*"Integration and unification may be necessary only for something that is not integral by itself, which is obviously wrong with respect to the nervous system and its functions. Maybe, there is an integrative function inherent to the nervous system, but only as the most ancient, elementary function ... that may be leading only at the earliest stages of the evolutionary process. Where can one observe this function? Only in a decapitated animal, in its orphan spinal system [...]. Integrative function of the nervous system reflects either its deep pathology or the pre-Cambrian antiquity [...]. Hence, the functioning of the contemporary nervous system of a highly developed vertebrate is not in integration, but in struggle against the prehistoric integration."*

*Nicholai Bernstein, 2003*

**University of Alberta**

# Touch and Balance During Walking

by

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# Dedication

*To Monica, for continuously showing me*
*the magic that has surrounded us*
*all along our journey together*

*And to Gregorio, for showing me the world*
*as he senses it and reminding me of the*
*wonders hidden within the simplest things*
*only a child can perceive*

# Abstract

In this thesis the participation of tactile feedback from the hands in the control of balance was investigated. In Chapter 2, I characterized arm and leg reactions to unexpected perturbations delivered through the arms during walking. Perturbations applied at the hands resulted in early latency responses in arm muscles that were accompanied by activation of muscles in the leg when subjects were instructed to oppose the perturbations. Although no responses were observed in the arms when subjects were instructed to comply to the perturbations, most subjects presented responses in muscles of the leg. Activation of muscles in the legs were present during the comply condition even though the perturbations did not result in a balance disturbance. In Chapter 3, I investigated the effect of light touch sensory cues on the earliest postural reactions to balance disturbances during walking. The results of this study revealed that corrective responses in leg muscles to perturbations during walking are modulated by light touch. In particular, it was found that the effect of light touch on the corrective responses was more apparent when walking with the eyes closed compared to walking with the eyes open. Finally, in Chapters 4 and 5, I studied the effect of light touch on the gating of neural pathways transporting sensory information associated with the touch surface. The results of the study presented in Chapter 4 showed that segmental cutaneous afferent pathways are facilitated in

the presence of touch if they transport sensory information from functionally relevant sensory cues (i.e. skin in contact with the surface). The results of the study presented in Chapter 5 showed that when tactile feedback associated with the touch surface is available interlimb sensorimotor pathways transporting sensory information from the skin in contact with the touch surface are facilitated. Altogether the results from this thesis revealed that sensory input from the hand can encode information describing the interaction between the body and the environment, hence plays a strong role in the control of balance.

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## Chapter 1

# General Introduction

## 1.1 Introduction

Human standing is a challenging task due to the inherently unstable nature of bipedal upright stance. In humans, the centre of mass is located well above the ground, and the upright posture is maintained over a relatively small base of support. Even in the absence of external disturbances, controlling the position of the centre of mass to maintain an erect posture is largely demanding. The inverted pendulum model is a simplified model that can accurately predict the movement of the whole-body centre of mass during standing (Gage et al., 2004), hence serves to exemplify the difficulty of maintaining an erect posture. In an inverted pendulum, a small rotation at the base can displace largely the centre of mass from its stable position. To recover balance of the pendulum, a torque opposing the rotation has to be applied at the base. In the human body, standing balance is maintained by constant corrections of the centre of mass position through organized patterns of muscle activation that result in the delivery of the balancing torque. Thus, maintaining the body in a chosen position, such as maintaining an erect posture, is not a simple task to be accomplished by the nervous system.

However, the goal in human postural control is not limited to maintaining the body in a chosen position (i.e. static equilibrium), it also includes allowing the body to perform a desired movement without losing balance (i.e. dynamic equilibrium) (Jones, 2000). Walking, one of the main gaits of human locomotion, provides a particular challenge to the nervous system. Human walking has been compared to a set of voluntary forward falls that get averted by safe placement of the swing foot (Winter, 1995). Once locomotion has started, the body pivots on the stance leg while the swing leg moves forward until the foot contacts the ground. At this moment, the swing leg becomes the stance leg to allow the other leg to begin a swing motion and start the walking cycle again. Human walking is composed of two major phases (i.e. stance and swing phases) linked by transition events. Each leg will be in contact with the ground during the stance phase, but, after transitioning from stance to swing, it will be swinging during the swing phase. Then, after transitioning from swing to stance, the leg will go back to the stance phase. The transition from swing to stance is known as heel-contact given that the heel is the part of the foot that first contacts the ground, while the transition from stance to swing is commonly referred as toe-off or take-off, given that the foot loses contact with the ground and the last contact occurs at the toes.

Contrary to standing, where balance is achieved by maintaining the centre of mass within the base of support, during walking the centre of mass is seldom contained within the base of support. For example, during walking at a normal speed the centre of mass is only within the base of support for ~20% of a stride, time during which both feet (i.e. double support) are in contact with the ground (Winter, 2005). Corrections to balance can be performed by the legs only when in contact with the ground, this is when the force resulting from muscle activation will have a direct mechanical effect on balance. Hence, to maintain dynamic equilibrium during walking, the nervous system is challenged with preserving balance at every step (i.e. postural control) while maintaining the rhythmic movement of the legs (i.e. locomotor activity).

Nevertheless, controlling balance during walking is mostly an extension of balance control during standing. This is clearly reflected in the development of independent walking in infants. On average, infants begin to stand with help by the age of 8 months, walk with help at 11 months, pull themselves to a standing position at around 12 months, stand alone at 14 months, and walk alone about one month after this. Infants are thus capable of walking alone by the age of 15 months, and by about 5 to 7 years of age they exhibit adult-like walking characteristics (Woollacott & Shumway-Cook, 1990). This is strong evidence that, in humans, learning to walk starts by learning how to maintain a standing posture. Although, the rhythmic movement of the legs necessary for walking appears long before humans are capable of standing, it is only after a stable standing posture can be maintained that walking occurs. It is then at this moment that balance control mechanisms are integrated within the ongoing locomotor activity to ultimately result in stable bipedal walking.

Among the several advantages of bipedalism is that the upper limbs become free for other uses. The ability of using the arms while walking is one of the arguments often proposed for the evolution of bipedal locomotion. In particular, Darwin (1871) wrote that "man could not have attained his present dominant position in the world without the use of his hands, which are so admirably adapted to act in obedience to his will". However, although not necessary for balance regulation during upright stance, the hands can participate in postural control. In particular, light touch of a stable surface has been shown to have a strong effect on postural control. It has been found in adults that body sway is attenuated by light touch (Holden et al., 1994). Moreover, the effect of light touch on body sway is also present in children that have just begin to walk (Chen et al., 2008). It has been suggested that infants use sensory information from touch to tune the sensorimotor relations for the control of balance (Metcalfe & Clark, 2000). How then is touch sensory information used by a mature nervous system, one that does not necessarily rely on the hands to maintain a standing posture?

The role of tactile information from the hands in modulating balance control during walking based upon sensory input sensations from the hands is an open question. The intention of my thesis is to provide a better understanding of the influence of tactile feedback from the hands in postural control during walking.

Although, a number of studies have focused on the influence of the arms and the hands in balance regulation during standing, the importance of tactile feedback from the hands in balance regulation during walking not been given much attention. In particular, it is not clear yet whether the effect of light touch on balance regulation during standing can be translated during walking. The focus of my thesis is to study the influence of the hands, in particular tactile information from the hands, on balance regulation during walking.

## 1.2 Reflexive control of balance

### 1.2.1 Balance control and simple reflexes

To maintain the body in a standing position the nervous system has to deal with maintaining a high centre of mass over a rather small base of support at the feet (i.e. static equilibrium) by constant delivery of postural adjustments. During walking, postural adjustments have to be carefully integrated within the ongoing locomotor activity to hold the body with an erect posture at the same time that the centre of mass is displaced forward (i.e. dynamic equilibrium). A first approach to the understanding of the mechanisms involved in human postural control was done by having subjects stand on a platform that could be displaced, either backwards or forwards, or tilted, either upwards or downwards (Nashner, 1971). Electromyographic responses from various muscles and movements at different joints were used to quantitatively evaluate the neuronal mechanisms underlying the control of posture by comparing the responses from the different types of perturbations (i.e. translation or rotation) among different groups of patients. Since the first use of this technique, different ways of perturbing posture, both during standing and walking, have been used to expand the understanding of how the nervous system deals with the challenges of the inherently unstable nature of bipedal upright stance.

Translation of the platform over which subjects stand results in rapid corrective responses involving primarily the musculature at the ankle (Nashner, 1976). Corrective reactions evoked in response to balance disturbances are intended to stabilize the sway induced by the disturbance. Because the responses occur short after the onset of the disturbance and involve primarily the stretched ankle muscles, it was suggested that postural control during standing was regulated by stretch reflex responses. The idea of stretch reflex responses as the main mechanism involved in balance regulation during standing was first proposed to explain balance regulation during quiet stance. Hellebrandt (1938) proposed the concept of the 'stretch reflex strategy', hypothesizing that the sway of the body around the ankle would stimulate stretch afferents from the stretched muscles that would then be contracted reflexively to regulate a standing posture. Similar to a spring, a deflection of the body from its equilibrium position would result in an opposing torque that would drive the body back to this position. Because little muscular activity is required to maintain balance during standing

(Bonnet et al., 1976), balance regulation could be associated with an essentially reflexive control mechanism such as the stiffness at the ankle associated with the spring-like properties of muscles.

However, there have been many arguments opposing the stretch reflex strategy. For example, if body sway was controlled exclusively by the stiffness of the ankle resulting from the neuro-mechanical characteristics of the muscle, then additional sensory input would not have an effect on body sway. It was then argued that the increase in body sway resulting from standing with the eyes closed could not be explained by that model. However, sensorimotor reflexes altogether with reflexes from the visual and the vestibular systems, are able to modulate ankle stiffness. Therefore, the maintenance of a standing posture can be regulated by local sensory reflexes and the influence of other sensory sources in the gain associated with these reflexes (Fitzpatrick et al., 1992). Due to its simplicity, the stretch reflex strategy has been attractive to many (Fitzpatrick et al., 1992; Winter et al., 1998; Winter et al., 2001). However, recent studies have proven this theory incorrect, mainly because it does not explain a number of findings. A recent study has shown that, although the intrinsic ankle stiffness does participate in the generation of a torque opposing body sway, it is not sufficient to stabilize balance during quiet stance (Morasso & Sanguineti, 2002). Moreover, the results from other studies have demonstrated that spinal stretch reflexes are not relevant to the maintenance of quiet stance. Soames and Atha (1981) found in standing subjects a constant activity in the muscles of the ankle, suggesting they were generating a constant torque about the ankles and not responding to changes in sway. Altogether, these results suggest that, although the intrinsic ankle stiffness may play a role during balance regulation, more complex sensorimotor interactions are necessary to control balance.

### 1.2.2 From reflexes to synergies

Even though balance during standing is not solely regulated by the reflexive torque resulting from joint stiffness, it is important to note that corrective responses to balance perturbations are automatic and highly stereotyped in humans. Rapid displacement of the platform over which subjects stand result in responses involving activation of particular groups of muscles (Nashner, 1977; Nashner et al., 1979; Diener et al., 1984). It has been argued that these stereotyped responses are guided by postural strategies aimed at restoring balance by repositioning the body to an equilibrium position, that is, by moving the centre of mass back into the base of support (Horak & Macpherson, 1996). Nashner & McCollum (1985) hypothesized the existence of two separate strategies that could be combined to generate more complex responses to balance disturbances generated in the antero-posterior direction. The 'ankle strategy' moved the body to the equilibrium position by generating a torque at the ankle by activating ankle joint muscles first, followed by activation of thigh and trunk muscles.

Conversely, the 'hip strategy' restored equilibrium by generating a movement at the hip by activating muscles from the trunk and thigh, antagonists to the those activated during the ankle strategy, in a proximal-to-distal ordering with a very modest activation of muscles in the ankle. The authors further expanded their observations suggesting that the hip strategy would be activated in situations where the generation of an ankle torque would be ineffective.

To implement a certain strategy in response to a balance disturbance, the nervous system needs to activate a large number of muscles, sometimes spanning across multiple joints, in a timely manner and with specific amplitudes. To control individually the activation from each muscle would require a high load on the nervous system. Hence, to generate the appropriate spatio-temporal pattern of muscle activation associated with a response strategy the nervous system makes use of motor synergies. In the cat, the isolated spinal cord is capable of generating complex movements such as scratching and locomotion (Sherrington, 1906). Sherrington believed that the spatial and temporal organization required for a specific movement was driven by afferent input and linked by spinal reflexes. Producing coordinated movements such as postural responses would only require activation of the centres associated with the specific movement, thus resulting in a very low load for the nervous system. In this view, the production of complex movements could result from coordinated activation of motor synergies defined by reflex networks located at the spinal cord.

Contrary to the anatomical view proposed by Sherrington, synergies were also studied from a functional approach. It was first proposed by Bernstein (1967), and later expanded by Macpherson (1991), that the nervous system acts in a hierarchical manner to control any complex movement and overcome the excessive number of degrees of freedom involved in the generation of such movement. In this view, the upper level in the hierarchy is responsible for the planning of the movement, whereas the lower levels are involved in the construction of the movement. The hierarchical control schema for motor control was initially proposed as the mechanism by which the nervous system generated and controlled voluntary movements. Human postural responses are also considered to be organized by the combination of synergies (Nashner, 1977; Horak et al., 1997). For instance, as was discussed earlier, the nervous system selects one of various synergies to counteract anteroposterior body sway induced from a balance perturbation (Nashner & McCollum, 1985). The particular synergy that is triggered depends on conditions such as the amplitude and velocity of the perturbation, as well as prior experience from the subject (Nashner & McCollum, 1985; Horak & Nashner, 1986). In this sense, the definition of a synergy spans beyond reflex networks located at the spinal cord into a mechanism involving multiple centres from the nervous system.

The presence of motor synergies, both from an anatomical and a functional point of view, reduces the complex task of activating several muscles to counteract the effect of postural disturbances down to the simple task of choosing the most appropriate combination of synergies necessary to restore balance. It was suggested, from platform perturbation studies with cats, that automatic postural responses (APRs) result from the combination of a few synergies, and that these synergies can be turned on and scaled independently to accommodate the response to the desired result (Macpherson, 1988a; Macpherson, 1988b). Ting & Macpherson (2005) found, by perturbing balance in standing cats with rapid multi-directional translations of the support platform, that 95% of the APRs could be accounted by as few as four synergies.

### 1.2.3 Sensory regulation of balance

The nervous system gathers information about the internal (i.e. body configuration) and external (i.e. surroundings) worlds from multiple sources of sensory information, and integrates it to regulate posture. Sensory input from multiple sensory modalities plays a major role in postural control. Among the different sensory modalities available to the nervous system, balance is strongly influenced by the visual, vestibular and somatosensory systems. For instance, stimulation of the visual (Berthoz et al., 1975; Nashner & Berthoz, 1978), vestibular (Njiokiktjien and Folkerts, 1971; Séverac Cauquil et al., 1998), and somatosensory (Jeka and Lackner, 1994; Jeka et al., 1997, Kavounoudias et al., 1998) systems has been shown to strongly affect body sway. Body sway, the result from constant changes in the level of muscle activation necessary to correct for the inherent stabilities in the mechanics of an upright posture, provides a measure of balance control performance. Thus, each one of the aforementioned sensory modalities has a clear impact on balance control.

The central nervous system ensures that balance is maintained by integrating the input from multiple sensory modalities describing the internal and external worlds into appropriate motor actions that will control stability by minimizing the risk of losing balance or by restoring equilibrium following a balance disturbance. The task of rapidly selecting and activating an appropriate corrective response to a balance disturbance is not simple. Misiaszek (2006) used a model based on finite state control theory (i.e. If-Then rules) to illustrate how the central nervous system could deal with the complicated task of integrating multiple sensory inputs into motor actions. In essence, in the If-Then rules model multiple sensory inputs are continuously evaluated to determine the state of the rules and accordingly generate the appropriate motor outputs. Sensory inputs can be added, removed or scaled according to the requirements of the balance task. For example, the vestibular system provides the central nervous system with information about the acceleration of the body and allows the control of an upright posture that results in alignment of the body with gravity (Day & Fitzpatrick, 2005). Njiokiktjien & Folkerts (1971) found that stimulation of the vestibular apparatus will affect balance but that in the presence of vision the effect will be inhibited. According to the If-Then rules model, input from every available sensory source will be integrated for the control of balance, but each source will be evaluated according to its relevance for the task.

During standing, balance is achieved by maintaining the centre of mass within the base of support. Therefore, loss of balance will occur when the centre of mass is moved away from the base of support, and corrective responses will be required to restore the centre of mass to its equilibrium position. Nevertheless, responses to balance perturbations are often triggered well in advance of a significant change in the position of the centre of mass (Patla, 2003). Moreover, changes in joint trajectory following perturbations applied at the waist during treadmill walking were only observed after the responses in the legs and arms were activated (Misiaszek, 2003). Although, visual, vestibular and somatosensory input can activate postural responses, rapid APRs are likely to be triggered by the latter. Evidence supporting somatosensory input in activating the initial APR is provided by the fact that the latency of the responses activated by visual and vestibular input are too long, and in the absence of visual and vestibular input APRs are still present (Rothwell, 1994).

Nonetheless, visual and vestibular input contributes to the fine tuning of postural responses. For the visual system, the responses evoked from a sudden displacement of the support platform under normal vision conditions are reduced when the visual field is manipulated to appear stationary. Even though body sway is induced from the displacement of the support, the absence of a change in the visual field results in a reduction of the response as if the perturbation was smaller compared to the normal condition (Nashner & Berthoz, 1978). For the vestibular system, patients with loss of vestibular input show no change in the responses to perturbations delivered by translating the support platform. However, these patients show a reduced response to platform rotations, thus depicting the influence of vestibular input on the final shape of the response (Greenwood & Hopkins, 1976). Postural responses are thus modulated by sensory input from different sensory modalities.

## 1.3 Integrating balance control and walking

### 1.3.1 Balance control modulation

Apart from being modulated by sensory input, balance control also adapts to the conditions of the task. For instance, Nashner (1976) developed a simple experiment that allowed the comparison of reflex responses to different postural disturbances that resulted in similar sensory stimuli. Subjects standing on a platform were perturbed by 1) a rapid backward displacement and 2) a rapid upward tilt of the platform. Although, only the rapid displacement of the platform resulted in a displacement of the centre of mass, both perturbations resulted in an imposed dorsiflexion of the ankle joint. Subjects perturbed with rapid displacement of the platform showed consistent activation of the medial gastrocnemius (MG) muscle, most likely driven by a stretch reflex response triggered from the rapid elongation of the muscle. A similar response was observed initially in MG when subjects were perturbed with rapid rotation, instead of a translation, of the platform. However, after a few repetitions of the rotation perturbation, the activation in MG was suppressed. The change in the response was explained by the mechanical effect of contracting the MG muscle. Activation of MG when the platform is displaced horizontally will result in a torque that will stabilize the sway induced by the perturbation. On the contrary, activation of MG when the platform rotates backwards will result in a torque that will increase the sway already induced by the perturbation. Therefore, the responses to perturbations were adapted to the 'usefulness' of the response for each type of disturbance. In other words, reflex gains can be modified according to the context so that a response that could destabilize posture would be suppressed.

Besides the effect of the conditions of the task, corrective responses to balance perturbations are also adapted to the behavioural context. A clear example of this comes from the strong association found between postural control and the fear of falling in the elderly. Maki et al. (1991) found that subjects who expressed a fear of falling showed poorer balance control of spontaneous sway in one-leg and blindfolded two-legs stance tests. The anxiety associated with the fear of falling may impose an additional demand to the nervous system that would affect postural control. Carpenter et al. (1999) extended the results observed in the elderly by examining the stability of healthy young subjects under different conditions of postural anxiety. The authors analyzed body sway for different heights of the support platform and found a strong influence between postural control performance and the level of postural anxiety associated with the height of the platform. These examples show that not only the raw information from sensory input affects balance, but rather it is the sensory information combined with the interpretation of that information that has a strong effect on postural control.

Cortical commands can affect the responses evoked in lower centres in the nervous system. Changes in the transmission in sensorimotor pathways necessary to suit a particular task or context were referred by Prochazka (1989) as the 'sensorimotor set'. The concept of sensorimotor set can be explained as the tuning of the nervous system to respond to a stimulus to reach a certain goal under certain restrictions defined by the context. It is important to annotate that rapid postural responses are considered to be automatic because they cannot be modified volitionally (Diener et al., 1991). However, the amplitude of the responses can be modified by the subject's sensorimotor set (Horak et al., 1989). "A sensorimotor set is a state in which transmission parameters in various sensorimotor pathways have been adjusted to suit a particular task or context.

This includes parameter adjustments evoked by conditioning, and parameter schedules in stereotyped tasks such as gait." (Prochazka, 1989).

### 1.3.2 Balance control during walking

Balance control has been mainly studied during standing. Although many principles translate also to balance control during walking, it is evident that responding to a balance disturbance while walking imposes a more difficult challenge to the nervous system. Successful walking is achieved by regulating postural control along with the displacement of the body. Thus, postural control and locomotion are closely related. For instance, the contribution to balance that can be provided by a leg during the swing phase is very different to the contribution that same leg can provide to balance during the stance phase. During the stance phase, activation of muscles in the leg will result in the generation of forces that will affect immediately the position of the centre of mass. This effect is absent when muscles of the leg are activated during the swing phase. As a result, it would be expected that when both feet are simultaneously in contact with the ground (i.e. double-support), activation of muscles in the legs would help to rapidly recovery balance. This is not the case. During the period of double-support the support base is not very firm because one foot is accepting weight while the other is pushing off (Winter, 1995). During walking, balance corrective responses have to be integrated within the constant change of support from one leg to the other, that is, the nervous system is challenged with the task of modulating balance control according to the step cycle.

Phase modulation of balance corrective responses has been demonstrated in different scenarios. For example, Patla (2003) showed that the same perturbation can trigger different balance corrective responses depending on whether perturbations were delivered at the right or left leg single support periods. Subjects walking on a treadmill were perturbed mechanically by unexpected pushes of the upper body to the right. Perturbations delivered when the left foot supported the body resulted in abduction of the right swing leg and subsequent increase in step width. Conversely, perturbations delivered when the right foot supported the body resulted in adduction of the left swing leg and subsequent decrease in step width. Although both strategies result in different muscle activation patterns (i.e. abduction or adduction of the swing leg), they both have the common goal of stabilizing balance by moving the base of support in the same direction the centre of mass is moving as a result of the perturbation. This goal can only be achieved if the balance corrective responses targeted at regaining balance are adjusted to the step cycle.

Balance corrective responses during walking are also modulated by the context. Misiaszek & Krauss (2005) measured the responses to perturbations delivered at different points in the step cycle to subjects walking on a treadmill under different conditions of arm restriction. The latency of the responses was not affected by the arm restriction condition, but the responses evoked when arms were crossed across the chest showed a strong facilitation compared to the normal condition. Thus, similar to balance corrective responses during standing, postural responses to perturbations delivered during walking are modulated according to the context-dependent needs of the task. However, the effect of restricting the arms was most relevant early in the stance phase, particularly at heel-strike. Therefore, the effect of the task on postural responses is not constant across the step cycle but instead is modulated by the step cycle. In other words, the nervous system integrates the requirements of the task within the ongoing locomotor activity to provide the appropriate response to a given balance disturbance occurring at a particular point in the step cycle. Postural responses during walking are stereotyped and adapt both to the sensorimotor set and to the step cycle.

