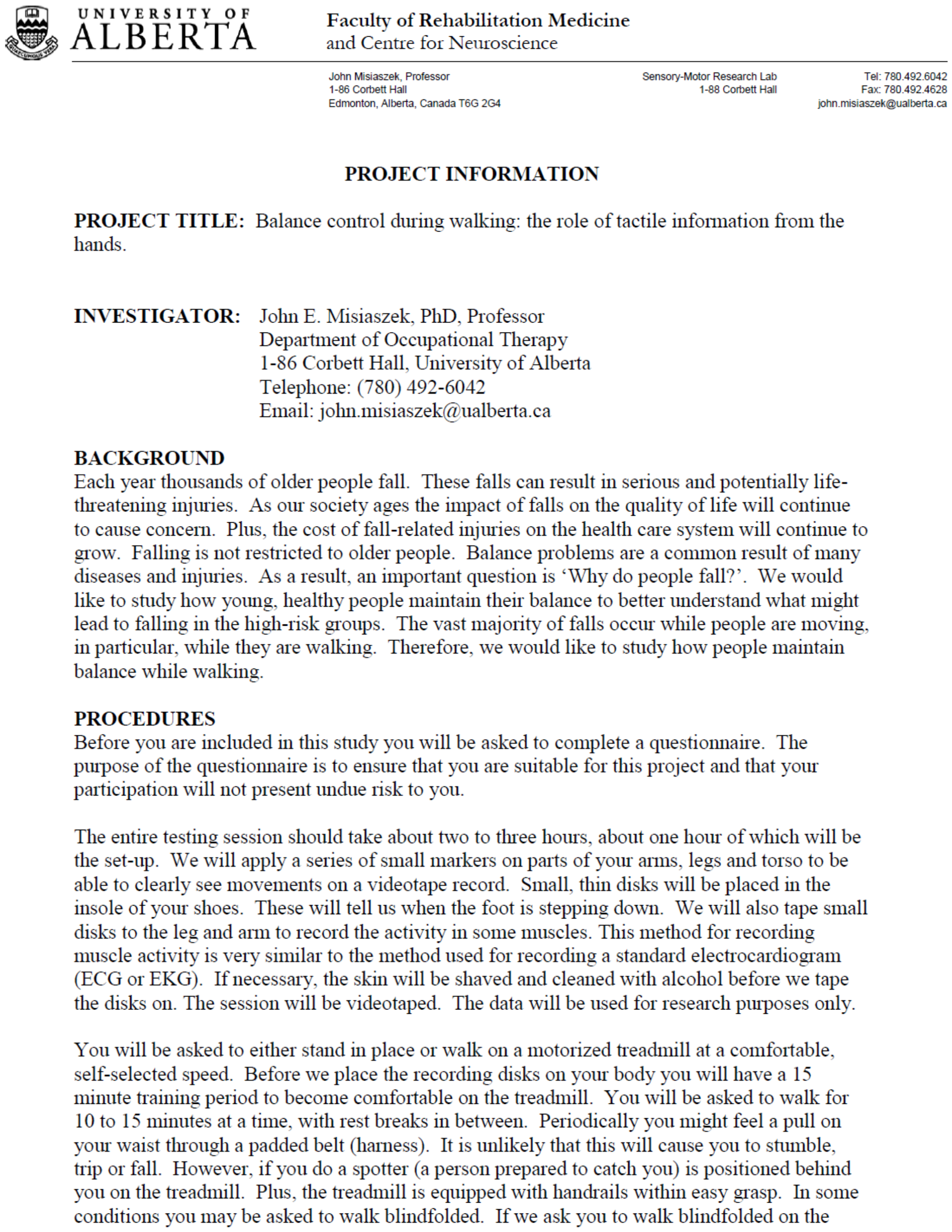
Yang, J. F., & Stein, R. B. (1990). Phase-dependent reflex reversal in human leg muscles during walking. *Journal of Neurophysiology, 63*, 1109-1117.