Corrective responses to perturbations delivered during walking have been studied for slips (Tang & Woollacott, 1998; Marigold et al., 2003), trips (Eng et al., 1994), translation perturbations of the support surface (Berger et al., 1984; Dietz et al., 1987; Tang et al., 1998), and perturbations at the waist (Misiaszek, 2003). Common to each one of these perturbation paradigms are the stereotyped reactions evoked in leg muscles in response to the disturbance. For example, similar to the responses evoked to perturbations delivered during standing (i.e. ankle strategy), responses to perturbations delivered early during the stance phase of walking will result in early activation of the ipsilateral tibialis anterior (TA) and vastus lateralis (VL) muscles whether perturbations resulted from sudden deceleration of the treadmill belt (Berger et al., 1984), forward translations of the support surface while walking along a walkway (Tang et al., 1998), or backward perturbations at the waist during treadmill walking (Misiaszek, 2003). The similarity in the strategies used by the nervous system to respond to balance perturbations, independently from the locus of application of the disturbance, strongly suggests the presence of a centrally coordinated response program.

## 1.4 The arms and the regulation of balance

### 1.4.1 Whole-body responses

Responses to perturbations to balance are not limited to activation of the musculature in the lower limbs. Instead, balance corrective responses involve the whole-body (Marigold & Misiaszek, 2009). For instance, activation of muscles in the torso have been reported in association with responses in leg muscles to perturbations delivered by forward displacement of the force plate over which subjects stepped (Tang et al., 1998). The most relevant evidence that corrective responses to balance perturbations involve activation of muscles besides those in the legs is that arm movements are evoked in conjunction with the reactions in the legs.

Activation of muscles in the arm have been reported for different perturbation paradigms. Responses in arm muscles have been studied for slips (Dietz et al., 2001; Marigold et al., 2003), trips (Roos et al., 2008) and perturbations at the waist (Misiaszek, 2003). For instance, the rapid activation of muscles in the supporting leg following a slip are accompanied by responses in muscles of the unperturbed leg altogether with muscles in the upper body and arms. During a slip, the responses in the arms occur at similar latencies as those measured from the responses in the legs (Marigold et al., 2003). Moreover, a similar response is observed when the balance disturbance results from a perturbation applied at a body segment other than the legs or the arms. Perturbations delivered at the waist result in activation of arm muscles that occur simultaneously with activation of leg muscles (Misiaszek, 2003). The concurrent activation of arm and leg muscles independent from the locus of the disturbance depicts a clear whole-body balance response strategy, most likely involving a motor synergy incorporating altogether muscles from the legs and the arms.

The movement of the arms play a role in maintaining stability. First, the arms can participate in balance regulation by dissipating the centre of mass momentum induced by a perturbation whether it results from a slip (Oates et al., 2005) or a trip (Roos et al., 2008). Second, arm movements can be activated to protect the body from injury by arresting a fall (Robinovitch et al., 2005; Feldman & Robinovitch, 2007). Finally, the movement of the arms could be targeted to reach for nearby rails when balance has been compromised (McIlroy & Maki, 1995; Maki & McIlroy, 2006). There is therefore a large repertoire of actions available to the arms to assist the legs to regain balance upon a perturbation.

Nevertheless, the arms also play a role in balance regulation that does not involve their movement. For instance, even though reaching to external objects for support is commonly used as a technique to regain balance after it has been disturbed (McIlroy & Maki, 1995; Maki & McIlroy, 1997; Maki et al., 1998), there are some contexts for which this protective response would be suppressed. Bateni et al. (2004) measured the responses in the arms to balance perturbations during standing when subjects were performing different grasping tasks. The authors found that holding an object in the hands will largely inhibit the reach-and-grasp responses targeted at enhancing balance, independently of whether the object being held provides balance support (e.g. a cane) or not (e.g. the handle of a cane). Misiaszek & Krauss expanded these observations with a series of experiments involving different tasks for the arms during walking. They found that the responses evoked in the legs from balance perturbations are modified according to the task the arms are involved in. When the arms are restricted to move by lightly folding them across the chest or clasping them behind the back, the amplitude of the responses in the leg muscles is amplified compared to when they are free to move (Misiaszek & Krauss, 2005). Conversely, holding on to stable handles will largely attenuate or even suppress the responses in leg muscles (Misiaszek & Krauss, 2004). Altogether, these results are evidence that corrective reaction strategies are also modulated by the task engaged by the arms.

### 1.4.2 Light touch and balance regulation during standing

The most compelling evidence of balance modulation from upper limb tasks is provided from experiments of balance and light touch. Body sway is inherent to standing. Body sway results from the constant changes in the level of muscle activation necessary to correct for inherent instabilities in the mechanics of an upright posture, and thus provides a measure for the performance of balance control. Holden et al. (1987) were the first to test the effect of light touch on balance during standing using body sway as a measure of balance control performance. They tested the effect of light touch on balance by having subjects standing on a platform maintaining precision contact of the index finger with a stationary bar. The authors found that the increase in body sway resulting from standing in the dark (i.e. eyes closed) was attenuated with the provision of light touch. Moreover, they found that light touch was able to stabilize body sway to a level comparable to that measured when subjects stood with full sight. The benefits of light touch in stabilizing body sway has been studied by many authors since (for reviews Jeka, 1997; Wing et al., 2011).

The effect of touch on balance could be associated with an increase in stability arising from the additional support available through the touch contact. However, light touch has been dissociated from mechanical support by having subjects maintaining contact force levels below 1 N, a value that is much below the necessary value to provide mechanical support (Holden et al., 1994). In addition, Kouzaki & Masani (2008) measured the effect of light touch on body sway during standing before and after applying tourniquet ischemia to the upper limb. Ischemia can induce a membrane depolarization, due to inhibition of the electrogenic $Na^+$/ $K^+$ pump and the consequent increase in extracellular $K^+$ ions (Bostock et al., 1994; Mogyoros et al., 1997). Hence, applying tourniquet ischemia to the upper limb would result in depression of the sensory signals transported via peripheral nerves from the arm. Kouzaki & Masani (2008) found that the stabilizing effect of light touch was abolished by applying tourniquet ischemia to the upper limb, providing direct support to the hypothesis that the effect of light touch on body sway is linked to tactile feedback from the fingertip, irrespective of mechanical support.

The first results depicting the stabilizing effect of light touch on balance during standing showed that contact cues from the hand were able to substitute for visual cues in balance control (Holden et al., 1994; Jeka et al., 1994; Clapp & Wing, 1999). Further studies showed that tactile feedback from the index finger in contact with a stable support was able to compensate for the loss or deterioration of other sensory systems providing inputs relevant to balance control. For instance, Lackner et al. (1999) found that subjects with bilateral vestibular loss showed a reduction in body sway with the provision of light touch through contact of the index finger with a stationary surface. Moreover, subjects with vestibular dysfunction showed a smaller sway when provided with light touch in the dark compared to when they were provided with vision but not touch. In addition, Dickstein et al. (2001) studied the effect of light touch on body sway in patients with somatosensory loss in the feet from diabetic peripheral neuropathy. They found the stabilizing effect of light touch on balance in the somatosensory patients was comparable to the effect observed in the healthy subjects. Thus, light touch can provide sensory cues that can be integrated into balance control during standing.

Further evidence showing that tactile feedback from light touch participates in balance control was provided from experiments where the contact surface moved instead of remaining fixed. Jeka et al. (1997) provided touch to subjects maintaining a tandem posture through a device that was able to oscillate sinusoidally from side to side at frequencies ranging from 0.1 Hz to 0.8 Hz. The authors found from spectral analysis of the sway that, for frequencies up to 0.5 Hz, body sway was entrained by the motion of the contact surface. In a later experiment, Wing et al. (2011) expanded these results by including, altogether with the fixed contact surface condition and 0.3 Hz and 0.5 Hz oscillating conditions, two more conditions to the experiment. First, a 'superimposed' condition was defined by having the contact surface moving with superimposed 0.3 Hz and 0.5 Hz oscillations. Similar to the single frequency entrainment, spectral analysis of body sway during the superimposed condition showed that body sway was also entrained with more complex oscillations of the contact surface. Second, a 'biological' condition was defined by having the contact surface move based on a previously recorded sway from another participant. The authors found for this condition that body sway was increased compared to the fixed condition but not compared to the single or the superimposed oscillations conditions. It is important to note that this result contrasted with the observations made by Johannsen et al. (2009) in their study on balance and interpersonal light touch (IPLT). They found that light touch, both with a fixed contact surface and with the finger of another participant (IPLT), showed a reduction in body sway compared to the no-touch condition, with a larger reduction observed during the fixed condition. Perhaps the interaction between two subjects during IPLT results in more complex internal dynamics that would account for the difference in the observations. Despite that, put together, the results from all three studies are evidence that sensory cues provided through tactile feedback from the hand affect balance control performance.

The effect of light touch on balance control has also been assessed from the responses to balance perturbations. Johanssen et al. (2007) studied the effect of light touch on voluntary and involuntary balance perturbations. Subjects self-initiated a perturbation (voluntary perturbations) by pulling a cable, and were exposed to involuntary perturbations from pulls imposed by the experimenter. The authors found for both perturbation paradigms that balance was restored faster when light touch was provided. In addition, Dickstein et al. (2003) studied the effect of light touch on corrective responses to perturbations in subjects with diabetic neuropathy. Patients with somatosensory loss due to diabetic neuropathy show a clear balance impairment. In particular, they cannot appropriately scale the magnitude of APRs to the velocity of the perturbation. However, the scaling of postural responses was improved when diabetic neuropathy subjects were provided with fingertip touch. These results thus suggest that tactile feedback from the finger has a dynamic effect on postural control.

During normal standing the arms hang by the side of the body. Does the change in posture necessary to maintain light touch result in an additional task constraint? Riley et al. (1999) tested the effect of light touch under different conditions of postural demand. They provided light touch through a hanging curtain, and defined two groups of subjects, one for the touch-relevant condition and another for the touch-irrelevant condition. Subjects on the touch-relevant group were instructed to touch and maintain the finger fixed on the curtain. On the contrary, the subjects from the touch-irrelevant group were positioned so that contact with the curtain was maintained but they were not instructed to focus on maintaining contact with the curtain. The authors found that sway was reduced with the provision of touch only when the participant's attention was driven toward maintaining contact with the curtain (touch-relevant group). In another experiment, Vuillerme et al. (2006) used a more direct approach to evaluate the attentional demands of light touch for postural control. Reaction time (RT) to an auditory stimulus was used in the experiment to quantify the attentional demand during the experiment. The authors found an increase in RT when touch was provided, suggesting an increase in attentional demands when using light touch in balance control. However, it is important to note that in these studies, the attentional demands of the task of responding to an auditory cue could themselves influence the findings. Similarly, maintaining contact with a curtain might be per se more attentional-demanding than maintaining touch with a fixed surface. Hence, the results from these studies do not fully support the hypothesis that the effect of light touch on balance control results exclusively from a change in postural demand associated with maintaining contact with the surface. In summary, although maintaining contact with a surface could be observed as an additional postural task, it is most likely that light touch provides additional cues that can contribute to balance control.

### 1.4.3 Light touch and balance regulation during walking

The effect of light touch on balance control has been predominantly studied during standing, and, as of the time of writing this thesis, only one publication has addressed the question of whether the effect of light touch on balance regulation exists also during walking. Dickstein & Laufer (2004) studied the effect of light touch on balance control during treadmill walking under different vision conditions. They found the effect of light touch on balance regulation during walking is comparable to the effect extensively reported during standing. When subjects walked with the eyes open, body sway, measured from the variance of the centre of mass around the mean position, was reduced with the provision of light touch. The most important result was that the inability of subjects to walk on a treadmill with the eyes closed for more than few steps was overcome with the provision of light touch of a stable surface. The authors suggested that light touch provides treadmill walkers with a somatosensory anchor that allows for spatial orientation in the absence of vision. This study clearly showed that light touch influences balance control during walking. But, due to the limitation to allow subjects to walk on the treadmill in the dark, the effect of touch could not be isolated from the visual feedback treadmill walkers rely upon. To better understand the role of tactile feedback from the hands when light touch is provided, it is important to isolate the effect of touch from that of vision. After all, humans, whether sighted or visually impaired, can walk overground in the absence of vision.

### 1.4.4 Cutaneous sensory input and light touch

Tactile information from the hand (i.e. touch) is encoded by sensory receptors located in the skin that respond to mechanical stimulation (i.e. mechanoreceptors). There are four types of structurally and functionally distinct tactile afferents serving the glaborous skin of the human hand (Knibestöl & Vallbo, 1970). These afferents have been grouped according to the basis of their adaptation and receptive field properties, and have been denoted slow- and fast-adapting type I and II afferents (SA-I, SA-II, FA-I and FA-II). The end-organs of these afferents are the Merkel, Ruffini-like, Meissner and Pacini endings respectively. Located superficially with a high density in the fingertips are the FA-I and SA-I afferents. FA-I afferents are particularly sensitive to dynamic skin deformations of high-frequency and insensitive to static forces, while SA-I afferents are sensitive to dynamic skin deformations of lower frequencies as well as to static deformations. FA-I and SA-I afferents are therefore capable of encoding representations of local spatial discontinuities from the touched surface (i.e. edge contours). Deeper in the skin with a uniform distribution are the FA-II and SA-II afferents. FA-II afferents are extremely sensitive to mechanical transients and high-frequency vibrations, making them able to respond to distant events acting on objects held in the hand. On the contrary, SA-II afferents have a low dynamic sensitivity, are particularly sensitive to static forces, and can respond to remotely applied stretching of the skin (Vallbo & Johansson, 1984). Altogether, tactile afferents in the hand can provide the central nervous system with detailed information about the surface in contact with the hand, not only related to the shape and texture of the contacted surface, but also related to the dynamics of the contact between the hand and the surface. The effect of light touch, specifically the effect of tactile feedback from the finger, in the control of balance was discussed in the previous section. That sensory input from the skin can provide information about the movement of the hand relative to the surface, as well as the forces present between the hand and the support, further supports the suggestion that tactile feedback from the finger has an effect on postural control. In particular, tactile afferents from the hand are able to measure shear forces at the point of contact and detect when a slippery contact with the surface is occurring (Macefield et al., 1996). Therefore, cutaneous sensory input from the hand, particularly from the skin in contact with a stable surface when light touch is provided, can encode information relevant for balance control (for review see Johansson & Flanagan, 2009).

Cutaneous reflexes have been suggested to contribute in the regulation of balance control. They can be evoked in muscles by electrical stimulation of nerves containing axons of afferents from mechanoreceptors in the skin (Zehr &

Stein, 1999). In humans, cutaneous reflexes are evoked by delivering trains of constant current to superficial electrodes placed over the predicted path of the nerve to be stimulated. The intensity of the stimulus is set to generate non-noxious paresthesia to the innervation area of the stimulated nerve. That is, the intensity of the stimulus has to be high enough to generate paresthesia but not to activate a nociceptive reflex that would initiate a withdrawal response. Electrical stimulation of cutaneous nerves has been primarily used to study the function of cutaneous afferents during different behaviours. Although, electrically evoked cutaneous reflexes are not relevant to coordination of the limbs during locomotion, they can be used to study different aspects of the function of cutaneous afferents and cutaneous reflex pathways during walking. In particular, cutaneous reflexes have been suggested to assist with movement coordination between the arms and legs during locomotor tasks (Zehr & Stein, 1999). One important characteristic of cutaneous reflexes is that they are modulated according to the conditions of the environment (task-modulation) or the characteristics of a movement (phase-modulation) such as walking (Zehr et al., 1997). The task and phase dependent modulation of cutaneous reflexes (and by extension cutaneous feedback) implies that these sensorimotor pathways serve a meaningful purpose in controlling movements. Whether tactile feedback arising from light touch participates in the regulation of walking balance movement is a question that will be addressed in this thesis. Electrically evoked cutaneous reflexes will be used as neural probes for testing this question.

## 1.5 Thesis outline

It is clear that the arms play an important role in postural control and balance regulation during walking. In particular it has been found that the influence of the arms is not limited to the mechanical support they can provide to enhance balance, but also that tactile feedback from the hands plays a relevant role in postural control. It is also clear that it is through the highly complex sensorimotor interactions in the nervous system that tactile feedback from the hands affects postural control. However, how do tactile cues provided by light touch modulate balance during walking?

To answer to this question and expand the understanding of the role of tactile feedback from the hands in balance regulation during walking, I have addressed in this thesis four different questions in four different projects about balance regulation and feedback from the hands. The first project is presented in Chapter 2. This project was designed to study how responses to perturbations are activated when disturbances are delivered at the arms during walking. Specifically, reactions in the arms and the legs were studied for different requirements of the task involving the direction of the perturbation, the step cycle progression and the instruction given to the subjects.

The influence of light touch on balance regulation has been largely studied during standing, but only partly analyzed in one study during walking. The second project of this thesis, presented in Chapter 3, aims at answering the questions that still remain unresolved about the effects of light touch on balance regulation. This project was designed to evaluate corrective responses to perturbations delivered during walking under different conditions involving light touch.

Tactile cues are gathered from cutaneous receptors in the skin and transmitted to the central nervous system through cutaneous sensory pathways. The last two projects are targeted at studying the effect of light touch on cutaneous sensory pathways. Cutaneous reflexes evoked from electrical stimulation of nerves serving the hand and the foot have been largely used to understand their influence on different behaviours such as locomotion (Zehr & Stein, 1999). The third and fourth projects of this thesis will be specifically targeted at studying the effect of light touch on cutaneous reflexes evoked in muscles of the arm (Chapter 4) and the leg (Chapter 5) by stimulating nerves serving the hand.

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## Chapter 2

# Balance Corrective Responses to Unexpected Perturbations at the Arms

## 2.1 Introduction

Perturbations to balance delivered during walking evoke complex responses involving activation of muscles in the legs, trunk and arms. Corrective reactions to perturbations delivered during walking have been studied for slips (Marigold et al., 2003), trips (Eng et al., 1994), translation perturbations of the support surface (Berger et al., 1984; Dietz et al., 1987; Tang et al., 1998), and also for perturbations delivered at the waist (Misiaszek et al., 2000). Independently from the locus of the perturbation, the responses to balance disturbances involve activation of muscles of the legs that are accompanied by activation of muscles of the arms. In general, corrective reactions to balance perturbations during walking trigger whole-body responses (Marigold & Misiaszek, 2009).

Mobility aids involving the use of the arms are largely used to improve balance control. Standing balance is achieved by maintaining the centre of mass within the base of support. The use of a mobility aid increases the base of support (Tagawa et al., 2000), hence allowing a greater range of motion for the centre of mass without loss of balance. However, walking aids can also destabilize balance.

For instance, Bateni & Maki (2005) reviewed the advantages and possible disadvantages associated with the use of mobility aids. Although they found strong clinical evidence about the effectiveness of the use of walkers and canes to improve balance in adults, they also found there is an increase in the risk of falling when using these devices. The increase in risk was mostly associated with changes in attentional demand that could result from the use of the walking aid. For instance, a strategy commonly used to avert a fall results from targeting the arms to reach for nearby safety handrails (McIlroy and Maki 1995; Maki and McIlroy 2006). However, in another study Bateni et al. (2004) demonstrated that subjects holding a 'cane' would not release it to reach for available handrails in order to recover balance upon delivery of a postural perturbation even if the 'cane' was unable to stabilize balance (i.e. falling backwards) or any value at all (i.e. the top of the cane). The authors concluded that the nervous system prioritizes the ongoing task of holding the object despite sacrificing balance performance and possibly falling. These results show that balance can be enhanced by using walking aids, but the task of holding an object in the hands can compromise balance performance.

When the arms are actively engaged in balance control, such as when utilizing a mobility aid to increase the base of support, then disturbances to the arms can also be a source of balance instability. Similarly, if the arms are engaged in additional tasks, such as carrying a load, then perturbations to the arms or the load can also result in a balance disturbance. Previous investigators have analyzed the responses to perturbations delivered at the arms during standing (Cordo & Nashner, 1982) and also during walking (Nashner & Forssberg, 1986; Hirschfeld & Forssberg, 1991). The majority of the work to date has investigated the balance adaptations to voluntary pushes or pulls to handles. This involves anticipatory postural adjustments associated with the voluntary arm actions (Massion, 1992). Whereas, unexpected perturbations to the arms will require compensatory reactions to the disturbances to prevent or correct for a balance disturbance. To date, only one study has investigated responses to unexpected arm pulls in two subjects (Nashner & Forssberg, 1986). Therefore, corrective balance reactions to disturbances of the arms is not well studied.

The purpose of the present study is to characterize arm and leg reactions to unexpected perturbations delivered through the arms during walking. For this purpose, perturbations will be delivered at random points across the step cycle in one of two directions (i.e. backwards, forward). We hypothesize that unexpected perturbations delivered to the arms will induce rapid onset balance corrective reactions in the muscles of the legs. Responses in the arms to unexpected pulls resulted in responses with latencies shorter than the voluntary reaction times when subjects were instructed not to resist the perturbation (Cordo & Nashner, 1982). Thus, two different conditions involving the 'need' to respond (i.e. oppose or comply to the perturbations) will be defined for the current study. We hypothesized that balance reactions induced by perturbations applied through the arms depend upon the task condition at the time of perturbation.

## 2.2 Methods

To evaluate the responses associated with perturbations at the arms during locomotion, a total of 9 subjects (three males and six females) were included in the experiment. Ages, heights and weights ranged from 26 to 31 years (mean ± s.d., 27.7 ± 1.80 years), from 158 to 175 cm (165.4 ± 5.48 cm), and from 50 to 76 kg (58.2 kg ± 9.24 kg) respectively. Subjects provided written consent of their participation. The procedures were approved by the University of Alberta Research Ethics Board.

### 2.2.1 Protocol

During the experiment subjects were asked to walk on a motorized treadmill. Each subject selected a comfortable walking speed (0.8 ± 1.2 m/s) which was maintained for the remainder of the experiment. Subjects were instructed to grasp two handles located in front of them without supporting their body weight on them, and to not release them upon their displacement. The handles were adjusted for each subject so that each hand was aligned laterally with the corresponding shoulder, and the height was set so that the elbows would be held at a 90 degrees position while the forearms were held horizontally. The handles were secured to a car mounted on rails that only allowed fore-aft displacements. A drum, located behind the subjects and connected to the car through a series of pulleys, was used to displace the handles in either the forward or backward directions by pushing or pulling the handle attached to it (Fig. 2-1). A few sample perturbations were delivered before beginning the experiment to familiarize the subjects with the protocol. Perturbations were delivered by displacing the handles in either the forward or backward directions.

Perturbations were delivered by rapidly rotating the drum, which in turn pulled the handles forward or backward producing the corresponding displacement. Rotations of the drum were manually generated through a rigid bar attached to it, so that pushing the bar would produce a forward displacement and pulling it a backward one. The maximum displacement of the handles never exceeded 15 cm in either direction, hence the arms were not extended beyond their maximum reach nor flexed as to hit the subject. The duration of the perturbation, measured from the onset until the maximum displacement was reached, never exceeded 250 ± 50 ms. Before each perturbation, the handles were repositioned at the centre of the rail track and the elbow position was verified to be at 90 degrees. Perturbations were delivered while the subjects performed one of two tasks. In the first task, subjects were instructed to react as rapidly as possible to “not allow the handles to move” (OPPOSE). In the second task, subjects were asked to allow the handles to freely be displaced, but not to release them (COMPLY). All subjects performed the OPPOSE task first, and were permitted to rest between tasks if needed.

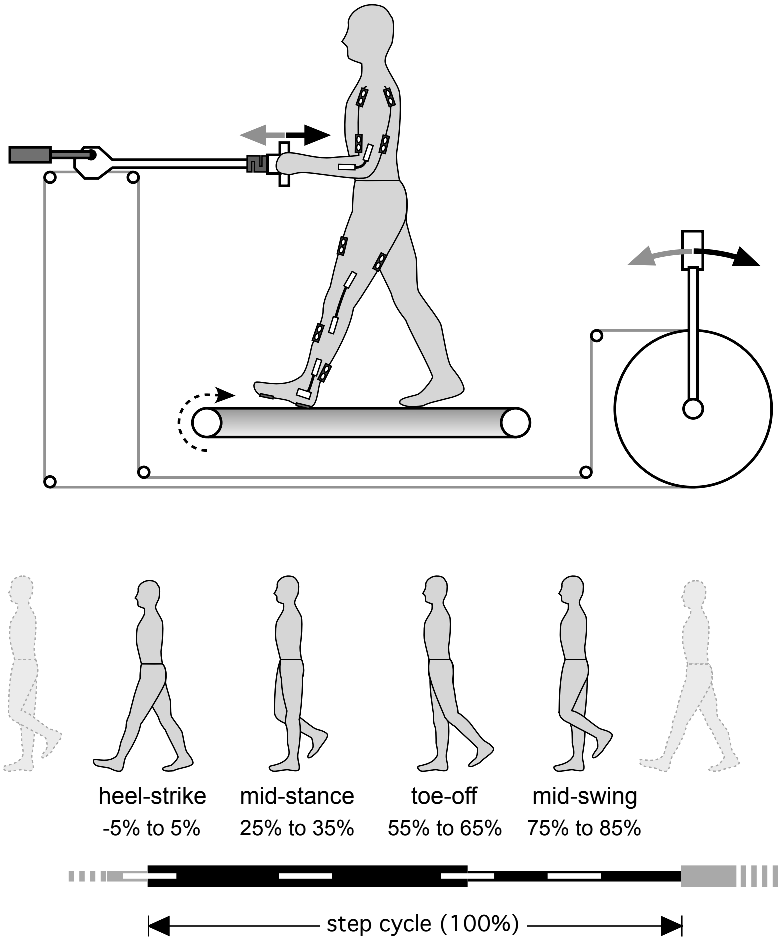

**Figure 2-1:** Schematic diagram of the general setup. Subjects walked on a motorized treadmill while grasping a pair of handles. The handles were positioned so that elbows would be held at a 90 degrees position while forearms were held horizontally when subjects were holding on to the handles. The handles were secured to a car mounted on rails that only allowed fore-aft displacements. A drum, located behind the subjects and connected through a series of pulleys to the car, was used to generate the perturbations in either the forward or backward directions. Perturbations were delivered at heel-strike, mid-stance, toe-off, and mid-swing of the step cycle for both task conditions. The order or presentation of the perturbations was randomized for each subject.

Perturbations were delivered in two directions (forward: FWD, backward: BWD) and at four different points in the step cycle (heel-strike: HS, mid-stance: MSt, toe-off: TO, mid-swing: MSw). The signals from the foot sensors and the handles position sensor were viewed on a two channel oscilloscope by the experimenter delivering the perturbations to verify the timing of the perturbation within the step cycle. In total 20 perturbations were delivered for each combination of direction (2) and step phase location (4), resulting in a grand total of 160 perturbations per task. The order of delivery for the perturbations was randomized before the beginning of the experiment for each subject and each task. Perturbations were delivered with 3 to 5 steps in between to allow the experimenter to reposition the handles back to the center of the rail and subjects to recover from a perturbation.

### 2.2.2 Measurements

A force transducer (Omega LCCA-500, Stamford, CT, USA) located at the handles allowed for the recording of the pulling/pushing force transferred through them, and a linear position sensor (Penny & Giles SLS320, Santa Monica, CA, USA) connected to the car measured the horizontal displacement of the handles. Two force-sensitive sensors were located at the heel and the metatarso-phalangeal joint on the left foot to record foot contact with the ground (Interlink Electronics, Camarillo, Calif., USA). Kinematic data were recorded from the ankle, knee and elbow joints using electrogoniometers (Biometrics Ltd, Gwent, UK). Electromyographic (EMG) recordings were obtained from the tibialis anterior (TA), soleus (SOL), vastus lateralis (VL) and biceps femoris (BF) of the left leg, and the anterior deltoid (AD), posterior deltoid (PD), biceps brachii (BB) and triceps brachii (TB) of the left arm. A pair of Ag/AgCl surface electrodes was placed over the bellies of each recorded muscle, 2 cm apart and aligned to the predicted direction of the muscle fibers. Two ground electrodes were placed over the left tibia and left clavicle. Raw EMG signals were preamplified and band-pass filtered (30 Hz - 1 kHz) using Grass P511 preamplifiers (Astro-Med Inc.; West Warwick, RI, USA). All signals were digitized online at 1 kHz and stored directly to hard drive using a custom-written LabVIEW v8.2 data acquisition routine and a National Instruments data acquisition card (National Instruments PCI-MIO-16E-4, Austin, TX, USA). Post processing of the signals was performed offline: EMG signals were full-wave rectified and low-pass filtered at 50 Hz (zero-lag 4th order Butterworth filter); and signals from the handle force transducer, goniometers and handle position sensor were low-pass filtered at 10 Hz (zero-lag 2nd order Butterworth filter).

### 2.2.3 Data analysis

The data stream from each task was divided into sweeps, each sweep starting 500 ms before left heel-strike, as determined by the foot sensor signal, and lasting for

2000 ms. A perturbed sweep was defined as a sweep within which a perturbation was delivered, and the sweep preceding it was used to define the corresponding control sweep. Control step durations were defined for each control sweep as the time between heel-strikes within that sweep. The average control step duration was calculated as the mean of the control step durations. The onset of a perturbation was defined at the point when a visible deflection in the handles position trace was observed. The perturbation delay was defined as the time elapsed between left heel-strike and the onset of the perturbation, expressed as a percentage of the average control step duration (%ASD). If a perturbation occurred less than 50 ms before heel-strike, its delay was defined by the negative value of the time elapsed between heel-strike and the onset of the perturbation. Perturbation sweeps were categorized according to their direction (BWD, FWD) and delay. Four different bins, spanning 10%ASD, were defined representing the four different points in the step cycle to be analyzed: heel-strike, 0 ± 5%ASD; mid-stance, 30 ± 5%ASD; toe-off, 60 ± 5%ASD; mid-swing, 80 ± 5%ASD (Fig. 2-1). Perturbations that could not be classified in any of the bins were removed from any further analysis. This sorting process resulted in 8 to 18 sweeps to be analyzed for each combination of direction and bin, for each task from each subject.

Perturbed and control data traces were captured accordingly from the perturbed and control sweeps, and grouped for each combination of direction, bin, subject and task. Perturbed traces for each data grouping were aligned to the perturbation onset and then averaged. Each average perturbed trace was then truncated to 500 ms duration, starting 100 ms before the onset of the perturbation. Control traces were aligned to heel-strike, and then normalized in time to the average control step duration using a linear time-normalization method to make their length equal to the average control step duration. From the time normalized control traces, averaged control traces and their 95% confidence bands were calculated. For each group, averaged control traces and their confidence bands were truncated to 500 ms starting 100 ms before the average perturbation onset time for that data grouping. Subtracted traces were then calculated by subtracting the averaged control traces from the corresponding averaged perturbed traces. Analysis of EMG and joint position data was performed using the subtracted traces.

The average control sweep duration before time normalization was used as a measure of the average step duration. Within a subject, a response to a perturbation was considered to be significant in any given muscle if the subtracted trace fell outside the 95% confidence band for more than 25 consecutive milliseconds. The onset of the response was defined as the point after the onset of the perturbation that the subtracted trace deviated from zero, and the response onset latency was measured as the time from the onset of the perturbation until the onset of the response. Muscle response amplitudes were calculated as the average amplitude of the subtracted trace for the first 200 ms of the response. Muscle background activity was calculated as the mean amplitude over a 50 ms window centred at the onset latency of the perturbation to assess muscle activity levels at the time when the perturbation was delivered. EMG amplitudes were normalized to the peak EMG amplitude for each muscle measured from the control steps. Similarly, ankle and knee joint position amplitudes were calculated as the mean amplitude over a 50 ms window centred at the onset latency of the perturbation.

### 2.2.4 Statistics

Data from the undisturbed steps was used to compare the effects of the task on the gait features. In addition, we compared the effects of the direction of the perturbation and the location within the step cycle on each outcome measure separately for each task. One-factor repeated measures ANOVAs were used to determine if gait features were modulated by the task, and also to determine for each muscle if the onset and amplitude of corrective responses were modulated by the step cycle and the direction of the perturbation. All measured values are presented as mean ± s.e.m. All comparisons were performed using a statistical significance level of 0.05.

## 2.3 Results

Perturbations applied at the arms produced corrective reactions that involved activation of arm and leg muscles. During the OPPOSE task, consistent activation of muscles in the arm were accompanied by activation of muscles in the leg in response to the displacement of the handles. On the contrary, during the COMPLY task, no measurable responses were evoked in muscles of the arm, and, only in some subjects, modest responses were observed in muscles of the leg.

### 2.3.1 Modulation of the responses in arm muscles when opposing the perturbations

Perturbations delivered in the BWD direction resulted in robust activation of AD and BB, with modest excitation of both PD and TB. Averaged traces and average subtracted traces from a representative subject responding to BWD perturbations delivered at heel-strike during the OPPOSE task are displayed in Fig. 2-2A and 2-2B respectively. The onset of the response in AD, PD, BB and TB evoked from BWD perturbations had mean latencies of 61 ± 3.5 ms, 56 ± 3.0 ms, 48 ± 3.6 ms and 64 ± 2.8 ms respectively. The data presented in Fig. 2-2 shows that FWD perturbations produced strong responses in PD and TB, but only modest excitation of both AD and BB. The onset of the evoked response in AD, PD, BB and TB from FWD perturbations had mean latencies of 72 ± 5.5 ms, 82 ± 2.2 ms, 75 ± 1.7 ms and 54 ± 3.0 ms respectively. The ANOVA revealed an effect of the direction

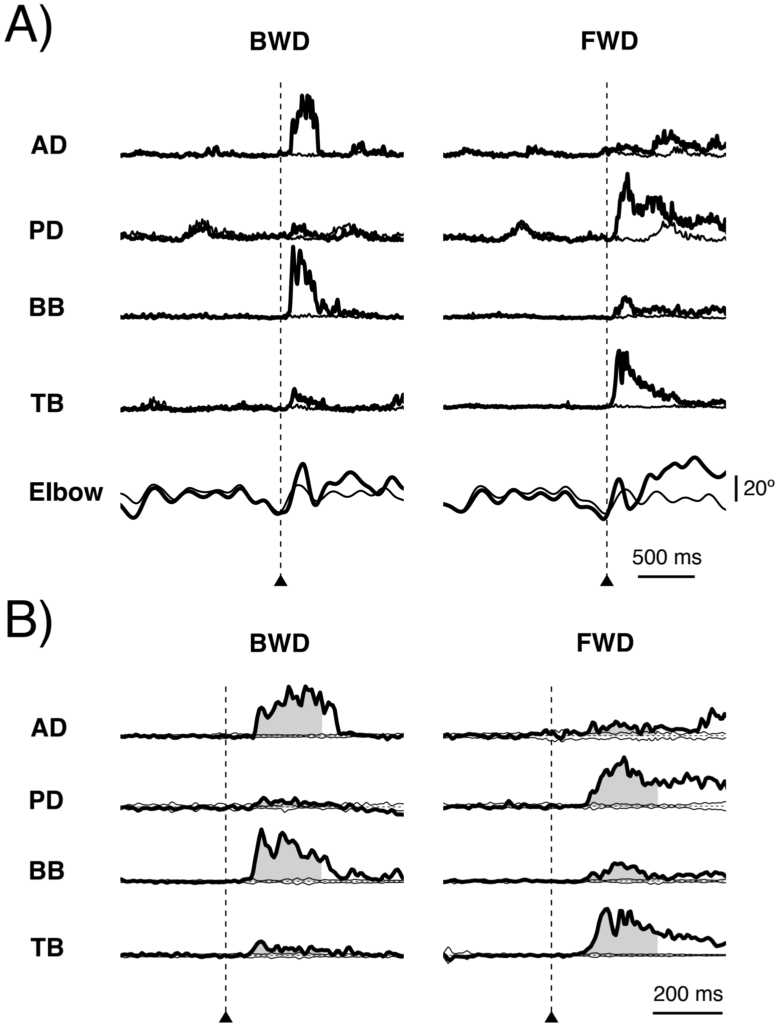

**Figure 2-2: A**, Sample data from one subject showing average electromyography and position traces for perturbed (thick traces) and unperturbed (thin traces) steps for perturbations delivered during the OPPOSE task. The vertical dashed line in each column is aligned to the onset of the perturbation. Upward deflections in the kinematic traces indicate extension for the elbow. **B**, The data shown in A are replotted as subtracted traces by subtracting the average unperturbed traces from the perturbed traces. The average subtracted traces are shown as thick lines. The two thin lines of each set represent the 95% confidence band around the average unperturbed trace. The vertical dashed line in each column is aligned to the onset of the perturbation (AD: anterior deltoid, PD: posterior deltoid, BB: biceps brachii, TB: triceps brachii).

of the perturbation on the onset latency of the response for AD (F=4.01, p=0.045), PD (F=7.82, p=0.005) and BB (F=13.12, p<0.001), but not for TB (F=1.05, p=0.305). Thus, although responses in muscles of the arm can be described as a co-contraction of shoulder and elbow muscles for perturbations delivered at heel-strike, arm muscles were activated earlier for perturbations delivered in the BWD direction compared to perturbations delivered in the FWD direction. In addition, it was found that the latencies of the onset of the responses in muscles in the arm were not altered across points in the step cycle (p>0.05).

The amplitude of the responses to perturbations delivered during the OPPOSE task averaged across subjects and scaled to the peak walking EMG amplitude are shown for different points in the step cycle in Fig. 2-3. It can be seen from the data presented in Fig. 2-3 that, although AD, PD, BB and TB are all activated in response to both BWD and FWD perturbations, activation of AD and BB appears to be more pronounced than the activation in PD and TB in response to BWD perturbations. In contrast, FWD perturbations evoked clear activation of PD, TB and BB, but only modest activation of AD. The amplitude of the responses evoked by both BWD and FWD perturbations varied across the step cycle. The ANOVA revealed a significant effect of the step cycle on the amplitude of the responses to BWD and FWD perturbations in AD (F=17.39, p=0.001 and F=15.96, p=0.003), PD (F=20.38, p<0.001 and F=39.16, p<0.001), BB (F=18.72, p<0.001 and F=15.46, p=0.003) and TB (F=34.02, p<0.001 and

F=20.63, p<0.001). Therefore, responses in the arms are not only modulated by the direction of the perturbation, but also by the position in the step cycle.

### 2.3.2 Phase-dependent modulation of the leg muscle responses during the OPPOSE task

Responses in the arm muscles evoked when subjects opposed the perturbations were accompanied by activation of muscles in the leg. Averaged traces and average subtracted traces from the same subject in Fig. 2-2 responding to perturbations delivered at heel-strike during the OPPOSE task are displayed in Fig. 2-4A and 2-4B respectively. Responses to BWD perturbations delivered at

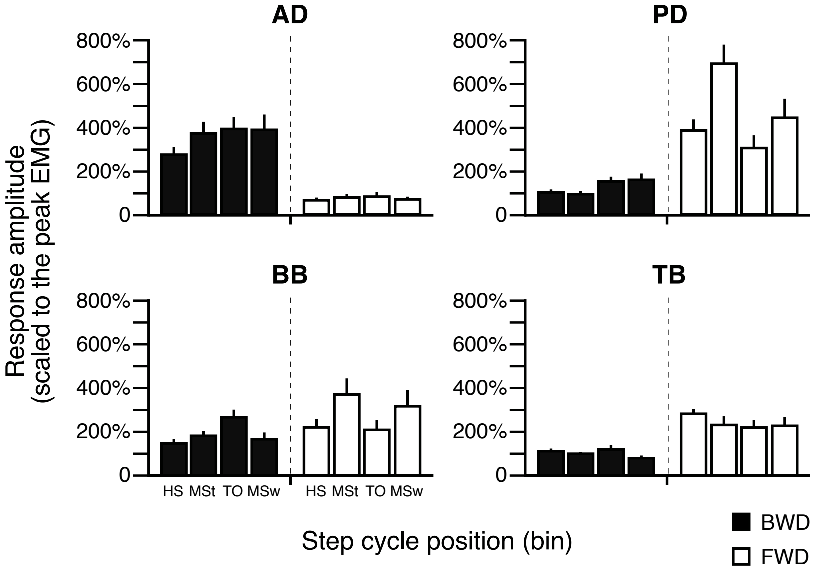

**Figure 2-3:** Means and standard errors of the response amplitudes for AD, PD, BB, and TB to perturbations delivered during the OPPOSE task. The data were standardized to the peak EMG amplitude observed during normal undisturbed walking for that muscle, for each subject. Solid bars represent the data from the backward perturbations. Open bars represent the data for the forward perturbations (HS: heel-strike, MSt: mid-stance, TO: toe-off, MSw: mid-swing).

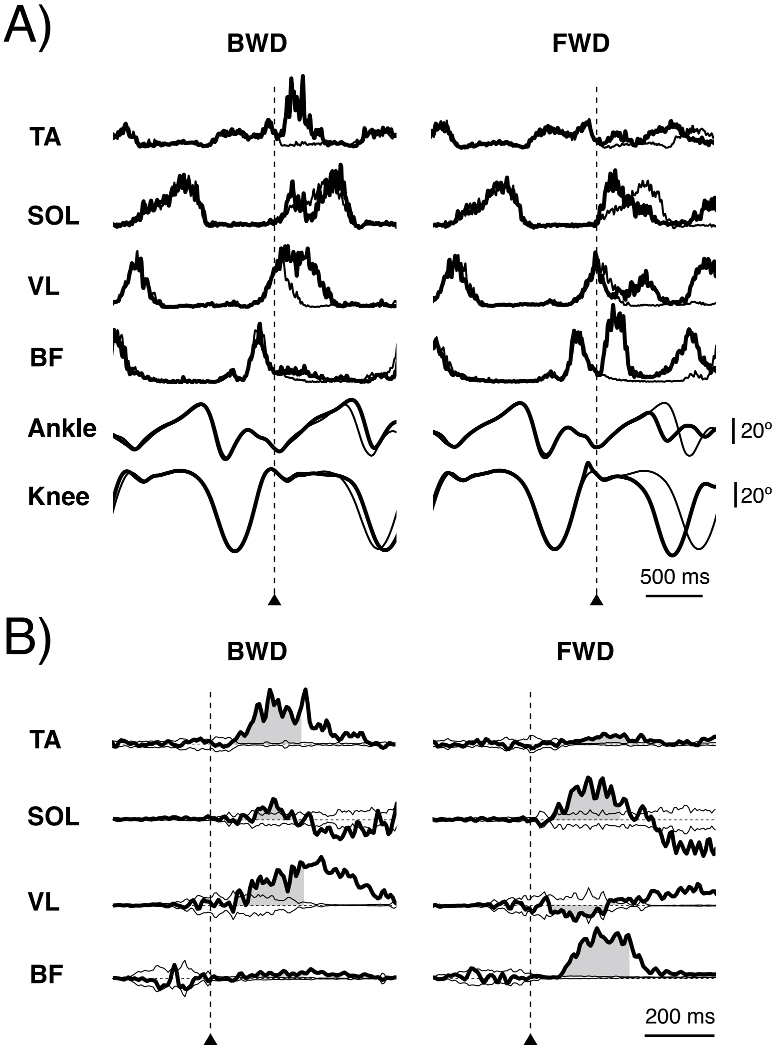

**Figure 2-4: A**, Sample data from one subject showing average electromyography and position traces for perturbed (thick traces) and unperturbed (thin traces) steps for perturbations delivered during the OPPOSE task. The vertical dashed line in each column is aligned to the onset of the perturbation. Upward deflections in the kinematic traces indicate dorsiflexion for the ankle and flexion for the knee. **B**, The data shown in A are replotted as subtracted traces by subtracting the average unperturbed traces from the perturbed traces. The average subtracted traces are shown as thick lines. The two thin lines of each set represent the 95% confidence band around the average unperturbed trace. The vertical dashed line in each column is aligned to the onset of the perturbation (TA: tibialis anterior, SOL: soleus, VL: vastus lateralis, BF: biceps femoris).

heel-strike consisted of robust activation of TA and VL, with a modest excitation of SOL and BF. The response elicited at heel-strike in TA, SOL and VL, but not that of BF, was consistent between subjects. Early responses following BWD perturbations delivered at heel-strike were exhibited in TA for all nine subjects, in VL for eight of nine, in SOL for seven of nine, and in BF for only two of nine (Fig. 2-5). Hence, only the responses in TA and VL were consistently expressed when perturbations were delivered in the backward direction at heel-strike. The average latency for the onset of the response was 55 ± 1.3 ms and 80 ± 4.2 ms for TA and VL respectively. The onset of the response in VL was significantly delayed compared to TA. Similar to previous reports for perturbations delivered

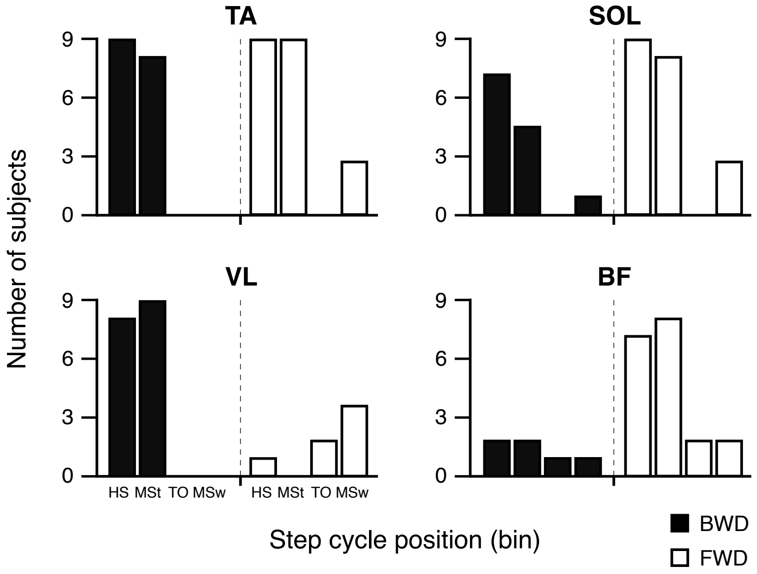

**Figure 2-5:** Frequency of occurrence of a response in each muscle of the leg to perturbations delivered during the OPPOSE task for each bin as indicated by the average subtracted traces.

at heel-strike from pulls at the waist (Misiaszek, 2003; Misiaszek & Krauss, 2005), leg muscle responses to perturbations delivered at the arms at heel-strike also follow a distal to proximal temporal organization.