Zehr, E. P., Komiyama, T., & Stein, R. B. (1997). Cutaneous reflexes during human gait: Electromyographic and kinematic responses to electrical stimulation. *Journal of Neurophysiology, 77*, 3311-3325.

Zehr, E. P., & Duysens, J. (2004). Regulation of arm and leg movement during human locomotion. *The Neuroscientist, 10*, 347-361.

APPENDIX

A1: Project Information Sheet



UNIVERSITY OF ALBERTA

Faculty of Rehabilitation Medicine
and Centre for Neuroscience

John Misiaszek, Professor
1-86 Corbett Hall
Edmonton, Alberta, Canada T6G 2G4

Sensory-Motor Research Lab
1-88 Corbett Hall

Tel: 780.492.6042
Fax: 780.492.4628
john.misiaszek@ualberta.ca

PROJECT INFORMATION

PROJECT TITLE: Balance control during walking: the role of tactile information from the hands.

INVESTIGATOR: John E. Misiaszek, PhD, Professor
Department of Occupational Therapy
1-86 Corbett Hall, University of Alberta
Telephone: (780) 492-6042
Email: john.misiaszek@ualberta.ca

BACKGROUND

Each year thousands of older people fall. These falls can result in serious and potentially life-threatening injuries. As our society ages the impact of falls on the quality of life will continue to cause concern. Plus, the cost of fall-related injuries on the health care system will continue to grow. Falling is not restricted to older people. Balance problems are a common result of many diseases and injuries. As a result, an important question is 'Why do people fall?'. We would like to study how young, healthy people maintain their balance to better understand what might lead to falling in the high-risk groups. The vast majority of falls occur while people are moving, in particular, while they are walking. Therefore, we would like to study how people maintain balance while walking.

PROCEDURES

Before you are included in this study you will be asked to complete a questionnaire. The purpose of the questionnaire is to ensure that you are suitable for this project and that your participation will not present undue risk to you.

The entire testing session should take about two to three hours, about one hour of which will be the set-up. We will apply a series of small markers on parts of your arms, legs and torso to be able to clearly see movements on a videotape record. Small, thin disks will be placed in the insole of your shoes. These will tell us when the foot is stepping down. We will also tape small disks to the leg and arm to record the activity in some muscles. This method for recording muscle activity is very similar to the method used for recording a standard electrocardiogram (ECG or EKG). If necessary, the skin will be shaved and cleaned with alcohol before we tape the disks on. The session will be videotaped. The data will be used for research purposes only.

You will be asked to either stand in place or walk on a motorized treadmill at a comfortable, self-selected speed. Before we place the recording disks on your body you will have a 15 minute training period to become comfortable on the treadmill. You will be asked to walk for 10 to 15 minutes at a time, with rest breaks in between. Periodically you might feel a pull on your waist through a padded belt (harness). It is unlikely that this will cause you to stumble, trip or fall. However, if you do a spotter (a person prepared to catch you) is positioned behind you on the treadmill. Plus, the treadmill is equipped with handrails within easy grasp. In some conditions you may be asked to walk blindfolded. If we ask you to walk blindfolded on the treadmill you will be given as much time as you feel you need to become comfortable walking before we resume testing. To help you feel comfortable on the treadmill a tone will provided through a set of headphones to indicate if you are moving too far forward or backward.

Throughout the session you may be asked to use your arms in very specific ways. You may be asked to:

1) lightly touch a rod
2) hold a set of stable handles
3) hold a pair of rods
4) hold a set of handles that can move
5) touch a surface that can move
6) stand or walk naturally.

If you feel that the pull at your waist will cause you to fall you are free to grasp the railing. A spotter will be near you at all times to help stop you from falling if you should stumble. If you feel any discomfort from the belt around your waist you will be given the opportunity to adjust the position of the belt or else stop the session.