The pattern of activation of leg muscles in response FWD perturbations at heel-strike was different from the one observed for BWD perturbation. Responses to FWD perturbations at heel-strike were characterized by a robust activation of SOL and BF, with a modest activation of TA, and a suppression of VL activity (Fig. 2-4B). The response evoked at heel-strike in TA and SOL, but not that in VL or BF, was consistent between subjects. All nine subjects exhibited an early response in TA and SOL, seven of nine showed a response in BF and only one of nine presented a response in VL following FWD perturbations delivered at heel-strike (Fig. 2-5). Therefore, the responses in TA, SOL and BF, but not in VL, was consistently expressed when perturbations were delivered in the forward direction at heel-strike. The onset of the response evoked in TA, SOL and BF had mean latencies of 71 ± 2.5 ms, 62 ± 1.4 ms and 56 ± 1.2 ms respectively. Contrary to the clear temporal organization of the responses evoked in TA and VL from BWD perturbations, differences in the onset latency of the responses for FWD perturbation in TA, SOL and BF do not expose a particular organization for the activation of leg muscles following perturbations delivered at heel-strike.

Early activation of the TA, SOL, VL and BF muscles was also observed at other points in the step cycle. In particular, the responses evoked at mid-stance were consistent between subjects (Fig. 2-5). All nine subjects exhibited an early response in VL, eight of nine showed a response in TA, and only four of nine presented a response in SOL following BWD perturbations delivered at mid-stance. Also, all nine subjects exhibited an early response in TA, and eight of nine showed a response in SOL and BF following BWD perturbations delivered at mid-stance. However, the amplitude of the responses decreased at mid-stance compared to heel-strike. Response amplitudes from perturbations delivered during the OPPOSE task averaged across subjects (only those presenting an early response to the perturbation were included) and scaled to the peak walking EMG amplitude are shown for different points in the step cycle for the muscles with the qualitatively most pronounced responses are presented in Fig. 2-6. In Fig. 2-6A, the amplitude of the response in TA and VL to BWD perturbations is shown. The amplitude of the response in TA and VL decreased in mid-stance compared to heel-strike, and was absent at toe-off and mid-swing. The amplitude of the response in SOL and BF to FWD perturbations also changed across the step cycle (Fig. 2-6B). However, these responses were modulated across the step cycle in a particular way. The response in BF remained unchanged at heel-strike, mid-stance and mid-swing, but presented a sharp reduction at toe-off. The response in SOL was particular in that, at mid-swing it presented a reduced activity compared to heel-strike, but at mid-stance FWD perturbations resulted in a suppression of the ongoing activity. It is important to note that the reduction in the amplitude of the responses evoked in leg muscles was mirrored by a reduction in the frequency of occurrence of an early response (Fig. 2-5). This was expected given that the absence of a response can also be described as a response with an amplitude of zero.

### 2.3.3 Task-modulation of the responses

Responses in muscles in the arms were absent when subjects were instructed to comply to the displacement of the handles. Contrary to the OPPOSE task, none of the nine subjects exhibited a significant response in AD, PD, BB or TB when

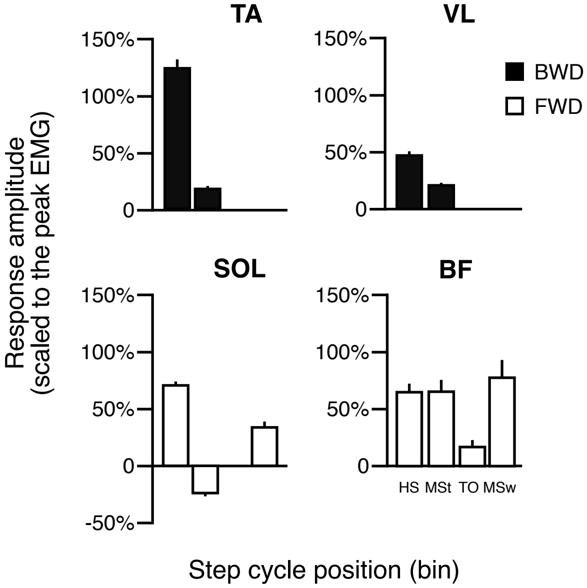

**Figure 2-6:** Means and standard errors of the response amplitudes to perturbations delivered during the OPPOSE task in the backward direction for TA and VL, and in the forward direction for SOL and BF. The data were standardized to the peak EMG amplitude observed during normal undisturbed walking for that muscle, for each subject. Solid bars represent the data from the backward perturbations. Open bars represent the data for the forward perturbations (HS: heel-strike, MSt: mid-stance, TO: toe-off, MSw: mid-swing).

perturbations were delivered during the COMPLY task. Nevertheless, early responses in leg muscles to perturbations delivered during the COMPLY task were still evoked in some subjects. Averaged traces and average subtracted traces from the same subject in Fig. 2-4 responding to perturbations delivered at heel-strike during the COMPLY task are displayed in Fig. 2-7A and 2-7B. Similar to the responses evoked during the OPPOSE task, BWD perturbations delivered at heel-strike during the COMPLY task resulted in activation of TA and VL. The response elicited at heel-strike in TA and VL was very consistent between subjects. Early responses following BWD perturbations delivered at heel-strike were exhibited in TA and in VL for seven of nine subjects (Fig. 2-8). The average latency for the onset of the response in TA and VL was 65 ± 12.3 ms and 97 ± 12.2 ms respectively. In addition to the responses in TA and VL, and contrary to the OPPOSE task, BWD perturbations delivered at heel-strike during the COMPLY task resulted in a suppression of the ongoing SOL activity. This suppression was present in six of the nine subjects (Fig. 2-8). The latency of this reduction in SOL was 88 ± 14.9 ms. Additionally, early responses were also observed in muscles of the leg for some subjects when FWD perturbations were delivered during the COMPLY task. Similar to the responses evoked during the OPPOSE task, FWD perturbations delivered at heel-strike during the COMPLY task resulted in activation of SOL and BF (Fig. 2-7). Responses in SOL were present in six of nine subjects, and in BF in eight of nine subjects (Fig. 2-8). The

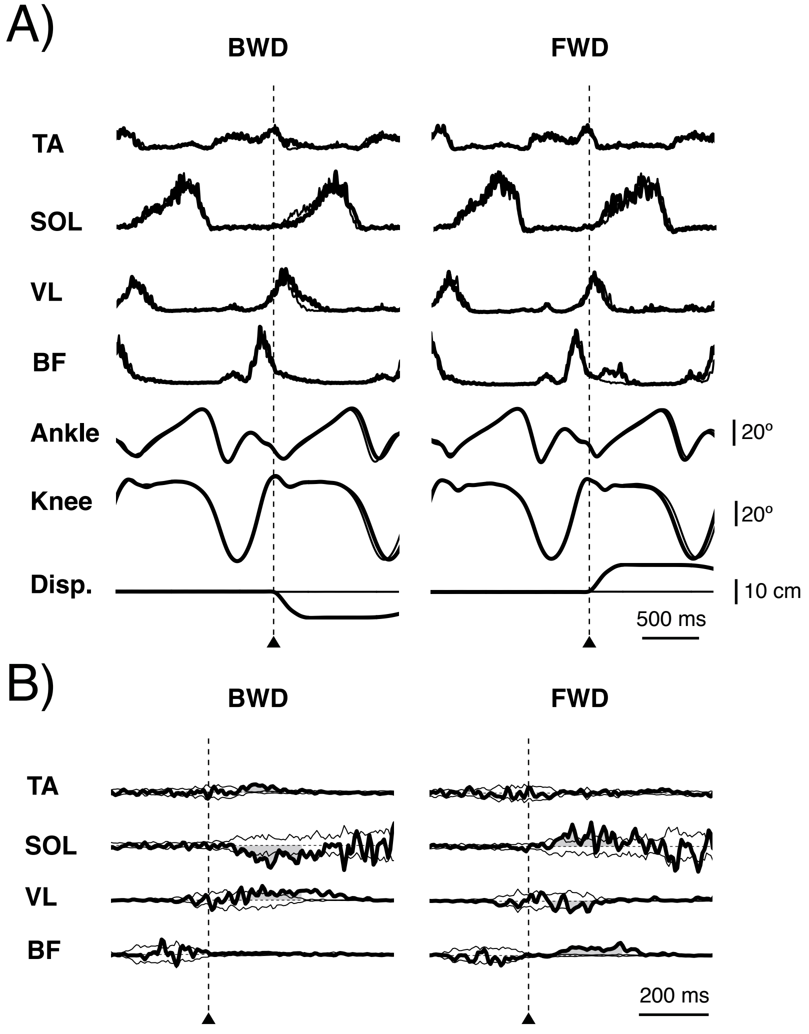

**Figure 2-7: A**, Sample data from one subject showing average electromyography and position traces for perturbed (thick traces) and unperturbed (thin traces) steps for perturbations delivered during the COMPLY task. The vertical dashed line in each column is aligned to the onset of the perturbation. Upward deflections in the kinematic traces indicate dorsiflexion for the ankle and flexion for the knee. Downward deflections in the position traces indicate a backward displacement of the handles. **B**, The data shown in A are replotted as subtracted traces by subtracting the average unperturbed traces from the perturbed traces. The average subtracted traces are shown as thick lines. The two thin lines of each set represent the 95% confidence band around the average unperturbed trace. The vertical dashed line in each column is aligned to the onset of the perturbation (TA: tibialis anterior, SOL: soleus, VL: vastus lateralis, BF: biceps femoris, Disp: handles displacement).

mean latency of the responses in SOL and BF were 102 ± 21.1 ms and 76 ± 15.3 ms respectively.

Early activation of the TA, SOL, VL and BF muscles during the COMPLY task was only observed at heel-strike and not at other points in the step cycle. Although the responses were of a similar latency compared to those measured during the OPPOSE task, the responses measured in the legs during the COMPLY task were of a significantly smaller amplitude. The ANOVA revealed that the amplitude of the response in TA and VL to BWD perturbations applied at heel-strike during the COMPLY task were significantly different from the amplitude of the responses measured during the OPPOSE task (F=261.70, p<0.001 and F=116.53, p<0.001). Similarly, the amplitude of the response in SOL and BF to FWD perturbations applied at heel-strike during the COMPLY task were significantly different from the amplitude of the responses measured during the OPPOSE task (F=304.75, p<0.001 and F=132.14, p<0.001).

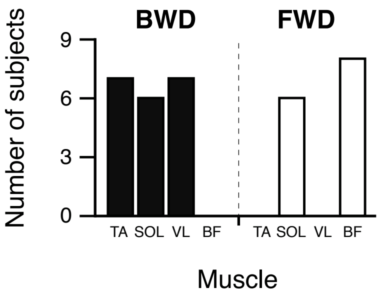

**Figure 2-8:** Frequency of occurrence of a response in each muscle of the leg to perturbations delivered at heel-strike during the COMPLY task as indicated by the average subtracted traces.

### 2.3.4 Effect of the task on gait kinematics

The duration of the step cycle (unperturbed steps) was affected by the task. The ANOVA indicated a significant effect of the task on the step cycle duration ($F=35.74$, $p<0.001$). The step cycle duration was increased when subjects where instructed to comply to the perturbations (COMPLY = 1404 ± 43.1 ms) compared to when they opposed the perturbations (OPPOSE = 1362 ± 33.1 ms). The change in step duration was accompanied by changes in joint kinematics. Joint position was measured for each joint by averaging the joint position over a window centred around each bin. The ANOVA indicated significant differences in knee joint angle at heel-strike ($F=6.73$, $p=0.009$), mid-stance ($F=25.78$, $p<0.001$), and toe-off ($F=4.49$, $p=0.033$). Changes in knee joint angle resulted in a consistent increase in knee extension when subjects were asked to comply to the perturbations compared to when they were asked to oppose them. In addition, a significant increase in ankle dorsiflexion was found at mid-swing ($F=4.78$, $p=0.028$) during the COMPLY task compared to the OPPOSE task.

### 2.3.5 Handles displacement and the load applied at the hands

The handles force and position traces showed the effect of activating or not the muscles in the arm in response to the perturbation. Averaged and subtracted average displacement and force traces from a single subject responding to perturbations delivered at heel-strike during both tasks are displayed overlapped in Fig. 2-9A and 2-9B respectively. The data from Fig. 2-9A shows that average displacement and force traces for both tasks overlap each other before the onset of the perturbation (vertical dashed line) and for the first ~150 ms (grey area) following it. While the handles remained at the centre of the rail track (initial position), the force at the handles had a mean value of zero (± 2.3%BW). The

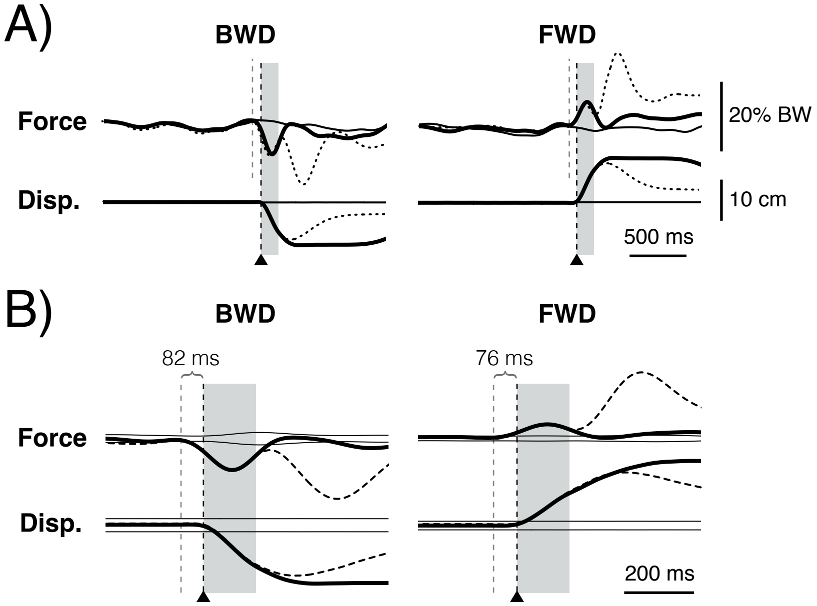

**Figure 2-9:** **A**, Sample data from one subject showing average force and position traces for perturbed and unperturbed steps. The average unperturbed traces are shown as thin solid lines. The average perturbed traces are shown as thick solid lines for the COMPLY task and as dotted lines for the OPPOSE task. The vertical black dashed line in each column is aligned to the onset of the perturbation. The vertical grey dashed line is aligned to the moment at which a change in the force becomes visible. Upward deflections in the force traces indicate pushes against the handles. Downward deflections in the position traces indicate a backward displacement of the handles. **B**, The data shown in A are replotted as subtracted traces by subtracting the average unperturbed traces from the perturbed traces. The average subtracted traces are shown as thick solid lines for the COMPLY task and as dashed lines for the OPPOSE task. The two thin lines of each set represent the 95% confidence band around the average unperturbed trace. The vertical black dashed line in each column is aligned to the onset of the perturbation. The vertical grey dashed line is aligned to the moment at which a change in the force becomes visible (Disp: handles displacement).

displacement of the handles in the backward direction resulted in a decrease in the force that reached a minimum at ~100 ms following the onset of the displacement. Forward displacements of the handles resulted in an increase in the force that reached a maximum at a similar latency after the onset of the displacement. When subjects complied to the perturbation, the force measured at the handles returned to the zero value after reaching the peak. On the contrary, when subjects opposed the perturbations, the force at the handles presented a second peak that occurred ~250 ms after the first peak was reached. In addition, when subjects complied to the perturbations, the position of the handles remain at the final position after they were displaced. Conversely, when subjects opposed the perturbations, the handles position returned to a position closer to the initial position. Both the handles force and position traces expose the effect of activating or not the muscles in the arm in response to the perturbation.

The measurement of the load applied to the hands when perturbations were delivered showed that the onset of the handles movements was preceded by a significant change in the load recorded from the sensors at the handles. It can be clearly seen from the subtracted traces depicted in Fig. 2-8B that a change in the force trace occurred before the onset of the handles movement. The mean value for the onset latency of the movement of the handles measured from the point where a change in the force was detected was 76 ± 1.8 ms when handles were displaced in the backward direction and 79 ± 2.2 ms when displaced forwards.

## 2.4 Discussion

The primary purpose of the current study was to investigate the reactions in muscles of the arm and the leg following perturbations delivered at the hands during walking. The main findings of this study were that 1) perturbations applied at the hands resulted in early latency responses in arm muscles when subjects were instructed to oppose but not when instructed to comply to the perturbations, 2) the responses evoked when opposing the perturbations involved activation of muscles in the arm as well as muscles in the leg, 3) when instructed to comply to the perturbations, most subjects presented responses in muscles of the leg notwithstanding that there was no activation of muscles in the arm.

### 2.4.1 How do these results compare to other studies?

Similar to other studies, responses in the arms and legs occurred within the first 100 ms following the onset of the displacement of the handles when subjects opposed the movement of the handles. Although these results are associated with an intentional arm movement, responses in arms and legs have been reported before when subjects were instructed to comply to the movement of the handles. In particular, only one other study has addressed this question. Cordo & Nashner (1982) compared the responses to perturbations delivered at the arms to standing subjects instructed either to 'resist' or to 'not resist' the disturbances. Contrary to their results, we did not see responses in the arms when subjects complied (did not resist) to the perturbations. The contrast between these results could be linked to differences in the experimental protocols. For instance, in Cordo and Nashner's study subjects were required to maintain a steady load on the handles (~1 kg or 3 − 5% of maximum effort), hence were sustaining tonic activation of muscles in the arm at the time of the disturbance. Conversely, in the current study subjects were unable to maintain such a steady load because they could not anticipate the direction of the perturbation (i.e. backward or forward). Although we cannot directly compare the EMG data from both studies, it is clear that subjects maintaining a steady load on the handles should present a larger activation in muscles of the arm. Maintaining tonic activation in a muscle results in an increase in activity that drives a rise in the excitability of the motoneuron pool potentiating stretch reflex responses associated with that muscle (Matthews 1986). It could be argued that the reduced activity in muscles of the arms in the current study decreased the probability for stretch reflexes to activate responses in the arms, hence resulting in the absence of a response when subjects were instructed not to respond (i.e. COMPLY).

### 2.4.2 Activation of responses to perturbations applied at the hands

Perturbations applied during walking by rapid displacement of a handle result in postural responses involving activation of muscles in the arms and the legs (Nashner & Forssberg, 1986; Hirschfeld & Forssberg, 1991). It has been argued that such perturbations trigger reflex responses in muscles of the arms and legs that are most likely activated from afferents in muscles of the arms. Our results could be interpreted with a similar approach. Perturbations delivered at the hands during the OPPOSE task resulted in direction-specific activation of muscles in the arm and the leg following the displacement of the handles. In particular, backward displacement of the handles led to stretch of AD and TB while forward displacement led to stretch of PD and BB. Responses to backward perturbations were characterized by strong activation of AD and BB, whereas responses to forward perturbations were dominated by activation of PD, TB and BB. One possible mechanism by which the direction-specificity in the activation of the muscle in the arms to perturbations delivered at the hands could be explained is that responses to backward perturbations could be cued by muscle afferents in AD and TB, while responses to forward perturbations could be cued by muscle afferents in PD and BB. However, in Fig. 2-9 it was shown that any appreciable movement of the handles did not occur until well after a change in load was applied at the handles (~80 ms). Changes in arm position capable of activating stretch reflex responses would only occur after the handles have been displaced. It is possible that a perturbation could be detected well in advance of any muscle stretch associated with the displacement of the handles. The extra time would thus allow for longer latency processes to be involved in the responses observed in the arms. The responses in the muscles of the arms could be related to synergies associated with the direction of the perturbation, probably cued by input other than that of a muscle stretch afferent.

One possibility is that the onset of the perturbation could be cued by the change in acceleration preceding the displacement of the handles. Muscle spindle afferents are not only sensitive to changes in length but also to velocity and acceleration (Prochazka, 1996). Thus, changes in acceleration associated with the onset of the displacement of the handles could be cued by muscle afferents from the stretched muscles. However, it would be expected that the most likely point at which a disturbance would be first detected is at the interface between a support surface and the body. Therefore, strong candidates for detecting the onset of the perturbation in association with the change in load and triggering the responses are cutaneous receptors in the skin of the hand. Mechanoreceptors in the skin can encode detailed information about the surface in contact with the hand, not only related to the shape and texture of the contacted surface, but also related to the dynamics of the contact between the hand and the surface. These receptors can respond to changes in shear forces with latencies under 25 ms (Johansson & Flanagan, 2009). Also, tactile feedback from the hand has been found to strongly influence postural control. Body sway is largely reduced by touch of a stable surface even when the load applied at the surface is not sufficient to provide mechanical support (Jeka and Lackner 1994; Krishnamoorthy et al. 2002; Kouzaki and Masani 2008). Hence, it is possible that cutaneous information from the hands can be used by the nervous system to cue perturbations delivered through the hands and participate in triggering the responses observed in the current study as well as in others.

If perturbations in the arms were to be cued by cutaneous receptors in the hands, it would then be possible that the responses evoked in the legs were activated based on prior experience of the multiple exposures to the experimental paradigm. For instance, the responses in the legs could be activated to limit the movement of the body's centre of mass resulting from the displacement of the handles. These responses could also be activated in anticipation of a balance disturbance that could result from activation of the muscles in the arms. The movement of a limb changes the body's centre of mass position, and this movement can potentially result in a balance disturbance (Horak & Macpherson, 1996). Such movements are usually preceded by postural adjustments targeted at minimizing the effect of the limb movement (Massion, 1992). In the current experiment the responses in the arms to the displacement of the handles were expected to result in a disturbance to balance that required postural adjustments and responses in the legs. Accordingly, responses in the legs were present not only when the arms were activated in response to the displacement of the handles (i.e. OPPOSE) but also when responses in the arms were absent following the displacement of the handles (i.e. COMPLY). Although the responses in the leg muscles were of smaller amplitude in the COMPLY task, the latencies of the responses were similar between tasks. It is therefore likely that the response evoked in the muscles of the leg were triggered by similar cues during both tasks. It is then possible that responses in the legs were activated in anticipation of the balance disturbance associated with the movement of the arms resulting from the displacement of the handles, and that the responses were scaled to the expected amplitude for the mechanical disturbance associated with the task.

### 2.4.3 Task adaptation of arm and leg responses

Important differences in the responses evoked in arms and legs from perturbations delivered at the hands were found in association with the task. In particular, responses in the arms were observed during the OPPOSE task but absent during the COMPLY task. During the COMPLY task, the arms were displaced without resistance. Indeed, as shown in Fig. 2-9, the displacement of the handles in the first 150 ms of the perturbation were comparable regardless of task. There was no change in the characteristic of the perturbations before the responses observed during the OPPOSE task in the arms were activated. In addition, there were no differences in background EMG in muscles of the arms associated with the task, suggesting that no changes in elbow or shoulder joint stiffness were linked to the task. Thus, the responses evoked in the EMG between tasks are not related to differences in perturbations characteristics or joint stiffness. Instead, the differences found in the responses between tasks could be related to the change in functional requirement of the COMPLY task. In other words, the responses might be suppressed as part of the instruction set to permit the handles to be moved without the resistance that would be generated by activation of the arm muscles. Alternatively, such responses during the OPPOSE task might be facilitated as a rapid means to apply resistance to the movement of the handles.

The responses in the arms during the OPPOSE task were accompanied with activation of muscles in the legs. In particular, the responses observed in the legs were comparable to those observed in other balance disturbance studies during walking. For example, corrective reactions evoked during walking from backward pulls applied at the waist (Misiaszek, 2003), sudden deceleration of the treadmill belt (Berger et al., 1984) or forward translations of the support surface (Tang & Woollacott, 1998) consist of early activation of TA and VL with a distal to proximal temporal organization. It has been argued that the fact that comparable corrective reactions are evoked independently from the locus of the perturbation suggests that the reactions are due to a common centrally coordinated response (Misiaszek, 2003). Accordingly, the results observed in the current study during the OPPOSE task suggest that balance corrective reactions evoked from the displacement of the handles activates the same response, suggesting that responses evoked in the legs to perturbations applied at the hands activate balance corrective responses.

However, similar to the OPPOSE task, responses in the legs were also observed during the COMPLY task. In particular, the displacement of the handles during the COMPLY task resulted in similar responses to the ones observed during the OPPOSE task. That is, the same muscles that were activated in response to backward (i.e TA and VL) and forward (i.e. SOL and BF) displacement of the handle applied at heel-strike during the OPPOSE task were also activated during the COMPLY task. Although the onset of the responses in the muscles of the legs was similar between tasks, their amplitudes were not. The amplitude of the responses evoked during the COMPLY task were of a markedly smaller magnitude. Similar to the modulation of the responses in the arms, the scaling of the responses in the legs could also be related to the change in functional requirement of the COMPLY task. For example, activation of muscles in the arms during the OPPOSE task would be expected to result in a remarkable displacement of the centre of mass that would strongly challenge balance. Although responses in the muscles of the arms would be absent during the COMPLY task, the movement of the arms resulting from the displacement of the handles will result in a reposition of the centre of mass. However, in this case the challenge to balance will be rather minimal. In summary, the responses in the legs might be activated in anticipation of the forthcoming perturbation associated with the centre of mass disturbance regardless of task. In addition, these responses will be scaled based on the task, specifically, the threat to balance associated with it.

### 2.4.4 Functional considerations

The results from this study showed that balance reactions can be elicited in the legs in response to perturbations at the arms. However, the task engaged by the arms influences expression of the responses in the legs. That is, when a demand to maintain stability at the arms is part of the task (OPPOSE) then the responses are facilitated. On the contrary, if the task does not require maintaining stability at the arms (COMPLY) then the disturbance does not evoke a large reaction, but only a modest one to accommodate for the small change in the centre of mass position. The functionality of this behaviour can be described in the responses associated with the use of a walking aid or while pushing a stroller. For instance, the walking aid (e.g. cane, walker) serves as an extension of the base of support hence responses intended to maintain it stable would be necessary. On the contrary, hitting an obstacle with a stroller will require compliance of the arms and only a response in the legs large enough to overcome the obstacle but not too large as to lead to unnecessary balance reactions. The link between the arms and the legs is task-dependent, based upon the demands of the task. However, the arms can also contribute meaningful signals and cues to the elicitation of relevant balance adjustments as well as balance corrections. Bateni & Maki (2005) found that altogether with the advantages associated with the use of mobility aids, there is an increase in the risk of falling when using these devices. If the use of a mobility aid requires maintenance of stability at the arms, it is possible that an inappropriate balance corrective reaction will be activated in a situation where compliance to the disturbance (e.g hitting an obstacle) would be a safer choice. Nevertheless, whether sensory input provided through tactile feedback from the hands can become the source of a perturbation to balance remains an open question that requires further study.

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## Chapter 3

# Light Touch and Corrective Reactions[1]

## 3.1 Introduction

The nervous system activates complex yet coordinated responses to perturbations to balance during walking. The mechanisms for reacting to such disturbances involve rapid whole-body responses that include activation of leg and arm muscles. Corrective reactions in leg muscles during locomotion have been studied for slips (Marigold et al. 2003), trips (Eng et al. 1994), translation perturbations of the support surface (Berger et al. 1984; Dietz et al. 1987; Tang et al. 1998), and perturbations at the waist (Misiaszek et al. 2000). In addition, reactions in the arms have been studied for slips (Dietz et al. 2001; Marigold et al. 2003) and perturbations at the waist (Misiaszek 2003). The arms have been shown to play an important role during responses to perturbations during walking (for review see Marigold and Misiaszek 2009).

The arms possess a large repertoire of actions to be used to regain balance upon a perturbation. They can act to dissipate the center of mass momentum

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[1] A version of this chapter has been published. Forero J, Misiaszek JE (2013) The contribution of light touch sensory cues to corrective reactions during treadmill locomotion. Exp Brain Res 226:575–584

induced by the perturbation (Oates et al. 2005; Roos et al. 2008), serve a protective role by arresting a fall (Robinovitch et al. 2005; Feldman and Robinovitch 2007), or be targeted to reach for nearby safety handrails (McIlroy and Maki 1995; Maki and McIlroy 2006). However, the arms do not only play a direct but also an indirect role in balance regulation. Previous work in our laboratory has shown that corrective responses in the legs during treadmill walking are influenced by the tasks engaged by the arms. When the arms are restricted to move by lightly folding them across the chest or clasping them behind the back, the amplitude of the responses in the leg muscles is amplified (Misiaszek and Krauss 2005). Conversely, holding stable handles will suppress the responses in leg muscles during walking (Misiaszek and Krauss 2004).

The increase in stability resulting from holding stable handles can be easily linked to the mechanical support provided from the additional support. However, it has been shown that an increase in stability is provided by the hands even in the absence of mechanical support. The influence of light touch on posture has been extensively studied. It has been shown during standing that lightly touching a stable contact with the index finger greatly reduces body sway, and that this effect is stronger in the absence of vision (Jeka and Lackner 1994; Krishnamoorthy et al. 2002; Kouzaki and Masani 2008). Further evidence of the relevance of light touch during standing balance has been demonstrated with experiments where the touch surface moved instead of remaining steady. In experiments where the contact surface oscillated sinusoidally, body sway was entrained by the surface motion as revealed by spectral analysis of the sway showing the presence of the contact surface oscillation frequency (Jeka et al. 1998; Wing et al. 2011). In experiments where the contact surface movement was linked to the participants own sway, body sway was found as large as, or larger than, the sway observed with no contact (Reginella et al. 1999; Wing et al. 2011).

Besides regulating body sway during standing, tactile input provided through light touch of a stable support has also been show to assist recovery from dynamic perturbations. Subjects standing on a platform will trigger rapid corrective responses to a sudden displacement of the platform, and the responses will be scaled to the velocity and amplitude of the disturbance (Dietz 1992). In addition, providing subjects with light touch of a stable surface affects the scaling of the responses to the velocity of the postural perturbation (Dickstein et al. 2003). In another experiment where subjects self-initiated a perturbation by pulling a cable or responded to a perturbation imposed by the experimenter, it was found for both cases that balance was restored faster when light touch was present (Johannsen et al. 2007).

The effects of light touch on balance have also been studied during walking. Although, to our knowledge, only one study investigated the relationship of balance regulation and touch during locomotion, the results are similar to standing. Subjects walking on a treadmill showed a reduction in body sway when light touch of a stable support was provided both with eyes open and eyes closed (Dickstein & Laufer 2004). In this same experiment, subjects walking on a treadmill with their eyes closed with no touch drifted backwards and stepped off the treadmill after a few steps. However, when touch was available they were able to walk normally on the treadmill.

Previous work in our lab has shown that subjects pulled at the torso while walking on a treadmill respond to the disturbance by activating muscles throughout the leg at short-latency (<150 ms) (Misiaszek 2003). These short-latency responses in the legs are robust and consistently expressed across subjects (Misiaszek 2003). Moreover, we have shown that these early responses are increased in amplitude when subjects walk with their arms restricted (Misiaszek and Krauss 2005) and suppressed, or abolished, when subjects hold stable supports (Misiaszek et al. 2000). Postural responses occurring at short-latencies are most likely to be of a spinal nature while later components of the evoked responses might include more complex responses mediated through the motor cortex and other supraspinal structures (Matthews 1991). In the present study, we wished to investigate if light touch sensory cues affect the earliest, presumably non-volitional, postural reactions to balance disturbances during walking. We hypothesized that sensory cues from the hands would modulate the short-latency responses in the legs to perturbations delivered at the waist during walking. To test our hypothesis we studied the short-latency (< 150 ms) responses to backward perturbations delivered at right heel-strike while subjects walked on a treadmill, and compared the results for touch and no-touch conditions both when subjects had their eyes open or closed.

## 3.2 Methods

A total of 12 subjects (six males and six females) were included in the experiment. Ages, heights and weights ranged from 23 to 39 years (mean ± s.d. 26.4 ± 4.21 years), from 160 to 180 cm (168.1 ± 5.84 cm), and from 51 to 90 kg (66.0 ± 10.51 kg) respectively. Subjects provided written consent of their participation. The procedures were approved by the University of Alberta Research Ethics Board.

During the experiment subjects were asked to walk on a motorized treadmill. Each subject selected a comfortable speed (0.9 to 1.3 m/s) which was maintained for the remainder of the experiment. Perturbations were delivered using a steel cable attached to the front and back of a harness worn by the subjects and firmly attached about the pelvis, and connected through a series of pulleys to a drum located behind the subjects (Fig. 3-1A). The height of the pulleys was adjusted for each subject so that the line of action of the perturbing force was maintained parallel to the ground. A strain gauge attached to the handle of the drum was used to measure the force applied with each perturbation. The investigator delivering the perturbations viewed the output of the strain gauge on an oscilloscope to ensure that the magnitude was of approximately 20% of body weight (BW). Perturbation forces of this magnitude consistently produce corrective reactions (Misiaszek 2003).

Backward perturbations (i.e. backward pulls) were delivered at different points in the step cycle, predominantly at heel-strike. Perturbations were delivered every 5 to 7 steps to allow subjects to fully recover from a perturbation before the next one would be applied. In total 30 perturbations were delivered during each condition, 15 of which were delivered at heel-strike of the right leg while the other 15 were delivered randomly at other points in the step cycle. Only those perturbations delivered at right heel-strike were used in the analysis. The perturbations delivered at other points in the step cycle were included to ensure subjects could not predict the timing of the perturbations. Because backward pulls were not delivered at fixed intervals nor at the same point in the step cycle, subjects were unable to anticipate the perturbations.

Two touch conditions (touch: t, no touch: n) were combined with two vision conditions (eyes open: EO, eyes closed: EC) to test the influence of touch sensory cues on corrective responses both in the presence and absence of visual sensory cues. In total four different conditions were used in the experiment: eyes open without touch (EOn), eyes open with touch (EOt), eyes closed without touch (ECn), and eyes closed with touch (ECt). The EOn condition was defined as the normal condition. A latin square design was used to define the order at which conditions were set for each subject to ensure that any potential variation associated with the order of exposure to the conditions would not affect the comparisons between conditions. During the no-vision conditions subjects wore a blindfold that fully obscured their vision. Subjects confirmed their vision was occluded when the blindfold was over their eyes.

An auditory biofeedback control was used to enable subjects to comfortably walk on the treadmill with their eyes closed. A linear displacement sensor (Penny and Giles SLS320, Santa Monica, Calif.) attached to the harness measured the fore-aft position of the subject on the treadmill. A pair of headphones worn by the subjects provided a feedback tone related to their position on the treadmill. The tone's volume and frequency varied according to the sigmoid and piecewise linear functions defined by Chiari et al. (2005) but linked to subject position instead of acceleration. The target position was defined at the center of the treadmill belt in the fore-aft direction. We defined a reference region and a safety region both centered on the target position and extending 2.5 cm and 20 cm in each direction respectively. These values were based on pilot data. For a position maintained within the reference region, a constant tone (420 Hz) was played on the headphones. If the subject drifted outside the reference region the tone and volume changed accordingly. If the subject drifted backward, a higher pitch tone (<840 Hz) was used and if they drifted forward a lower pitch tone (>200 Hz) was delivered. The volume increased the further away from the reference region the subject drifted. The maximum volume of the tone was set to a level comfortable to the subject. The safety region was defined by mechanical stops to avoid subjects from stepping beyond the treadmill belt. Every subject was trained for 10 minutes before the measurements began to ensure they were able to walk comfortably on the treadmill with the eyes closed when touch was unavailable. All the subjects were able to walk comfortably on the treadmill with the eyes closed even when perturbations were delivered to them. To account for any influence auditory cues could have on the responses to the perturbations, the auditory feedback was present during all four tested conditions.

The touch reference was provided by a rigid rod (i.e. touch surface) positioned in front of the subject's right arm. During the touch conditions, subjects were asked to maintain light touch by extending their right index finger to reach the touch surface. The surface was adjusted for each subject so that it was aligned laterally with the right shoulder of the subject, and the height was set so that the elbow would be held at a 90 degrees position while the forearm was held horizontally and aligned with the extended hand and finger. During the no-touch conditions the arm was left free to move to avoid adding the task of maintaining a fixed posture. A force transducer (Omega Engineering LCCA-500, Stamford, Connecticut, USA) was used to record the touch force applied by the subject to the touch surface. If during the touch conditions the subject exceeded a 1 N load over the touch surface, an alarm tone was fed to the left speaker on the headphone to warn them so that they would reduce the load. None of the subjects presented any difficulty maintaining touch without exceeding the maximum load allowed.

Two force-sensitive sensors were located at the heel and the metatarso-phalangeal joint on the right foot to record foot contact with the ground (Interlink Electronics, Camarillo, Calif. USA). Kinematic data were recorded from the ankle joint using an electrogoniometer (Penny and Giles, Santa Monica, Calif. USA). Electromyographic (EMG) recordings were obtained from the tibialis anterior (TA) and soleus (SOL) muscles on the right leg. A pair of Ag/AgCl surface electrodes was placed over the bellies of each recorded muscle, 2 cm apart and aligned with the predicted direction of the muscle fibers. The ground electrode was placed over the tibia. All recordings were made on the right leg. Raw EMG signals were pre-amplified and band-pass filtered (30 Hz - 1 kHz) using Grass P511 preamplifiers (Astro-Med, Inc. West Warwick, R.I. USA). All signals were digitized online at 1 kHz and stored directly to hard drive using a custom-written LabVIEW v8.20 data acquisition routine and a National Instruments data acquisition card (National Instruments PCI-MIO-16E-4, Austin, Tex. USA). Post-processing of the signals was performed offline: the EMG signals were full-wave rectified and low-pass filtered at 50 Hz (zero-lag 4th order Butterworth filter) and signals from the position sensor, strain gauge, force sensors and the goniometer were low-pass filtered at 10 Hz (zero-lag 2nd order Butterworth filter).

The data stream from each trial was divided into sweeps, each sweep defining a single step starting 100 ms before right heel-strike and ending 100 ms before the subsequent right heel-strike as determined by the foot sensor signal. A perturbed sweep was defined as a sweep within which the perturbation was delivered, and the step preceding it was used to define the corresponding control sweep. Only those sweeps when the perturbation was delivered around heel-strike (i.e. inside a window of ±5% of the average control step duration), the perturbation peak force was within 5% of the target force (i.e. 15% - 25% BW) and the time to reach the peak force was shorter than 250 ms were included in the analysis. After screening the data according to the inclusion criteria an average of 13 perturbed sweeps and their corresponding control sweeps remained to be analyzed for each subject for each condition. Perturbed and control data traces were captured accordingly from the perturbed and control sweeps. From the control traces, average control traces and their 95% confidence bands were calculated. Before averaging, the control traces were normalized in time using a linear time-normalization method to make their length equal to the average control sweep duration for each subject for each group. Subtracted traces were then calculated by subtracting the average control traces from the corresponding stimulated traces. Analysis of EMG and joint position data was performed using the subtracted traces.

The average control sweep duration before time normalization was used as a measure of the average step duration. The peak to peak amplitude of the oscillating fore-aft movement of the subject on the treadmill, measured from the linear sensor used to control the auditory position cue, was measured from the control traces and used as an estimate of body sway (Fig. 3-1B, bottom trace). Within a subject, a response to a perturbation was considered to be significant in any given muscle if the subtracted trace fell outside the 95% confidence band for more than 50 consecutive milliseconds. The onset latency of the response was taken as the time following the onset of the perturbation that the average subtracted trace began to deviate from the zero level. This was selected instead of the time the trace exceeded the 95% confidence band, as the more active a muscle is the greater the 95% confidence band will be creating a lag in the estimated latency. Muscle background activity was measured from the control traces. To estimate the excitability of the motoneuron pool at the time of the evoked responses, the background activity was calculated as the mean amplitude over a 100 ms window centered at the average response onset latency for each condition, for each subject. Muscle response amplitudes were calculated as the average amplitude of the subtracted trace for the first 200 ms of the response. EMG amplitudes were normalized to the average peak control EMG amplitude occurring during the step cycle for each muscle, and then expressed as a ratio of the amplitude measured for the normal condition (i.e. EOn).

We compared the effects of touch and vision for each outcome measure. All measured values are presented as mean ± s.e.m. Two-factor repeated measures ANOVAs (touch condition [2] × vision condition [2]) were used to determine if the gait features or corrective responses were modulated by touch or vision. If a

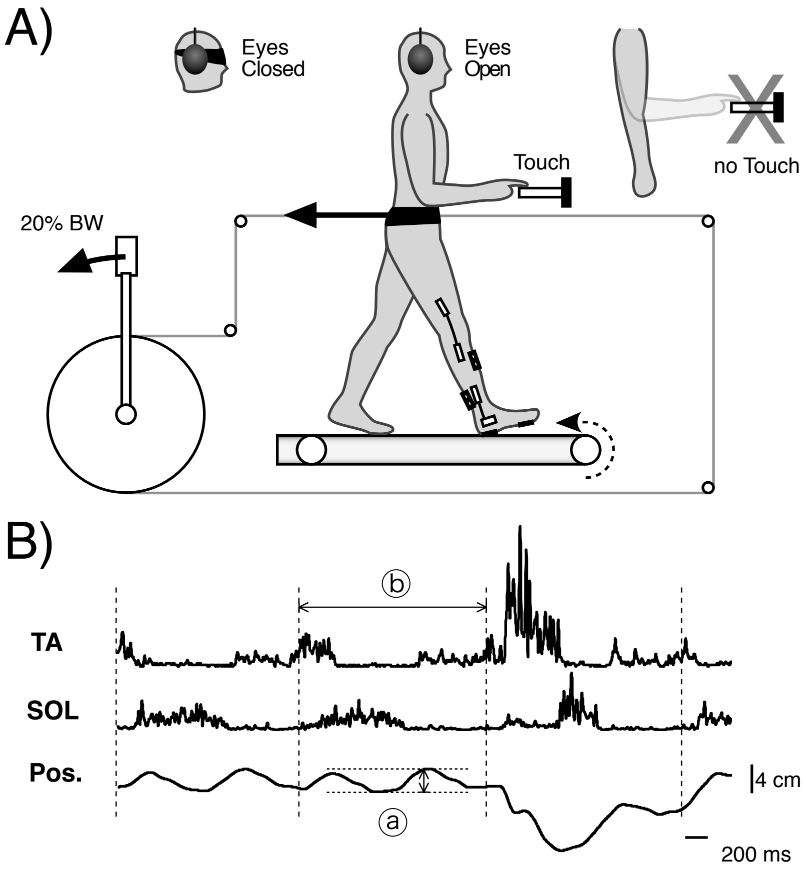

**Figure 3.1:** **A**, Schematic diagram of the general setup. Subjects walked on a motorized treadmill. A steel cable was attached to the front and back of a harness and wrapped around a drum. Rotating the drum backward would cause the subject to be perturbed backward. Vision was occluded with a blindfold. Touch was provided by a rigid rod positioned in front of the subject. **B**, Sample data from one subject showing electromyography and position traces for one perturbed step and the two steps preceding it. The peak to peak amplitude of the oscillation of the body position (a) was used to define body sway. The steps preceding a perturbed step were used as control steps, and their duration (b) was used to calculate average step durations.

significant interaction between touch and vision was found, Tukey's post-hoc comparisons were used to identify differences between conditions. All comparisons were performed using a statistical significance level of 0.05.

## 3.3 Results

In this study, we were interested in measuring the effect of touch and vision sensory cues on corrective responses to perturbations delivered during walking. The data revealed an effect of touch and vision in the responses to the perturbations delivered at heel-strike during walking. However, touch and vision also led to changes to the undisturbed gait. We will present first the results from undisturbed gait, and then describe the effects of touch and vision on the corrective responses.

### 3.3.1 Effect of touch on undisturbed gait

The peak-to-peak amplitude of the fore-aft movement of the body was used as a measure of body sway during walking (Fig. 3-1B). Body sway amplitudes are presented for each condition averaged across subjects in Fig. 3-2A. The ANOVA revealed a significant main effect of both touch ($F=14.33$, $p<0.001$) and vision ($F=11.09$, $p<0.001$) on the amplitude of the oscillation with no interaction between these factors ($F=0.66$, $p=0.42$). Lightly touching a stable reference significantly reduced the amplitude of the oscillations, regardless whether the eyes were open or closed. The average amplitude of the oscillations during the control condition (EOn) was 3.52 ± 0.109 cm, which was reduced to 3.32 ± 0.117 cm when subjects walked while lightly touching a stable contact (EOt). In the absence of vision, the addition of touch reduced the amplitude of the oscillations from an average of 3.82 ± 0.134 cm (ECn) to 3.51 ± 0.117 cm (ECt). In summary, the largest oscillations occurred when subjects walked on the treadmill without either vision or light touch, whereas the smallest oscillations occurred when subjects walked with the eyes open and lightly touching the contact surface.

The duration of the step cycle was also affected by the condition. Step cycle duration values are presented for each condition averaged across subjects in Fig. 3-2B. The ANOVA indicated a significant interaction between the vision and

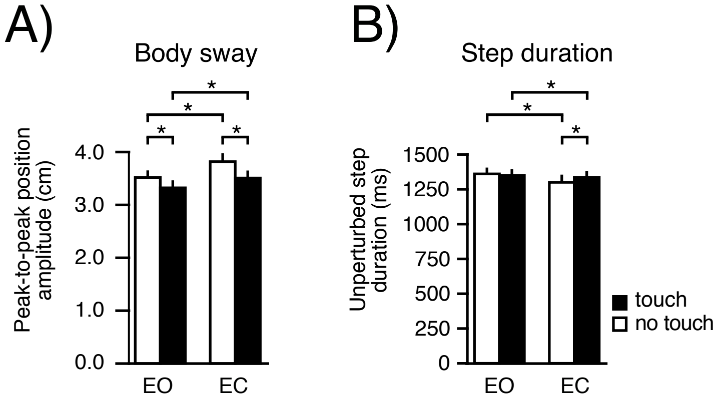

**Figure 3.2:** Means and standard errors of the measures for body sway presented in cm (A) and step duration presented in ms (B) for each combination of the touch and vision conditions. Open bars represent the data for the no-touch conditions. Solid bars represent the data for the touch conditions. The asterisks indicate average response amplitudes that are significantly different between conditions.

touch conditions (F=35.32, p<0.001). Post-hoc comparisons revealed that step cycle durations were significantly reduced (p<0.001) when subjects walked with their eyes closed without touching the contact (ECn = 1309 ± 49.9 ms), compared with walking normally with the eyes open (EOn = 1367 ± 39.3 ms). Allowing the subjects to lightly touch the stable contact while walking without vision significantly increased (p<0.001) the step cycle duration, compared to the ECn condition, returning the step cycle duration to an average of 1347 ± 39.9 ms (ECt). Touching the stable contact while walking with the eyes open (EOt = 1361 ± 38.1 ms) did not alter the step cycle duration (p=0.26), compared to normal walking (EOn).