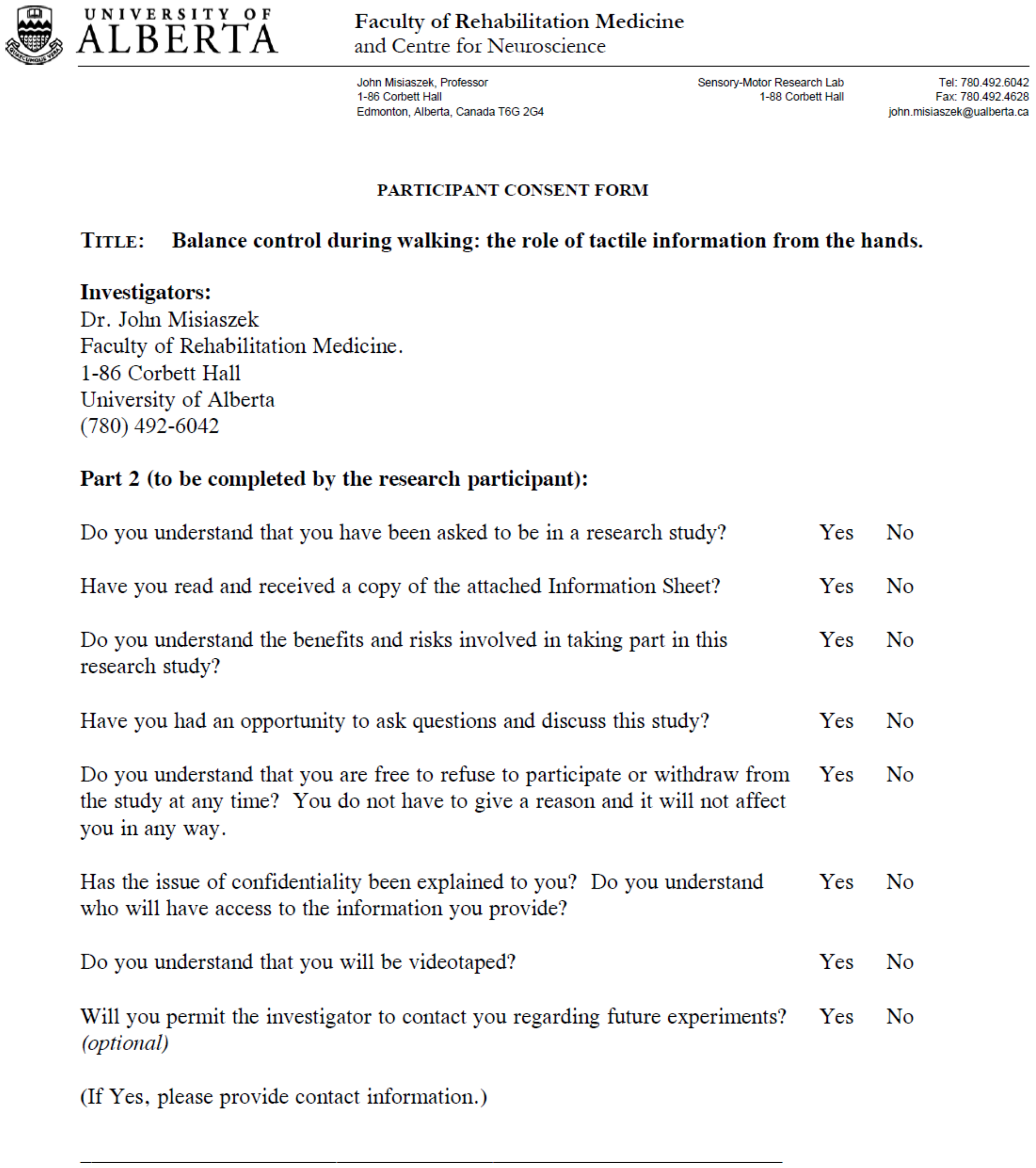
POTENTIAL RISKS OF YOUR PARTICIPATION
In this study we will push and pull you while you stand or walk. As a result, you might stumble, trip or fall. However, this risk is very small as you will be wearing a harness and a person will stand nearby to catch you if you appear to be falling. Some parts of the skin preparation might cause minor irritation. This occurs rarely and lasts only a day or two in those people affected. The equipment we use to record our data is either battery powered, or electrically isolated. This means it is very unlikely you can be harmed by the equipment. The equipment is inspected every year for safety.

CONFIDENTIALITY
Your identity will remain confidential. All data collected from you will be coded by letter or number. Data will be stored in locked cabinets and computers within a secured area. Only the investigator will have access to the code, the data and the videotapes. After 5 years, this data will be destroyed (in accordance with ethical guidelines at the university).

You are free to ask questions at any time. You may withdraw from the study at any time without any consequence to you. Your participation is entirely voluntary; there will be no pay. It is unlikely that your participation in the study will result in any direct benefit to you. Information gained from the study will further our understanding of how the nervous system controls balance during walking. The results of the study, once completed, can be provided to you at your request.

If you have any questions about this study, you may contact Dr. John Misiaszek (780-492-6042) at your convenience. You may also contact the Associate Dean of Research, Dr. Tammy Hopper (780-492-0836), who is not involved with this study if you have any other questions or concerns. You may also contact the Research Ethics Office of the University of Alberta at 780-492-0459 should you have any concerns or questions about the nature or conduct of this study.

A2: Participant Consent Form



UNIVERSITY OF ALBERTA
Faculty of Rehabilitation Medicine
and Centre for Neuroscience

John Misiaszek, Professor
1-86 Corbett Hall
Edmonton, Alberta, Canada T6G 2G4

Sensory-Motor Research Lab
1-88 Corbett Hall

Tel: 780.492.6042
Fax: 780.492.4628
john.misiaszek@ualberta.ca

PARTICIPANT CONSENT FORM

TITLE: Balance control during walking: the role of tactile information from the hands.

Investigators:
Dr. John Misiaszek
Faculty of Rehabilitation Medicine.
1-86 Corbett Hall
University of Alberta
(780) 492-6042

Part 2 (to be completed by the research participant):

Do you understand that you have been asked to be in a research study?	Yes	No
Have you read and received a copy of the attached Information Sheet?	Yes	No
Do you understand the benefits and risks involved in taking part in this research study?	Yes	No
Have you had an opportunity to ask questions and discuss this study?	Yes	No
Do you understand that you are free to refuse to participate or withdraw from the study at any time? You do not have to give a reason and it will not affect you in any way.	Yes	No
Has the issue of confidentiality been explained to you? Do you understand who will have access to the information you provide?	Yes	No
Do you understand that you will be videotaped?	Yes	No
Will you permit the investigator to contact you regarding future experiments? *(optional)*	Yes	No

(If Yes, please provide contact information.)

____

This study was explained to me by: ______________________________

I agree to take part in this study.