The amplitude of TA and SOL EMG was measured over a 100 ms window centred at the average onset latency of the evoked response. The ANOVA revealed a significant main effect of both touch (F=3.86, p<0.05 and F=12.12, p<0.001) and vision (F=7.48, p<0.01 and F=6.86, p<0.01) on the amplitude of the background EMG in TA and SOL respectively, with no interaction between these two factors (F=0.14, p=0.71 and F<0.01, p=0.99). As can be seen in Fig. 3-4A, light touch led to a reduction in the ongoing EMG of both TA and SOL, whereas closing the eyes led to a significant increase in the activity of both muscles.

Manipulation of the vision and touch conditions had only modest effects on the motion of the ankle joint during walking. An ANOVA on the range of motion at the ankle across the step cycle revealed significant interaction between the touch and vision factors (F=5.04, p=0.025). Post-hoc comparisons revealed that this effect was due to a significantly smaller range of motion during the ECn condition, compared with all other conditions ($p<0.001$). On average, the ankle joint range of motion in the normal condition with eyes open (EOn) was $28.8 \pm 2.56^{o}$, which was reduced to $26.8 \pm 2.01^{o}$ in the absence of either vision or touch (ECn). When touch was provided in the absence of vision (ECt), the ankle joint range of motion was $28.8 \pm 2.28^{o}$.

### 3.3.2 Effect of touch on compensatory reactions

Subjects were displaced away from the reference region upon delivery of the perturbations (Fig. 3-1B, bottom trace). All subjects were able to recover balance and return to the reference region within one step after the perturbation in all but the ECn condition, during which an additional 1 to 3 steps were required. The initial response to the perturbations was a consistent short-latency (<100 ms) activation of the TA muscle, with a later onset (>200 ms) suppression of the SOL muscle activity in all subjects for every tested condition. Average traces and average subtracted traces from a single subject are displayed in Fig. 3-3A and 3-3B respectively. As can be seen from the data in Fig. 3-3B, the appearance and onset of the evoked responses was consistent across the four conditions in this subject. Responses in TA were evoked at around 90 ms for this subject in all four conditions, ranging between 90 ms (EOn) and 93 ms (EOt). Similar results were observed in all subjects. When the data from all subjects were tested with

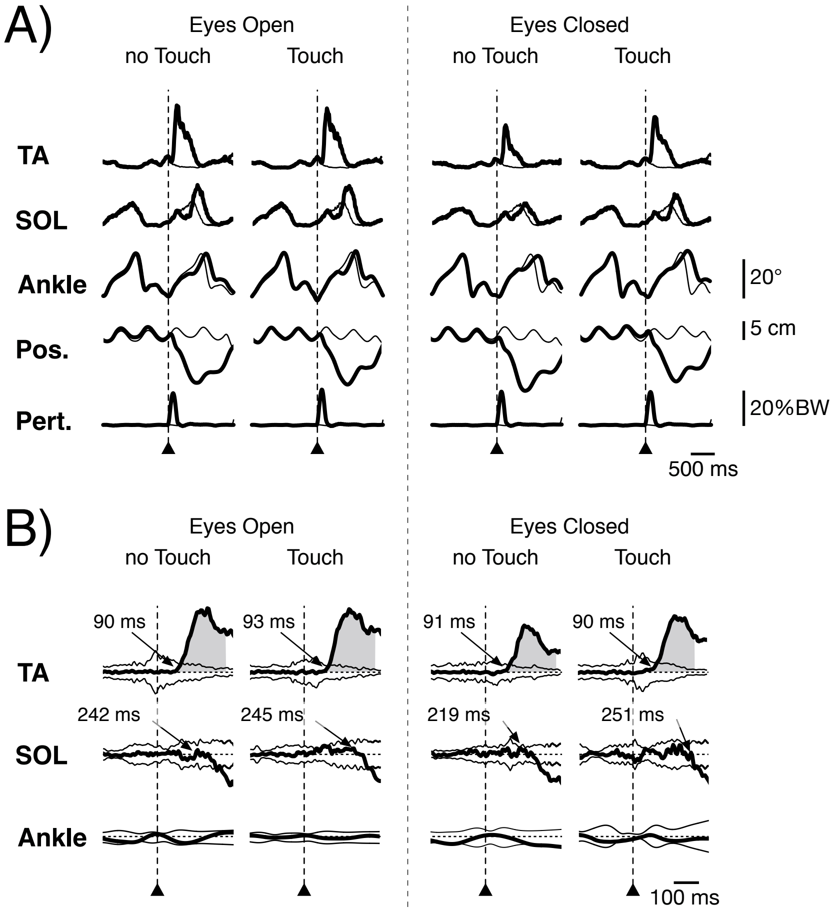

**Figure 3.3:** **A**, Sample data for one subject showing average (n=14) electromyography, kinematic, position and perturbation traces for perturbed (thick traces) and unperturbed (thin traces) steps for all four conditions. The vertical dashed line in each column is aligned to the onset of the perturbation. Upward deflections in the kinematic traces indicate dorsiflexion for the ankle. Downward deflections in the position traces indicate a backward displacement of the subject on the treadmill. **B**, The data shown in A are replotted as subtracted traces by subtracting the average unperturbed traces from the perturbed traces. The average subtracted traces are shown as thick lines. The two thin lines of each set represent the 95% confidence band around the average unperturbed trace. The vertical dashed line in each column is aligned to the onset of the perturbation. The average response onset latency is presented for the electromyography traces for each muscle (TA: tibialis anterior, SOL: soleus, Pos. position, Pert: perturbation).

ANOVA, no significant main effects of touch (F<0.01, p=0.93) or vision (F<0.21, p=0.66) were identified in TA response onset latencies.

The amplitudes of the evoked responses in TA were affected by the conditions. In Fig. 3-3A and 3-3B, the example data from one subject show an apparent suppression of the evoked response in TA when the subject was disturbed while walking with the eyes closed, without touch (ECn), compared with the other conditions. When the subject was permitted to touch the stable surface, the amplitude of the response increased, but not as large as the responses when the eyes were open. This observation is further confirmed by the group averaged data displayed in Fig. 3-4B. In Fig. 3-4B, the amplitude of the evoked response in TA is averaged across subjects, normalized to the peak walking EMG in TA. The ANOVA revealed a significant interaction effect between touch and vision on the response amplitudes in TA (F=16.10, p<0.001). Post-hoc comparisons revealed that the responses in TA were significantly reduced (p<0.001) in amplitude when subjects walked with their eyes closed without touching (ECn), compared to when walking normally with the eyes open (EOn). Moreover, allowing the subjects to touch a stable surface while their eyes were closed (ECt) resulted in responses in TA that were significantly larger (p<0.001) than in the ECn condition. In contrast, allowing the subjects to touch the stable surface while walking with the eyes open (EOt) resulted in no difference (p=0.73) in response amplitude, compared with EOn.

The perturbations resulted only in small ankle joint trajectory deviations from normal within the time frame of the analysis. For the subject's data displayed in Fig. 3-3 it can be seen that the motion of the ankle joint was not affected (in other words, did not deviate beyond the 95% confidence interval in the subtracted traces, Fig. 3-3B) by the applied perturbations within the first 300 ms following the perturbation onset.

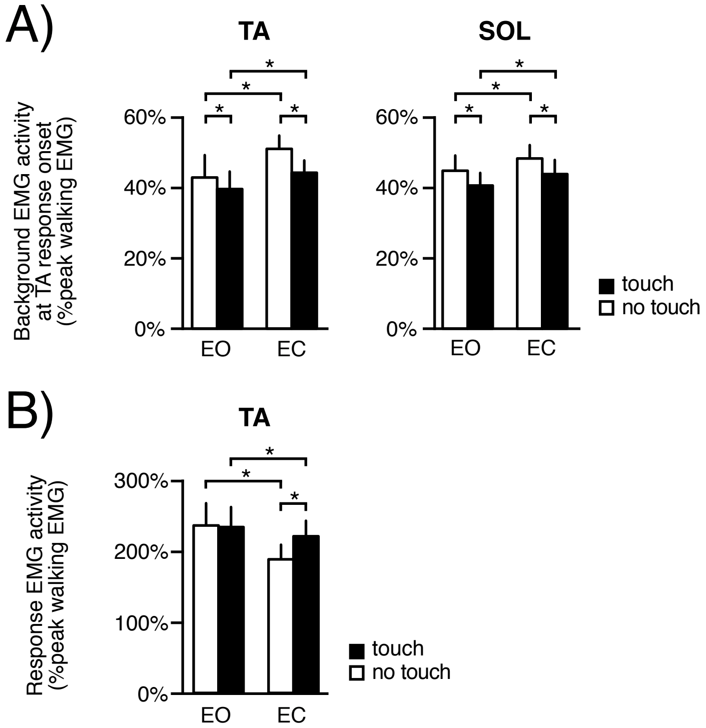

**Figure 3.4:** Means and standard errors of the background EMG for TA and SOL (**A**) and the response amplitudes for TA (**B**). The data were standardized to the maximum EMG amplitude observed during normal undisturbed walking for that muscle, for each subject. Open bars represent the data for the no-touch conditions. Solid bars represent the data for the touch conditions. The asterisks indicate average response amplitudes that are significantly different between conditions.

## 3.4 Discussion

The primary purpose of the current study was to investigate the effect of light touch on corrective responses to backward perturbations during treadmill walking. The main finding of this study is that corrective responses in leg muscles to perturbations during walking are modulated by light touch. There was a strong effect of touch on the corrective responses to perturbations, which was more apparent when walking with the eyes closed.

### 3.4.1 Light touch facilitates balance corrective responses during walking

The response evoked in TA following a backward perturbation of the waist at heel-strike was used as a probe to test the influence of light touch and vision on the regulation of balance corrective responses during walking. In previous studies we have shown that the response in TA to this type of disturbance is very robust, being expressed vigorously in all subjects (Misiaszek 2003; Misiaszek and Krauss 2005; Bolton and Misiaszek 2012). The evoked response in TA has been shown to change in amplitude, but not latency, when subjects have been asked to walk with their arms folded across their chest (Misiaszek and Krauss 2005) or when holding a set of stable handles (Misiaszek and Krauss 2004). Similar effects of light touch are demonstrated here as the amplitude, but not the latency, of the evoked responses varied with the presence or absence of the light touch. The effect of light touch on the amplitude of the response was easily evident when the subjects were asked to walk with the eyes closed. As seen in Fig. 3-4B, the response amplitude was significantly increased when subjects were permitted to touch the contact with the eyes closed, compared to the no touch condition with the eyes closed. The effect of touch in the eyes open condition (the left pair of bars in Fig. 3-4B) is less obvious as the average amplitude of the response in the eyes open touch and no touch conditions appear to be unchanged. However, the responses in the eyes open touch condition are of equal amplitude despite a significantly lower background level of EMG in TA. It would have been expected that with a decrease in background EMG in TA the amplitude of the evoked response would also be decreased as a result of the decrease in excitability of the motoneuron pool (Matthews 1986). Therefore, we argue that the gain of the evoked response in TA was larger in the eyes open touch condition, compared with eyes open no touch. Consequently, in both the eyes open and eyes closed conditions the provision of light touch resulted in an increase in the gain of the evoked response in TA.

### 3.4.2 Light touch as a spatial reference for stability during walking

The effect of light touch and vision on the amplitude of the corrective responses is not mirrored by the effect of light touch and vision on the other gait parameters measured. Allowing subjects to touch a stable contact led to decreased fore-aft oscillation on the treadmill and decreased amplitude of both TA and SOL EMG activity. Whereas, removing vision led to increased fore-aft oscillation on the treadmill and increased amplitude of both TA and SOL EMG activity. Therefore, it would appear that providing light touch cues leads to greater stability when walking on a treadmill and removal of visual cues leads to instability when walking on a treadmill. This is similar to the conclusion of Dickstein and Laufer (2004) who showed that subjects were able to stabilize their walking on a treadmill with their eyes closed so long as they had a touch reference. The difference between our study and that of Dickstein and Laufer (2004) is that our subjects received an auditory positional reference that permitted the subjects to walk on the treadmill with their eyes closed without drifting off the back of the belt. Nevertheless, that the subjects walked with less fore-aft oscillation and lower levels of ongoing EMG activity when touching a stable contact indicates that the provision of the light touch offered the subjects an additional somatosensory anchor, permitting stronger spatial orientation and positional reference.

The suppression of the responses in TA when walking with the eyes closed without touch was also accompanied by a requirement of taking multiple steps following the perturbation in order to regain a stable stepping pattern, which was not the case for any other walking condition. We suggest that the suppression of the short-latency (<100 ms) response in TA indicates that under these circumstances the more automatic postural reactions are suppressed (Misiaszek 2006) in favour of greater cognitive control of the balance reaction (Huffman et al. 2009). Prochazka (1989) referred to this as the ‘sensorimotor set’, whereby the transmission in sensorimotor pathways is adjusted to suit a particular task or context. In this context, subjects have a limited reference of their position on the treadmill, but are aware that they could step off the back or the side of the treadmill and therefore foot placement is a critical factor for future successful stepping. Moreover, the subjects are forced to continue to step as the treadmill belt continues to move. Therefore, attention and cognitive resources are allocated to estimating their position on the treadmill with limited information. When the subjects are then permitted to touch a stable contact point they are provided with an additional somatosensory anchor (Dickstein and Laufer, 2004), providing additional, concrete information about their spatial orientation within the context of the moving treadmill belt. In this way, the touch cues replace the spatial orientation information that is lost in the absence of the visual cues and the automatic responses to the balance disturbance (the evoked response in TA in this instance) can be scaled to correct for the disturbance within a single step, with the assurance that the correction will not lead to a misplacement of the foot or of drifting off the treadmill.

The adaptations we observed in the amplitude of the balance corrective response evoked in TA might also be related to the level of postural anxiety associated with each condition. Although we did not measure postural anxiety in our study, the evoked responses in TA were substantially suppressed in the absence of vision, when the postural threat would be expected to be high.

Response amplitudes were then restored to near normal when spatial orientation was provided through touch, when the postural threat would be expected to be low. There is now considerable evidence that postural anxiety or postural threat is related to profound adaptations to postural control during standing (Adkin et al. 2000; Carpenter et al. 2001; Carpenter et al. 2004) and adaptations to walking (Llewellyn et al., 1990; Brown et al. 2002; Delbaere et al. 2009). In addition, simple reflexes have been shown to be adapted to postural threat during standing (Sibley et al. 2007) and walking (Haridas et al. 2005; 2008). In our study, postural anxiety is likely related to the level of certainty of spatial orientation within the confines of the moving treadmill belt. Therefore, the contribution of the touch cues to the selection of the appropriate sensorimotor set would be expected to reflect both the level of anxiety and the spatial reference.

### 3.4.3 Touch as a task?

Light touch has been linked to balance regulation improvement due to its ability to reduce body sway during standing and walking (Jeka and Lackner 1994, Dickstein and Laufer 2004). However, it has been suggested that light touch of a stable surface can also be observed as a postural task requiring postural adjustments to maintain touch contact while standing (Riley et al. 1999). Our results might be interpreted with a similar approach. That is, the adaptations in the evoked responses and the changes in the measured gait parameters might well be related to a desire or perceived task requirement by the subjects to maintain contact with the support in the touch conditions. Indeed, Bateni et al. (2004) demonstrated that subjects holding a “cane” would preferentially continue to hold the cane rather than grasp an available handrail when standing balance was threatened. We cannot completely discount such an influence from contributing to the change in response amplitudes we observed. For example, in a previous study we demonstrated that if the arms are folded across the chest, and unable to contribute to the balance reaction, then the response in TA is increased (Misiaszek and Krauss 2005). It could be argued that by asking the subjects to maintain touch of the contact we have restricted the use of the arm from contributing to the balance correction in much the same way. However, this seems an unlikely explanation for the results of the present study as it would not account for the substantial reduction in response amplitude that is observed when the subjects walked with the eyes closed without touch. A more likely explanation is that walking with the eyes closed creates uncertainty and induces a more cautious gait that is then ameliorated by touching the positional reference.

### 3.4.4 Functional considerations

In our study, subjects walked on a moving treadmill belt, while receiving perturbations to balance. As a result, the subjects were required to continue stepping and were required to step within a confined location. The threat of falling off the treadmill or stepping to the side of the moving belt is unique to this experimental paradigm. Therefore, whether these findings would translate to overground walking is an open question. Although these findings are unlikely to translate directly to overground walking, it would be expected that the principles described here would. For example, the effect of light touch on body sway during standing has been well characterized (Jeka and Lackner 1994; Krishnamoorthy et al. 2002; Kouzaki and Masani 2008). Our results, along with those of Dickstein and Laufer (2004), confirm comparable influences of light touch are observed during treadmill walking. Therefore, it would be reasonable to expect that this principle would further translate to overground walking. The effect of light touch on balance recovery to perturbations delivered during standing has also been studied. For example, Dickstein et al. (2003) showed that touch of a stable surface improves the scaling of the responses to the velocity of the postural perturbation. Similarly, Johannsen et al. (2007) presented evidence that the presence of touch helps restore balance faster both after self-initiated or externally-imposed perturbations. Here, we have demonstrated that light touch can lead to a scaling of balance corrective reactions during treadmill walking in much the same way. Consequently, we would expect that light touch would scale responses during overground walking too.

## 3.5 References

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## Chapter 4

# Light Touch and Cutaneous Reflexes in the Arms

## 4.1 Introduction

Balance control during walking is not only regulated by the action of the legs but also by the action of the arms. Compensatory reactions to balance disturbances delivered during locomotion present a generalized response independent from the locus of the perturbation. Perturbations resulting from slips (Marigold et al., 2003), trips (Eng et al., 1994), and pulls at the waist (Misiaszek et al., 2000) will all trigger corrective responses in leg muscles that are accompanied by activation of arm muscles. In general, perturbations to balance delivered during locomotion trigger whole-body corrective responses (for review see Marigold & Misiaszek, 2009).

The arms participate during balance regulation in different ways. For instance, they might participate in balance regulation by dissipating the centre of mass momentum induced by a perturbation (Oates et al., 2005; Roos et al., 2008), protecting from injury by arresting a fall (Robinovitch et al., 2005; Feldman & Robinovitch, 2007), or reaching for nearby rails when balance has been compromised (McIlroy & Maki, 1995; Maki & McIlroy, 2006). Also, responses in leg muscles to perturbations delivered at the waist during locomotion are stronger when arm movement is restricted (Misiaszek & Krauss, 2005), but are largely suppressed and can be abolished if subjects hold on to stable handles (Misiaszek & Krauss, 2004). A direct mechanical effect of the arms over balance is revealed when they are free to move. However, restricting the arms from moving eliminates the direct effect and exposes an indirect effect on balance control. These results are evidence that corrective responses in the legs are modulated according to the task engaged by the arms.

The suppression of the leg reflex responses observed when subjects hold onto stable handles is evidence of an adaptation of the reflexes in order to accommodate to the new context. Changes in the transmission of sensorimotor pathways associated with reflex responses have been referred to as changes in the sensorimotor set (Prochazka, 1989). The general change in postural set could be associated with the confidence provided by the stable support at the hands (Misiaszek & Krauss, 2004). However, body stabilization may not result exclusively from the mechanical support available to the arms. In particular, the effect of light touch on balance regulation has been studied during standing and, to a lesser extent, during walking. During standing, postural sway in the absence of vision has been shown to be reduced by active (Jeka et al., 1997; Jeka et al., 1998; Wing et al., 2011) and passive (Rogers et al., 2001) touch of a stable surface. During walking, light touch has been shown to prevent subjects from drifting off the treadmill belt when walking on a treadmill with their eyes closed (Dickstein and Laufer, 2004). In addition, it was shown in Chapter 3 that corrective responses to perturbations delivered at heel-strike during walking are significantly affected by the presence of light touch of a stable surface. In each of these studies the effect of touch has been dissociated from mechanical support by maintaining the load applied to the touch surface below 1 N, a non-mechanically supportive level (Holden et al., 1994). The non-mechanical effect of touch on standing balance control has also been studied when afferents from the arm were blocked. Kouzaki & Masani (2008) found the effect of light touch was diminished when peripheral nerves from the arm were paralyzed by applying tourniquet ischemia to the upper limb, hence providing further support for a link between the effect of touch and tactile feedback from the skin in contact with the stable surface. Altogether, these results suggest that, besides mechanical support from the arms, cutaneous feedback from the hands may also be important in balance regulation.

Electrically evoked reflexes have been widely used as a tool to probe into the nervous system circuit organization mainly because they are repeatable and occur at a fixed latency following the stimulus (Burke, 1999). For instance, stimulation of cutaneous nerves in the lower and upper limbs evoke reflex responses that can be recorded in a variety of muscles in the body (Zehr et al., 2001). The inter-limb reflex responses evoked from stimulation of cutaneous nerves serving the hand and foot have been shown to be phase-modulated during the walking cycle, hence they have been suggested to be functionally relevant in the coordination of the legs and arms during walking (Haridas & Zehr, 2003). Cutaneous reflexes evoked during walking are also modulated according to the level of postural threat (Haridas et al., 2006). In particular, in a study involving light touch of a handrail under different levels of threat, the inter-limb reflexes evoked in arm muscles that were functionally able to contribute to mechanical stabilization were facilitated (Lamont & Zehr, 2007). Similarly, segmental reflexes from the hand can be used as neural probes into the excitability of the sensory channels from the fingertips. If the sensory information transported via the stimulated reflex pathway is functionally relevant for a given condition, then changes in gain should be observed for these reflexes.

The effect of light touch on balance regulation is well documented, and its influence has been linked to tactile feedback apart from mechanical support. The purpose of the current study was to use segmental cutaneous reflexes as a probe to examine the effect of light touch of a stable surface on the gain in the transmission of sensory information from cutaneous afferents from the skin of the hand in contact with the touch surface. The median and radial nerves serve cutaneous afferents from the palmar and dorsal sides of the hand respectively. We hypothesized that cutaneous reflexes would be modulated differently depending on whether the stimulated nerve contains afferents from the skin in contact with the touch surface. We provided touch through the tip of the index finger, hence we expected that touch would have an effect on cutaneous reflexes in the arms if they were evoked from stimulation of the median nerve, but not if they were evoked from stimulation of the radial nerve.

## 4.2 Methods

### 4.2.1 Subjects

A total of 11 subjects (7 females and 4 males) were included in the experiment. Ages, heights and weights ranged from 23 to 40 years (mean ± s.d., 30.3 ± 5.15 years), from 154 to 190 cm (167.4 ± 12.14 cm), and from 49 to 88 kg (64.6 ± 11.83 kg) respectively. Subjects provided written consent of their participation in a protocol approved by the University of Alberta Research Ethics Board.

### 4.2.2 Protocol

During the experiment subjects were asked to walk on a motorized treadmill. Each subject selected a comfortable speed (0.8 to 1.1 m/s) which was maintained for the remainder of the experiment. To increase the level of postural threat during walking, perturbations were delivered randomly across the step cycle (Haridas et al., 2006). Perturbations were created from backward pulls were applied through a steel cable fastened to the front and back of a harness worn by the subjects and firmly attached about the pelvis. The magnitude of the perturbations was maintained around 20% of body weight, a value that is high enough to accentuate postural threat without having subjects tripping nor falling (Haridas et al., 2006). Perturbations were delivered randomly between 12 and 20 seconds apart.

Cutaneous reflexes were examined by stimulating two nerves in the arms. Electrical stimulation was delivered to 1) the median nerve (MED) which innervates the palmar surface and the distal thumb, the index and middle finger, and 2) the superficial radial nerve (RAD) which innervates the skin on the dorsum of the thumb, index, and middle finger. Subjects visited the lab on two different occasions, one for each nerve stimulation protocol. The order of presentation of the nerve stimulation protocols was randomized between subjects. The influence of touch sensory cues on cutaneous reflexes in the arms was evaluated both in the presence and absence of vision. For this purpose, two touch conditions (touch: t, no-touch: n) were combined with two vision conditions (eyes open: EO, eyes closed: EC). On each visit, subjects were exposed to the four different conditions: eyes open without touch (EOn, normal condition), eyes open with touch (EOt), eyes closed without touch (ECn) and eyes closed with touch (ECt). The order at which conditions were exposed to each subject was randomized using a latin square design to minimize any effect the order of exposure to the conditions could have over the comparisons. Subjects were allowed to rest between conditions if needed.

The touch reference was provided by a rigid rod (i.e. touch surface) positioned in front of the subject's right arm. During the touch conditions, subjects were asked to maintain light touch by extending their right index finger to reach the touch surface. The surface was aligned laterally with the right shoulder of the subject, and the height was set so that the elbow would be held at a 90 degrees position while the forearm was held horizontally and aligned with the extended hand and finger. A force transducer was used to measure the vertical component of the touch force applied by the finger. None of the subjects presented any difficulty in maintaining light touch (touch load below 1 N) for the duration of the experiment. Average touch load traces from a single subject are shown for a complete walking cycle in Fig. 4-1. Although during the touch condition the touch load varied with the step cycle, the amplitude was maintained within a range that satisfies the requirements for light touch (~ 0.25 to 0.75 N). During the no-touch conditions, subjects were asked to hold the arm in a position

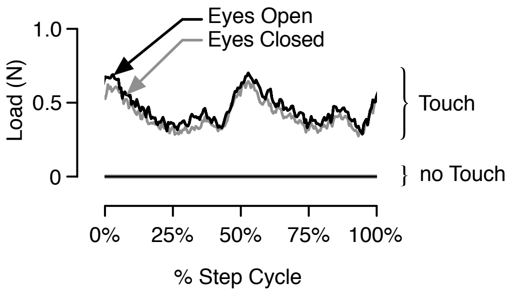

**Figure 4.1:** Average touch load traces across the complete walking cycle for each combination of touch and vision conditions from a single subject.

similar to the one maintained for the touch conditions. During the eyes closed conditions subjects wore a blindfold that fully occluded their vision.

An auditory feedback linked to the subject's fore-aft position on the treadmill was provided to allow them to walk comfortably with their eyes closed. The position feedback tone was provided using a pair of headphones. The target position was defined at the centre of the treadmill belt, with a reference region spanning 2.5 cm in both directions. The tone’s volume and frequency were maintained constant if subjects remained within the reference region, but varied if subjects moved outside of it. The volume of the tone increased if subjects moved away from the reference region, being the tone of a higher pitch if the displacement was in the forward direction, but of a lower pitch if it was in the backward direction (further details on the auditory feedback setup can be found in Chapter 3). Each subject was trained for 10 minutes before the measurements began to ensure they were able to walk comfortably on the treadmill with the eyes closed. A safety region was defined in the fore-aft direction 20 cm around the target position using mechanical stops to limit the subject’s displacement within the treadmill belt. To account for any influence the auditory cues could have on reflex responses the auditory feedback was present during all four conditions.

### 4.2.3 Electrical stimulation

Nerve stimulation was delivered by trains of isolated constant current applied to the MED or RAD of the right arm using flexible 1 cm disposable Ag/AgCl surface electrodes. Both nerves were stimulated with trains of 5×1.0 ms pulses at 300 Hz. The electrodes for the MED were placed on the ventral surface of the forearm just proximal to the crease of the wrist joint. The electrodes for the RAD were placed on the dorsal surface of the forearm just proximal to the distal radial head and the crease of the wrist. The intensity of the stimulation was set as a multiple of the radiating threshold (RT) for each subject. RT was estimated as the lowest stimulation amplitude necessary for the subject to perceive a clear radiating cutaneous parasthesia into the innervation area of the stimulated nerve (MED, palmar surface of the hand; RAD, dorsum of the hand). Overall, a value of approximately 2 to 3×RT was required for the stimulus to be strong enough to evoke a reflex, yet not be perceived as painful by subjects.

In Chapter 3, I showed that corrective responses in the legs to perturbations delivered at heel-strike were increased in the presence of light touch. To integrate those results with the ones from the current experiment, reflex responses were measured in arm muscles at heel-strike. The delivery of the stimuli was controlled by a computer to ensure they were randomly delivered between 3 to 5 steps apart, and triggered at right heel-strike as measured from the foot contact sensors (see Data Acquisition). The first stimulus was delivered one minute after data recording started, and stimuli were delivered for five more minutes. This technique resulted in 20 to 30 stimuli to be analyzed for each subject and each condition.

### 4.2.4 Data acquisition

Two force-sensitive sensors were located at the heel on the right foot to record foot contact with the ground (Interlink Electronics, Camarillo, Calif. USA). Touch force was recorded from the force transducer used to measure the vertical component of the force applied by the finger. In addition, electromyographic (EMG) recordings were obtained from the anterior (AD) and posterior (PD) deltoids, the biceps brachii (BB), the triceps brachii (TB), the flexor carpi radialis (FCR) and the flexor carpi ulnaris (FCU) of the right arm. A pair of Ag/AgCl surface electrodes were placed over the bellies of each recorded muscle, 2 cm apart and aligned with the predicted direction of the muscle fibres. The ground electrode was placed over the clavicle on the right side. Raw EMG signals were pre-amplified and band-pass filtered (30 Hz - 1 kHz) using Grass P511 preamplifiers (Astro-Med, Inc., West Warwick, RI, USA). All signals were digitized online at 1 kHz and stored directly to hard drive using a custom-written LabVIEW v8.20 data acquisition routine and a National Instruments data acquisition card (National Instruments PCI-MIO-16E-4, Austin, TX, USA). Touch force signals were digitally low-pass filtered at 10 Hz (zero-lag 2th order

Butterworth filter), and EMG signals were first digitally full-wave rectified and then low-pass filtered at 150 Hz (zero-lag 4th order Butterworth filter). Post processing of the signals was done offline.

### 4.2.5 Data analysis

The data stream from each trial was divided into sweeps, each one associated with a single step starting 50 ms before right heel-strike and lasting for 300 ms. A stimulated sweep was defined as a step during which a stimulation was delivered, and the step preceding it was used to define the corresponding control sweep. If a perturbation was present less than 3 steps before a stimulation was delivered, then the stimulated sweep and the corresponding control sweep were removed from the analysis. Stimulated and control traces were captured accordingly from the stimulated and control sweeps. Average control traces and their 95% confidence bands were calculated from the control traces. Subtracted traces were then calculated by subtracting the average control traces from the individual stimulated traces.

Cutaneous reflexes were calculated from the subtracted traces. A reflex response was identified and included in the analysis if the average subtracted trace fell outside the 95% confidence band for more than 5 continuous milliseconds. Average subtracted traces were calculated separately for each muscle, subject and condition. In Fig. 4-2A are presented the average subtracted traces from a single subject for PD, BB and TB recorded during the MED stimulation protocol for all tested conditions. The data presented in Fig. 4-2A show clear reflex responses evoked at the early latency (~50-80 ms) in all three muscles, and reflect the general behavior observed across subjects.

The reflex latency was measured at the peak of the response. Although the latency of the response will be larger with this method compared to others, the peak response latency has been argued to be more reliable across muscles and subjects (Zehr & Chua, 2000). Thus, the latency of the reflex was defined for each muscle, subject and condition at the time at which the average subtracted trace reached its maximum after escaping the 95% confidence band. To compare reflexes across conditions, an average reflex latency was calculated for each muscle and subject by averaging the latencies from the four conditions (see gray bars on Fig. 4-2A). The amplitude of the reflex was measured from each individual subtracted trace and calculated as the mean amplitude over a 10 ms window centered around the average latency of the reflex. Cutaneous reflex amplitudes were first normalized across conditions for each subject and muscle to the average peak control EMG amplitude occurring during the step cycle, and then standardized to the normal condition (i.e. EOn) for each subject to allow for group comparisons.

Due to the proximity of the stimulation site to the recording electrodes, strong stimulus artifacts were present in each EMG recording. Inspection of the recorded EMG traces showed that stimulus artifacts vanished within the first 50 ms after the delivery of the stimulation in AD, PD, BB and TB. However, stimulus artifacts were present in the EMG traces from FCR and FCU even 85 ms after the stimulation was delivered. Early latency responses in FCR and FCU were indistinguishable from the artifact, hence were excluded from the analysis. Only the responses recorded for AD, PD, BB and TB were reliable and included for analysis in this study.

Muscle background activity was estimated from individual control traces for each muscle, subject and condition. Background EMG amplitude was calculated from the control traces as the mean amplitude over a 50 ms window centred around the average latency of the reflex for each subject and muscle. Background EMG amplitudes were normalized to the average peak control EMG amplitude occurring during the step cycle for each muscle.

### 4.2.6 Statistics

Statistical comparisons were performed using the normalized values for the cutaneous reflex amplitudes and the background EMG amplitudes. Separate two-factor repeated measures ANOVAs (touch condition [2] × vision condition [2]) were used to determine if there was an effect of touch and vision on the amplitude of the reflex response or the background activity in the muscle for each nerve stimulation protocol and each muscle studied. If a significant interaction between touch and vision was found, Tukey's post-hoc comparisons were used to test the effect of touch and vision separately. All comparisons were performed using a statistical significance level of 0.05.

## 4.3 Results

In this study we were interested in measuring the effect of touch and vision sensory cues on cutaneous reflexes evoked in muscles of the arm from electrical stimulation of nerves serving the hand during walking. Cutaneous reflexes were evoked in different muscles of the arm by stimulating the MED and RAD at heel-strike. Reflex responses were clearly evoked in PD, BB and TB but not AD, hence data comparisons were performed only for PD, BB and TB. We found that reflex responses were affected by both touch and vision, but the effect observed was different depending on the nerve being stimulated.

### 4.3.1 MED stimulation protocol

Electrical stimulation of the MED resulted in early latency responses in PD, BB and TB. The average response traces from a single subject are presented in Fig. 4-2A as an example of the reflexes evoked from the stimulation. Each trace represents the average of 22 to 25 individual subtracted traces. Thin traces represent the average trace for the no-touch conditions (EOn/ECn) and the thick traces represent the average trace for the touch conditions (EOt/ECt). The top pair of traces in each grouping represents the response traces for the EO conditions and the bottom pair of traces represents the response traces for the EC conditions.

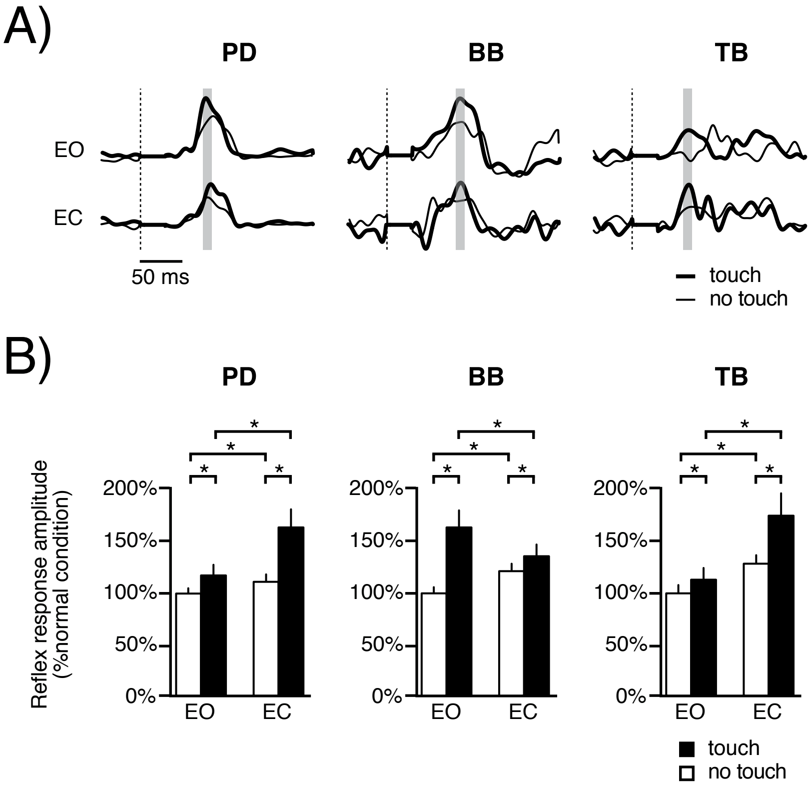

**Figure 4.2:** **A**, Subtracted electromyographic (EMG) traces for PD, BB and TB after median nerve stimulation for a single subject following electrical stimuli occurring at heel-strike. The top pair of traces in each grouping represents the response traces for the eyes open conditions and the bottom pair of traces represents the response traces for the eyes closed conditions. Thin traces represent average traces for the no-touch conditions and thick traces for the touch conditions. Rectangular boxes indicate the poststimulus time window in which the middle-latency reflex was analyzed. The vertical dashed line in each column is aligned to the onset of the stimulation. **B**, Means and standard errors of the middle-latency cutaneous reflexes arising from median nerve stimulation delivered at heel-strike for PD, BB, and TB for each combination of the touch and vision conditions. The data were standardized to the normal condition for each subject. Open bars represent the data for the no-touch conditions. Solid bars represent the data for the touch conditions. The asterisks indicate average response amplitudes that are significantly different between conditions (PD: posterior deltoid, BB: biceps brachii, TB: triceps brachii).

The grey boxes centred at the average peak reflex response latency represent the window over which reflex response amplitudes were measured. It is clear from the data from the subject in Fig. 4-2A that the presence of touch results in an increase in reflex response amplitudes common to all muscles. This observation is further confirmed from the group data.

Early latency reflex response amplitudes from stimulation of the MED are presented averaged across subjects in Fig. 4-2B. In general, both vision and touch influenced the responses evoked in all muscles. The ANOVA for BB revealed a significant interaction effect between the touch and vision conditions (F=20.33, p<0.001). Post-hoc comparisons revealed a significant increase in the amplitude of the reflexes when touch was provided while walking with the eyes open (EOn → EOt). The provision of touch showed the same effect while walking with the eyes closed (ECn → ECt), suggesting a general facilitation of the responses in BB from the provision of touch. In addition, responses in BB were facilitated with the removal of vision when touch was absent (EOn → ECn). Conversely, in the presence of touch, the removal of vision resulted in a suppression of the response in BB (EOt → ECt). The effect of touch and vision on the responses in PD and TB was different from the effect found for the responses in BB. The ANOVAs for PD and TB revealed a significant main effect of touch (F=10.87, p<0.001 and F=4.89, p=0.026) and a significant main effect of vision (F=4.58, p=0.032 and F=7.21, p=0.007) with no significant interaction between these two factors

(F=2.89, p=0.088 and F=2.30, p=0.128). Reflex responses measured in PD and TB were of a larger amplitude when subjects walked with the eyes closed compared to when they walked with the eyes open. In addition, allowing the subjects to touch a stable surface while walking resulted in an increase in the amplitude of the response in PD and TB compared to the response evoked when subjects were holding the arm extended in a position similar to the one maintained during the touch conditions without touching the touch surface. In summary, the reflexes evoked in PD, BB and TB from stimulation of the MED showed adaptation to the vision and touch conditions. In general, reflexes were facilitated with the removal of vision as well as with the addition of touch.

### 4.3.2 RAD stimulation protocol

Electrical stimulation of the RAD also resulted in early latency responses in PD, BB and TB. The average response traces from the same subject presented in Fig. 4-2A are presented in Fig. 4-3A as an example of the reflexes evoked from the stimulation of the RAD. Each trace represents the average of 21 to 25 individual subtracted traces. The same convention used for the data presented in Fig. 4-2A was used for the data presented in Fig. 4-3A. The reflex responses evoked from stimulation of the RAD also showed adaptation to the conditions, but the effect of the condition on the amplitude of the responses differed from the one previously described for the reflex responses evoked from stimulation of the MED. The responses evoked from stimulation of the MED were consistently stronger during the touch conditions (Fig. 4-2A). However, the data presented in Fig. 4-3A shows

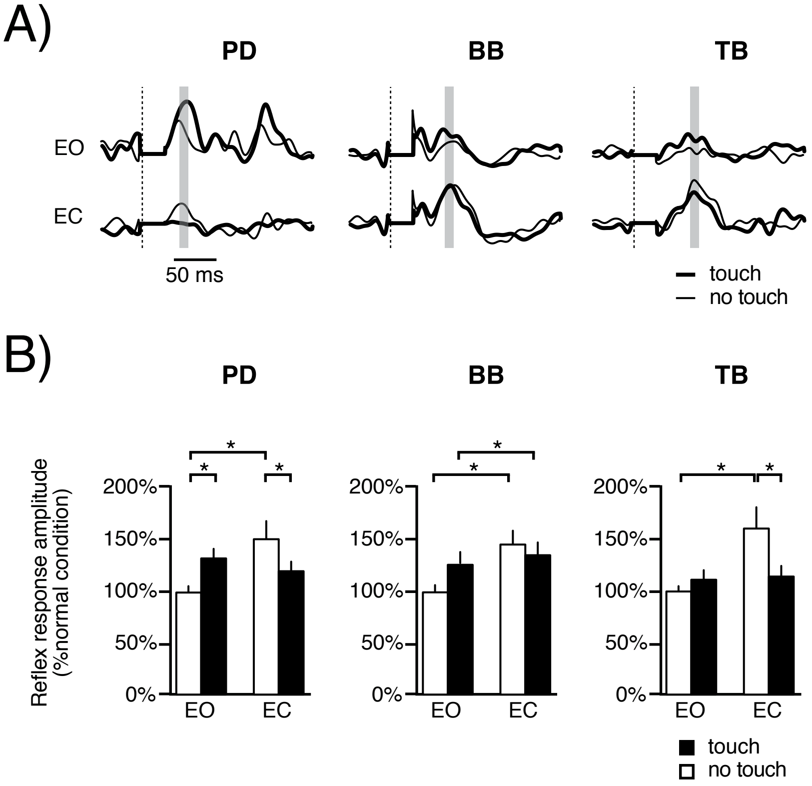

**Figure 4.3:** **A**, Subtracted electromyographic (EMG) traces for PD, BB and TB after radial nerve stimulation for a single subject following electrical stimuli occurring at heel-strike. The top pair of traces in each grouping represents the response traces for the eyes open conditions and the bottom pair of traces represents the response traces for the eyes closed conditions. Thin traces represent average traces for the no-touch conditions and thick traces for the touch conditions. Rectangular boxes indicate the poststimulus time window in which the middle-latency reflex was analyzed. The vertical dashed line in each column is aligned to the onset of the stimulation. **B**, Means and standard errors of the middle-latency cutaneous reflexes arising from median nerve stimulation delivered at heel-strike for PD, BB, and TB for each combination of the touch and vision conditions. The data were standardized to the normal condition for each subject. Open bars represent the data for the no-touch conditions. Solid bars represent the data for the touch conditions. The asterisks indicate average response amplitudes that are significantly different between conditions.

that the responses evoked from stimulation of the RAD are stronger during the touch condition only when vision is present. In the absence of vision, the reflex response evoked in PD and TB was stronger when touch was unavailable, and in BB the response traces from the touch and no-touch conditions seemed to overlap each other.

Early latency reflex response amplitudes from stimulation of the RAD are presented averaged across subjects in Fig. 4-3B. A general effect of touch and vision was observed in the responses evoked in all muscles. The ANOVAs for PD and TB revealed a significant interaction effect between the touch and vision conditions (F=5.22, p=0.022 and F=4.83, p=0.278). Post-hoc comparisons revealed that the amplitude of the reflex responses in PD and TB were significantly increased with the removal of vision (EOn → ECn) but then significantly reduced with the addition of touch (ECn → ECt). Post-hoc comparisons also revealed that, with the addition of touch, the amplitude of the responses in PD were significantly increased in the presence of vision (EOn → EOt) but reduced when vision was absent (ECn → ECt). A trend similar to the one described for PD and TB was observed in the responses in BB. However, the ANOVA revealed only a significant main effect of vision (F=6.50, p=0.011) but not touch (F=0.29, p=0.5854) for BB. Reflex responses measured in BB were facilitated when subjects walked with the eyes closed compared to when walking with the eyes open. In summary, the reflexes evoked in PD, BB and TB from stimulation of the RAD also adapted to the vision and touch conditions. However, the reflexes evoked during the RAD stimulation protocol were modulated differently from those evoked during the MED stimulation protocol.

### 4.3.3 Background activity

While walking on the treadmill, subjects were asked to hold the arm in a flexed position during all four conditions (see Methods). Background activity was measured over a 50 ms window centred around the average onset latency of the response for each muscle. In Fig. 4-4, the background EMG amplitude for PD, BB, and TB normalized to the peak EMG amplitude recorded during unperturbed walking and averaged across subjects is shown. A general trend is observed for the background activity presented in Fig. 4-4 for PD, BB and TB. This trend can

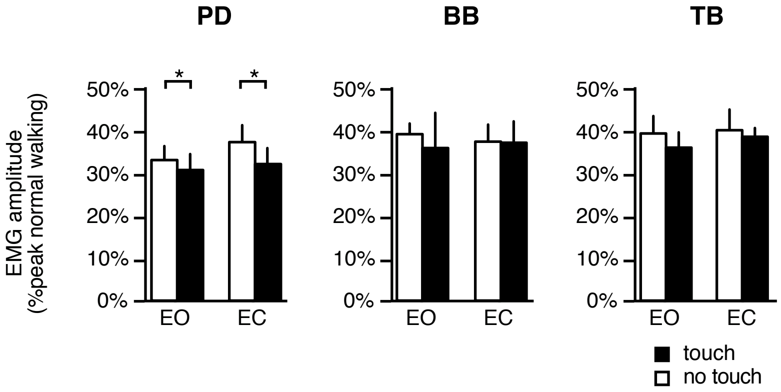

**Figure 4.4:** Means and standard errors of the background EMG for PD, BB and TB. The data were standardized to the maximum EMG amplitude observed during normal undisturbed walking. Open bars represent the data for the no-touch conditions. Solid bars represent the data for the touch conditions. The asterisks indicate average response amplitudes that are significantly different between conditions.

be described as a reduction of the background EMG amplitude resulting from the addition of touch. The ANOVA showed a significant main effect of touch for the background EMG in PD (F=4.11, p=0.042) but not in BB (F=1.34, p=0.246) or in TB (F=1.54, p=0.214). In addition, the ANOVA showed no significant main effect of vision for the background EMG for the background EMG in PD (F=3.50, p=0.061), BB (F=0.780, p=0.077) or TB (F=0.71, p=0.397), nor an interaction between factors (F=2.02, p=0.154; F=0.14, p=0.708; F=0.56, p=0.456). Although the averaged background EMG in PD, BB and TB showed a smaller amplitude during the touch conditions compared to the no touch conditions, the difference was found significant only for PD.