____ ________________________________

Signature of Research Participant Date Witness

________________________________ ________________________________

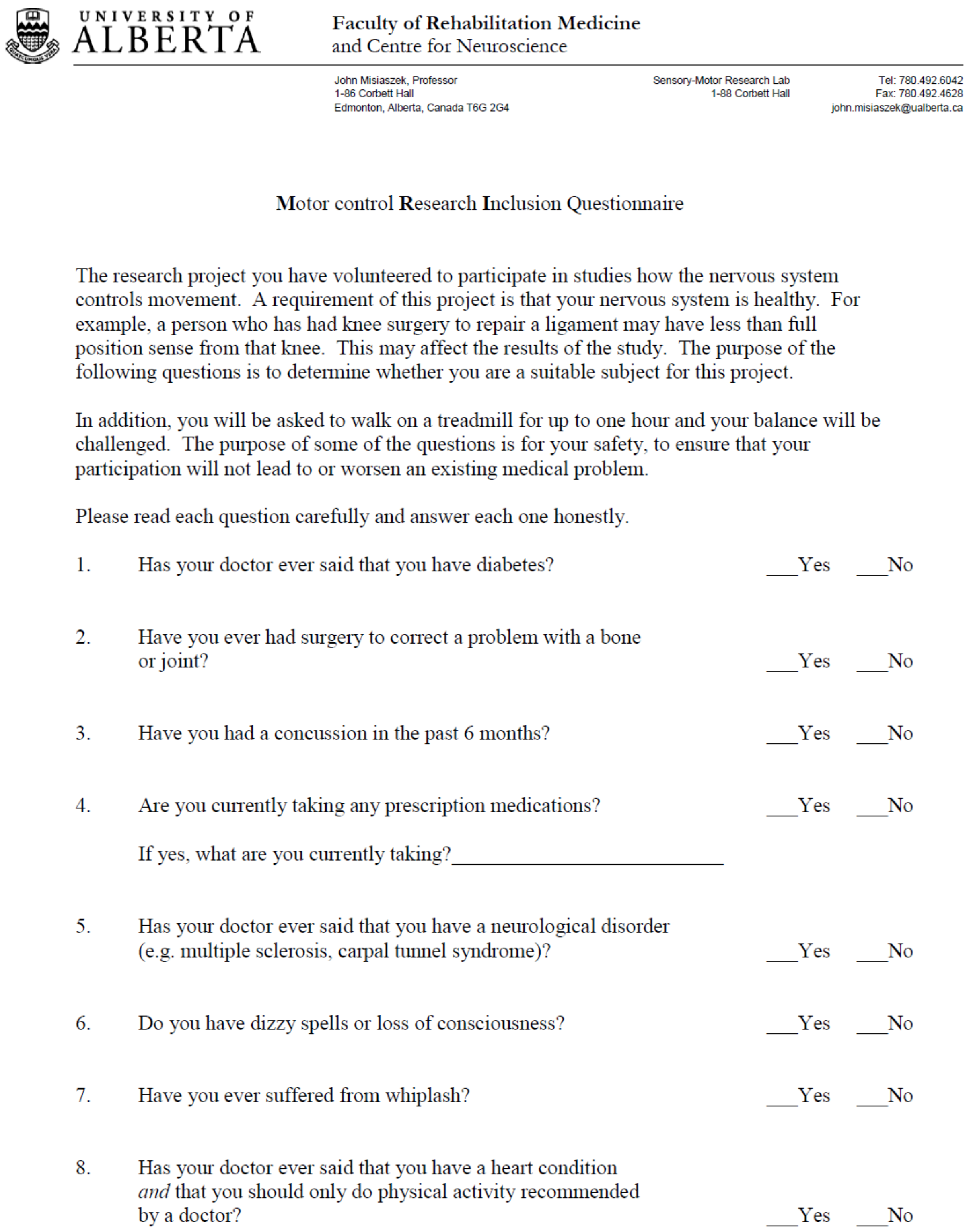
Printed Name Printed Name

I believe that the person signing this form understands what is involved in the study and voluntarily agrees to participate.

___________________________________ ___________________

Signature of Investigator or Designee Date

A3: MRIQ Questionnaire



UNIVERSITY OF ALBERTA
Faculty of Rehabilitation Medicine
and Centre for Neuroscience

John Misiaszek, Professor
1-86 Corbett Hall
Edmonton, Alberta, Canada T6G 2G4

Sensory-Motor Research Lab
1-88 Corbett Hall

Tel: 780.492.6042
Fax: 780.492.4628
john.misiaszek@ualberta.ca

Motor control **R**esearch **I**nclusion Questionnaire

The research project you have volunteered to participate in studies how the nervous system controls movement. A requirement of this project is that your nervous system is healthy. For example, a person who has had knee surgery to repair a ligament may have less than full position sense from that knee. This may affect the results of the study. The purpose of the following questions is to determine whether you are a suitable subject for this project.

In addition, you will be asked to walk on a treadmill for up to one hour and your balance will be challenged. The purpose of some of the questions is for your safety, to ensure that your participation will not lead to or worsen an existing medical problem.

Please read each question carefully and answer each one honestly.

1. Has your doctor ever said that you have diabetes? ___Yes ___No

2. Have you ever had surgery to correct a problem with a bone or joint? ___Yes ___No

3. Have you had a concussion in the past 6 months? ___Yes ___No

4. Are you currently taking any prescription medications? ___Yes ___No

   If yes, what are you currently taking?__________________________

5. Has your doctor ever said that you have a neurological disorder (e.g. multiple sclerosis, carpal tunnel syndrome)? ___Yes ___No

6. Do you have dizzy spells or loss of consciousness? ___Yes ___No

7. Have you ever suffered from whiplash? ___Yes ___No

8. Has your doctor ever said that you have a heart condition *and* that you should only do physical activity recommended by a doctor? ___Yes ___No

9. Do you feel pain in your chest when you do physical activity? ___Yes ___No

10. Do you have a bone or joint problem that could be made worse by walking for an extended period of time? ___Yes ___No

11. Have you had any back pain in the past 6 months? ___Yes ___No

12. Have you ever suffered a broken bone? ___Yes ___No

13. Do you have arthritis? ___Yes ___No

I have read, understood and completed this questionnaire. Any questions I had were answered to my full satisfaction.

Name_______________________________________

Signature____________________________________ Date___________________________

Investigator________________________________ Date___________________________

Witness____________________________________ Date___________________________

A4: Post-Experiment Questionnaire

Post-Experiment Questionnaire

In this study we are most interested in the last trial where you were walking with your eyes closed and touching the touch plate. Please answer the following questions reflecting on your experience during the last trial **ONLY**.

1. During this last trial we added one or more disturbances to test your balance. Did you become aware of the disturbance(s)? **Yes No (circle)**

    i. If yes, when did you become aware of what was happening? How did you figure it out? *(use the page back if you need more space)*

2. During this last trial, did you notice a sudden change of speed of the treadmill?

    Yes No (circle)

    i. If yes, circle the number below that best estimates the number of times the treadmill speed was changed throughout this trial.

    1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

    ii. If you circled 1 speed change, circle the choice below that best describes when the speed change occurred within the trial.

    a. Towards the beginning of the trial
    b. Towards the middle of the trial
    c. Towards the end of the trial

    iii. If you circled 2 or more speed changes, circle the choice below that best describes when the speed changes occurred within the trial.

    a. Clustered at the beginning of the trial
    b. Clustered at the middle of the trial
    c. Clustered at the end of the trial
    d. Distributed throughout the trial

    iv. If you circled 2 or more speed changes, would say that the last speed change was faster, slower or about the same as the first speed change?

    faster slower about the same (circle)

3. During this last trial, did you feel that you had been pushed or pulled at the waist?

   Yes No (circle)

   i. If yes, circle the number below that best estimates the number of times you were pushed or pulled throughout this trial.

      1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

   ii. If you circled 1 push or pull, circle the choice below that best describes when the push or pull occurred within the trial.

      a. Towards the beginning of the trial
      b. Towards the middle of the trial
      c. Towards the end of the trial

   iii. If you circled 2 or more pushes or pulls, circle the choice below that best describes when the push or pull occurred within the trial.

      a. Clustered at the beginning of the trial
      b. Clustered at the middle of the trial
      c. Clustered at the end of the trial
      d. Distributed throughout the trial

   iv. If you circled 2 or more pushes or pulls, would say that the last push or pull was stronger, weaker or about the same as the first push or pull?

      stronger weaker about the same (circle)

4. During this last trial, did you notice a rapid movement of the touch plate?

   Yes No (circle)

   i. If yes, circle the number below that best estimates the number of times the touch plate was rapidly moved.

      1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

   ii. If you circled 1 touch plate movement, circle the choice below that best describes when the touch plate was moved within the trial.

      a. Towards the beginning of the trial
      b. Towards the middle of the trial
      c. Towards the end of the trial

   iii. If you circled 2 or more touch plate movements, circle the choice below that best describes when the touch plate movements occurred within the trial.

      a. Clustered at the beginning of the trial
      b. Clustered at the middle of the trial
      c. Clustered at the end of the trial
      d. Distributed throughout the trial

   iv. If you circled 2 or more touch plate movements, would say that the last touch plate movement was faster, slower or about the same as the first touch plate movement?

      faster slower about the same (circle)

   v. If you circled 2 or more touch plate movements, would say that size of the last touch plate movement was bigger, smaller or about the same as the first touch plate movement?

      bigger smaller about the same (circle)