## 4.4 Discussion

The primary purpose of the current study was to investigate the effect of light touch on reflex responses evoked in muscles of the arm from stimulation of two nerves serving the hand, i. e. the median and radial nerves, during walking under an increased level of postural threat. The main findings were that 1) cutaneous reflexes were modulated by touch and vision, 2) the effect of touch on cutaneous reflexes was dependent on the stimulated nerve, and 3) the effect of touch was not related to changes in motoneuronal pool excitability.

### 4.4.1 Contribution of touch and vision to the regulation of postural anxiety during walking

Walking with the eyes closed is a challenging task that has been associated with changes in gait patterns into a more cautious walking (Hallemans et al., 2009). The data presented in Chapter 3 showed an adaptation in postural reactions to the vision condition, and the data presented in the current chapter further confirms those observations. The data from the current experiment showed a strong effect of vision on the responses evoked in muscles of the arm from stimulation of both the MED and RAD when subjects walked with the eyes closed compared to the normal condition (i.e. EOn). Walking on a treadmill with eyes closed leads to instability related to the potential threat of drifting off the back of the belt (Dickstein & Laufer, 2004). Postural control has been shown to adapt in response to the changes in the perceived postural threat during standing (Adkin et al. 2000; Carpenter et al., 2001; Carpenter et al. 2004) and walking (Brown et al. 2002; Delbaere et al. 2009). Also, simple reflexes have shown adaptation to the level of postural threat during standing (Sibley et al., 2007) and walking (Llewellyn et al., 1990; Haridas et al. 2005; 2008). The underlying premise is that anxiety levels would be heightened under conditions of increased postural threat that would alter the consequences of a possible fall (Brown et al., 2002). Changes in behaviour associated with the context have been referred before as changes in the postural set necessary to accommodate to the specifics of a particular task

(Prochazka, 1989). Thus, the increase in amplitude observed in the cutaneous reflexes evoked in PD, BB and TB by stimulating the MED and RAD in the absence of vision can be explained by a general change in the postural set associated with the challenge of walking with the eyes closed on a treadmill. It could be argued that the changes in amplitude measured for the cutaneous reflexes evoked in muscles of the arm would be associated with changes in the excitability of the motoneuron pool (Matthews 1986). However, there was no effect of vision on the background EMG in PD, BB or TB, hence the increase in reflex amplitude resulting from the removal of vision was not associated with changes in background EMG levels in PD, BB and TB. Instead, the results suggest that the increase in reflex amplitude resulting from walking with the eyes closed is a consequence of a facilitation of cutaneous reflexes, most likely in response to the increase in postural threat.

Reflexes evoked in PD and TB during the RAD stimulation protocol when walking with the eyes closed (i.e. ECn) showed a consistent reduction in amplitude when subjects were provided with light touch of a stable surface. The data presented in Chapter 3, altogether with the conclusion of Dickstein & Laufer (2004), suggested that the provision of light touch of a stable reference helps to stabilize walking on a treadmill in the absence of vision. Postural anxiety is probably associated with the level of confidence provided from the cues available to orient the body within the boundaries of the treadmill belt. In this sense, the increase in postural anxiety resulting from the added challenge of orienting the body with the eyes closed would most likely be reduced with the provision of light touch of a stable surface (Chapter 3). Accordingly, the data from the current experiment showed that providing light touch in the absence of vision resulted in a reduction in the amplitude of the responses evoked from stimulation of the RAD. Hence, that reflexes adapted to the level of postural threat associated with the touch could mean that the provision of touch resulted in a change in the sensorimotor set to stabilize walking when vision is not available.

### 4.4.2 Nerve-dependent modulation of cutaneous reflexes

Cutaneous reflexes evoked in the arms were used as a probe to test the transmission along sensorimotor pathways originating from the area of the skin in contact with the touch surface. The amplitude of the responses evoked in the muscles of the arm was affected differently depending on the nerve being stimulated. In the eyes open condition, reflexes from stimulation of both the MED and RAD were facilitated during the touch condition. In contrast, in the eyes closed condition, when the postural threat was greater, the effect of touch on the cutaneous reflexes differed depending upon which nerve was stimulated. Reflexes evoked in PD and TB by stimulating the MED when walking with the eyes closed showed an increase in amplitude when subjects were provided with light touch of a stable surface. Conversely, reflexes evoked in the same muscles by stimulating the RAD when walking with the eyes closed showed a consistent reduction in amplitude with the provision of light touch. Previous experiments involving stimulation of different nerves serving the foot (Zehr et al., 1997; Komiyama et al., 2000; Haridas et al., 2006) and the hand (Zehr & Kido, 2001) have reported nerve specificity before. It has been argued that cutaneous reflexes could be modulated according to the area they innervate and its relevance for the ongoing task. In the current experiment light touch was provided through the palmar surface of the index finger, hence sensory information from the tip of this finger would be expected to be relevant when light touch was provided. The area of skin of the tip of the index finger is exclusively innervated by the MED. Therefore, the nerve specificity depicted from the differences observed for the effect of touch on reflexes evoked from stimulation of the MED and RAD suggests that cutaneous afferent pathways are facilitated in the presence of touch if they transport sensory information from functionally relevant sensory cues.

### 4.4.3 The role of touch as a position reference

It was discussed above that an increase in postural anxiety resulting from walking in the absence of vision could be overcome with the provision of touch. This would suggest a generalized effect of touch on reflex adaptation. However, the inhibition of reflexes evoked in the RAD could, on the contrary, depict a specific effect of touch on reflex adaptation. In particular, this is supported from the effect of touch on the reflexes evoked in the MED when vision was absent. Although, during the eyes closed conditions the provision of touch inhibited the reflexes in the RAD, the reflexes in the MED were instead facilitated. This suggests that the provision of touch does not result in a generalized change in anxiety, but rather indicates a specific functional adaptation of the reflexes. A number of studies on the influence of light touch during standing have demonstrated that somatosensory cues from the finger are a strong orientation reference for postural control of upright stance (for review see Jeka, 1997). In addition, it has been suggested that light touch during walking provides a somatosensory anchor that allows for spatial stability in the absence of vision (Dickstein & Laufer, 2004). However, in contrast it has also been suggested that light touch could result in an increase in postural demand associated with the task of maintaining contact with the touch surface (Riley et al., 1999; Vuillerme et al., 2006). In the current study, the position of the touch surface was fixed with respect to the treadmill. Hence, by maintaining the finger in contact with the surface the position of the body will necessarily remain within the treadmill boundaries. Thus, the results from the present study indicate that the specific facilitation of reflexes in the MED (compared to the RAD) is most likely associated with the functional use of the contact surface for body (or finger) positioning instead of a general adaptation linked to the level of postural anxiety.

### 4.4.4 Functional considerations

Cutaneous reflexes were used as a probe to test the effect of light touch of a stable surface on cutaneous afferent pathways. It was found that light touch modulates the gain in the transmission of sensory information from cutaneous afferents from the skin of the hand. In another study, Lamont & Zehr (2007) showed that interlimb cutaneous reflex responses in TB and BB were facilitated when subjects held an earth-referenced rail. They suggested that neural pathways to these muscles are gated to incorporate the rail into the automatic recovery strategy. In particular, they proposed that reflexes are selectively facilitated to make use of an object that is perceived to provide stability. It could be argued that maintaining contact with the touch surface enhances balance depending on the nature of the surface. However, the results from the current study showed that cutaneous reflex responses in TB and BB were also facilitated when subjects were provided with light touch of a surface that was unable to provide mechanical support. Because the touch surface cannot be incorporated into the automatic recovery strategy, neural pathways to selected muscles in the arms could instead be gated to facilitate sensory input from the hands and enhance the information being incorporated and used in the integration process for the control of balance. Bateni et al. (2004) showed that standing subjects perturbed with rapid platform translations would not release an object held in the hand to reach for nearby handles to regain balance. They suggested that the nervous system prioritizes the ongoing task of holding an object even if the object is unable to help stabilizing balance. Thus, when light touch is available, sensory input from the hands would be expected to be facilitated whether the touch surface is capable or not of providing mechanical support.

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## Chapter 5

# Light Touch and Interlimb Cutaneous Reflexes in the Legs

## 5.1 Introduction

Perturbations delivered during walking evoke corrective responses in the legs that are accompanied by activation of arm muscles (Marigold & Misiaszek, 2009). Arm responses can assist in balance control by dissipating the centre of mass momentum generated from the perturbation (Roos et al., 2008), protect from injury by arresting a fall (Feldman & Robinovitch, 2007), reaching for nearby handles (Maki & McIlroy, 2006), or protecting from injury by absorbing the impact of a fall (Feldman & Robinovitch, 2007). However, besides the clear direct role played by the arms during balance regulation, they also play an indirect role. When arms are restricted to move, responses in leg muscles to perturbations delivered at the waist during walking are stronger than when arms are free to move (Misiaszek & Krauss, 2005). On the contrary, holding on to stable handles will attenuate or even suppress the responses in the legs (Misiaszek & Kraus, 2004). Corrective responses in the legs are strongly modulated by the task engaged by the arms.

Light touch has been shown to have a strong effect on balance regulation. During standing, natural body sway is increased in the absence of vision, but largely reduced by active (Holden et al., 1994; Jeka & Lackner, 1994; Wing et al., 2011) and passive (Rogers et al., 2001) light touch of a stable surface. The effect of touch has been dissociated from mechanical support by maintaining the load applied to the touch surface below 1N, a non-mechanically supportive level (Holden et al., 1994). Moreover, the effect of touch was abolished when tactile sensory feedback from the hand was blocked when peripheral nerves from the arm were paralyzed by applying tourniquet ischemia to the upper limb (Kouzaki & Masani, 2008). The implication is that cutaneous feedback from the hands in the absence of mechanical support is important during balance control.

The effect of light touch on balance regulation is also present during walking. The provision of light touch of a stable surface during treadmill walking results in a reduction of body sway whether subjects walk with the eyes open or closed (Dickstein & Laufer, 2004). In addition, corrective reactions to balance perturbations delivered during walking are adapted with the provision of touch. Responses in the legs to perturbations delivered with backward pulls applied at the waist were facilitated with the provision of touch both when vision was present and absent (Chapter 3). It was shown in Chapter 3 that, in the absence of vision, subjects required multiple steps to restore balance upon being perturbed, but the number of steps was smaller when touch was provided in the absence of vision. These results indicated that the provision of light touch provided sensory cues capable of adapting balance regulation for the lack of visual inputs. Therefore, light touch from the hands can be used as a relevant sensory cue in balance control.

Arm and leg movements have been argued to be correlated during walking. Dietz (2002) suggested that upper and lower limb movements are coordinated during human gait as a residual function of quadrupedal locomotion. There is evidence of a neuronal linkage between upper and lower limbs. In particular, cutaneous reflex responses are evoked in various muscles in the body after stimulation of nerves serving the hands and feet of subjects maintaining tonic contractions (Zehr et al., 2001), as well as of subjects performing locomotor activities such as walking (Zehr & Haridas, 2003) and cycling (Sakamoto et al., 2006). In addition, interlimb cutaneous reflex responses evoked when subjects perform a locomotor activity show a phase-modulation (Haridas & Zehr, 2003). These results suggest that interlimb cutaneous reflexes are relevant in assisting movement coordination between the arms and legs during motor tasks (for review, see Zehr & Duysens, 2004).

It was already discussed in Chapter 4 that the gain in the transmission of sensory information from cutaneous afferents from the skin of the hand in contact with the touch surface is regulated depending upon whether afferents transport information associated with a stable reference point. It was argued that the sensorimotor set adapted to accommodate to the change in context associated with light touch. Additionally, cutaneous reflexes have been suggested to assist with movement coordination between the arms and legs during locomotor tasks (Zehr & Stein, 1999). The purpose of the current study was to use cutaneous reflexes elicited in muscles of the legs from stimulation of nerves serving the hand as a neural probe to test the effect of light touch of a stable surface on sensorimotor pathways that could link the actions of the arms and legs, and that are involved in the transmission of sensory information from cutaneous afferents from the skin of the hand in contact with the touch surface. We hypothesized that a sensorimotor link that involves the contact surface would be regulated in a manner consistent with task demands i.e. balance control, whereas the sensorimotor link not involved with the contact surface would not be regulated so. Considering the median and radial nerves serve cutaneous afferents from the palmar and dorsal sides of the hand respectively, we expected that cutaneous reflexes in the legs resulting from stimulation of the median nerve would be modulated by touch differently from those resulting from stimulation of the radial nerve when, in the absence of mechanical support, light touch was provided through the tip of the index finger.

## 5.2 Methods

### 5.2.1 Subjects

A total of 10 subjects (seven males and four females) were included in the experiment. Ages, heights and weights ranged from 21 to 36 years (mean ± s.d., 27.5 ± 5.16 years), 154 to 190 cm (169.6 ± 9.87 cm), 52 to 87 kg (66.6 ± 11.30 kg) respectively. Subjects provided written consent of their participation in a protocol approved by the University of Alberta Research Ethics Board.

### 5.2.2 Protocol

During the experiment subjects were asked to walk on a motorized treadmill. Each subject selected a comfortable speed (0.8 to 1.1 m/s) which was maintained for the remainder of the experiment. To increase the level of postural threat during walking, perturbations were delivered randomly across the step cycle (Haridas et al., 2006). Perturbations were created from backward pulls applied through a steel cable fastened to the front and back of a harness worn by the subjects and firmly attached about the pelvis. The magnitude of the perturbations was maintained around 20% of body weight, a value that is high enough to accentuate postural threat without having subjects tripping nor falling (Haridas et al., 2006). Perturbations were delivered randomly between 12 and 20 seconds apart.

Interlimb cutaneous reflexes were examined by stimulating two nerves in the arms. Electrical stimulation was delivered to 1) the median nerve (MED) which innervates the palmar surface and the distal thumb, the index and middle finger, and 2) the superficial radial nerve (RAD) which innervates the dorsum of the thumb, index, and middle finger. Subjects visited the lab on two different occasions, one for each nerve stimulation protocol. The order of presentation of the nerve stimulation protocols was randomized between subjects. The influence of touch sensory cues on cutaneous reflexes in the arms was evaluated both in the presence and absence of vision. For this purpose, two touch conditions (touch: t, no-touch: n) were combined with two vision conditions (eyes open: EO, eyes closed: EC). On each visit, subjects were exposed to the four different conditions: eyes open without touch (EOn), eyes open with touch (EOt), eyes closed without touch (ECn) and eyes closed with touch (ECt). A latin square design was used to randomize the order of presentation of the condition to each subject before beginning the study. Subjects were allowed to rest between conditions if needed.

The touch reference was provided by a rigid rod (i.e. touch surface) positioned in front of the subject's right arm. During the touch conditions, subjects were asked to maintain light touch by extending their right index finger to reach the touch surface. The surface was aligned laterally with the right shoulder of the subject, and the height was set so that the elbow would be held at a 90 degrees position while the forearm was held horizontally and aligned with the extended hand and finger. A force transducer was used to measure the vertical component of the touch force applied by the finger. None of the subjects presented any difficulty in maintaining light touch (touch load below 1 N) for the duration of the experiment. Although, during the touch condition the touch load varied with the step cycle, the amplitude was maintained within a range that satisfies the requirements for light touch (~ 0.25 to 0.75 N). During the no-touch conditions, subjects were asked to hold the arm in a position similar to the one maintained for the touch conditions. During the eyes closed conditions subjects wore a blindfold that fully occluded their vision.

An auditory feedback linked to the subject's fore-aft position on the treadmill was provided to allow subjects to walk comfortably with their eyes closed. The position feedback tone was provided using a pair of headphones. The target position was defined at the center of the treadmill belt, with a reference region spanning 2.5 cm in both directions. The tone's volume and frequency were maintained constant if subjects remained within the reference region, but varied if subjects moved outside of it. The volume of the tone increased if subjects moved away from the reference region, being the tone of a higher pitch if the displacement was in the forward direction but of a lower pitch if it was in the backward direction (further details on the auditory feedback setup can be found in Chapter 3). Every subject was trained for 10 minutes before the measurements began to ensure they were able to walk comfortably on the treadmill with the eyes closed. A safety region was defined in the fore-aft direction 20 cm around the target position using mechanical stops to limit the subject's displacement within the treadmill belt. To account for any influence the auditory cues could have on reflex responses the auditory feedback was present during all four conditions.

### 5.2.3 Electrical stimulation

Nerve stimulation was delivered by trains of isolated constant current (Grass S88 stimulator with SIU5 and CCU1 isolation and constant current units, Warwick, RI) applied to the MED or RAD of the right arm using flexible 1 cm disposable Ag/AgCl surface electrodes. Both nerves were stimulated with trains of 5×1.0 ms pulses at 300 Hz. The electrodes for the MED were placed on the ventral surface of the forearm just proximal to the crease of the wrist joint. The electrodes for the RAD were placed on the dorsal surface of the forearm just proximal to the distal radial head and the crease of the wrist. The intensity of the stimulation was set as a multiple of the radiating threshold (RT) for each subject. RT was estimated as the lowest stimulation amplitude necessary for the subject to perceive a clear radiating cutaneous parasthesia into the innervation area of the stimulated nerve (MED, palmar surface of the hand; RAD, dorsum of the hand). Overall, a value of approximately 2 to 3×RT was required for the stimulus to be strong enough to evoke a reflex, yet not be perceived as painful by subjects.

In Chapter 3, I showed that corrective responses in the legs to perturbations delivered at heel-strike were increased in the presence of light touch. To integrate those results with the ones from the current experiment, reflex responses in muscles of the right leg were measured at heel-strike. Hence, electrical stimuli were delivered in synchrony with heel-strike from the right foot. The delivery of the stimuli was controlled by a computer to ensure stimuli were randomly delivered between 3 to 5 steps apart. The first stimulus was delivered one minute after data recording started, and stimuli were delivered for five more minutes. This technique resulted in 25 to 39 stimuli to be analyzed for each subject and each condition.

### 5.2.4 Data acquisition

Touch force was recorded from the force transducer used to measure the vertical component of the force applied by the finger. In addition, electromyographic (EMG) recordings were obtained from the tibialis anterior (TA), the soleus (SOL), the vastus lateralis (VL), and the biceps femoris (BF) of the right leg. A pair of Ag/AgCl surface electrodes were placed over the bellies of each recorded muscle, 2 cm apart and aligned with the predicted direction of the muscle fibres. A common ground electrode was placed over the right clavicle. Raw EMG signals were pre-amplified and band-pass filtered (30 Hz - 1 kHz) using Grass P511 preamplifiers (Astro-Med, Inc., West Warwick, RI, USA). All signals were digitized online at 1 kHz and stored directly to hard drive using a custom-written LabVIEW v8.20 data acquisition routine and a National Instruments data acquisition card (National Instruments PCI-MIO-16E-4, Austin, TX, USA). Touch force signals were digitally low-pass filtered at 10 Hz (zero-lag 2th order Butterworth filter), and EMG signals were first digitally full-wave rectified and then low-pass filtered at 150 Hz (zero-lag 4th order Butterworth filter). Post processing of the signals was done offline.

### 5.2.5 Data analysis

The data stream from each trial was divided into sweeps, each one associated with a single step starting 50 ms before right heel-strike and lasting for 300 ms. A stimulated sweep was defined from a step during which a stimulation was delivered, and the step preceding it was used to define the corresponding control sweep. If a perturbation was present less than 3 steps before a stimulation was delivered, then the stimulated sweep and the corresponding control sweep were removed from the analysis to ensure the response recorded at the time of the stimulus was not associated with the muscles responses associated with balance restoration from a perturbation. Traces for the touch load and EMG data were captured as defined by the stimulated and control sweeps for each subject. Control traces were used to define average control traces and their 95%

confidence bands. Subtracted traces were defined by subtracting the average control traces from the individual stimulated traces.

Cutaneous reflexes were calculated from the subtracted traces. Average subtracted traces were calculated separately for each muscle, subject and condition. In Fig. 5-1A are presented the average subtracted traces from an exemplar subject for TA and SOL recorded during the MED stimulation protocol for all tested conditions. The data presented in Fig. 5-1A depicts clear reflex responses evoked in TA and SOL at the middle (80 − 120 ms) latency window, showing positive and negative values within the defined window. Reflexes were quantified as the RMS value for the time window of 80 − 120 ms post-stimulus. Cutaneous reflex amplitudes were first normalized across conditions for each subject and muscle to the average peak control EMG amplitude occurring during the step cycle, and then standardized to the normal condition (i.e. EOn) for each subject to allow for group comparisons.

Muscle background activity was estimated from individual control traces for each muscle, subject and condition. Background EMG amplitude was calculated from the control traces as the RMS amplitude over the same window defined for the middle component of the response.

### 5.2.6 Statistics

Statistical comparisons were performed using the normalized values for the cutaneous reflex amplitudes and the background EMG amplitudes. For each nerve stimulation protocol and each muscle studied, two-factor repeated measures ANOVAs (touch condition [2] × vision condition [2]) were used to determine if there was an effect of touch and vision on the amplitude of the reflex response or the background activity in the muscle. If a significant interaction between touch and vision was found, post-hoc comparisons were done to test the effect of touch and vision separately. All comparisons were performed using a statistical significance level of 0.05.

## 5.3 Results

In this study we were interested in measuring the effect of touch and vision sensory cues on interlimb cutaneous reflexes evoked in muscles of the leg from electrical stimulation of nerves serving the hand during walking. Cutaneous reflexes were evoked in different muscles of the leg by stimulating the MED and RAD at heel-strike. Every subject showed significant responses in TA and SOL during both stimulation protocols. Conversely, responses in VL and BF were found significant only in seven and four of the ten subjects tested respectively. Because the data from VL and BF did not describe a generalized behavior, data comparisons were performed only for TA and SOL. We found that reflex responses in TA and SOL were affected by both touch and vision, but the effect observed was different depending on the nerve being stimulated. We will present first the results from the MED stimulation protocol, second the results from the RAD stimulation protocol, and then the results from comparisons made on the muscle background activity.

### 5.3.1 MED stimulation protocol

Electrical stimulation of the MED resulted in clear middle latency responses in TA and SOL. The average response traces from a single subject are presented in Fig. 5-1A as an example of the reflexes evoked from the stimulation. Each trace represents the average of 30 to 39 individual subtracted traces. Thin traces represent the average trace for the no-touch conditions (EOn/ECn) and the thick traces represent the average trace for the touch conditions (EOt/ECt). The top pair of traces in each grouping represents the response traces for the EO conditions and the bottom pair of traces represents the response traces for the EC conditions. The data presented in Fig. 5-1A are presented in Fig. 5-1B rearranged. Solid lines represent the average traces for the EC conditions (ECn/ECt) and the dotted lines represent the traces for the EO conditions (EOn/EOt). The top pair traces in each grouping represents the response traces for the no-touch conditions and the bottom pair of traces represents the response traces for the touch conditions. In both Fig. 5-1A and 5-1B the grey boxes represent the window over which middle

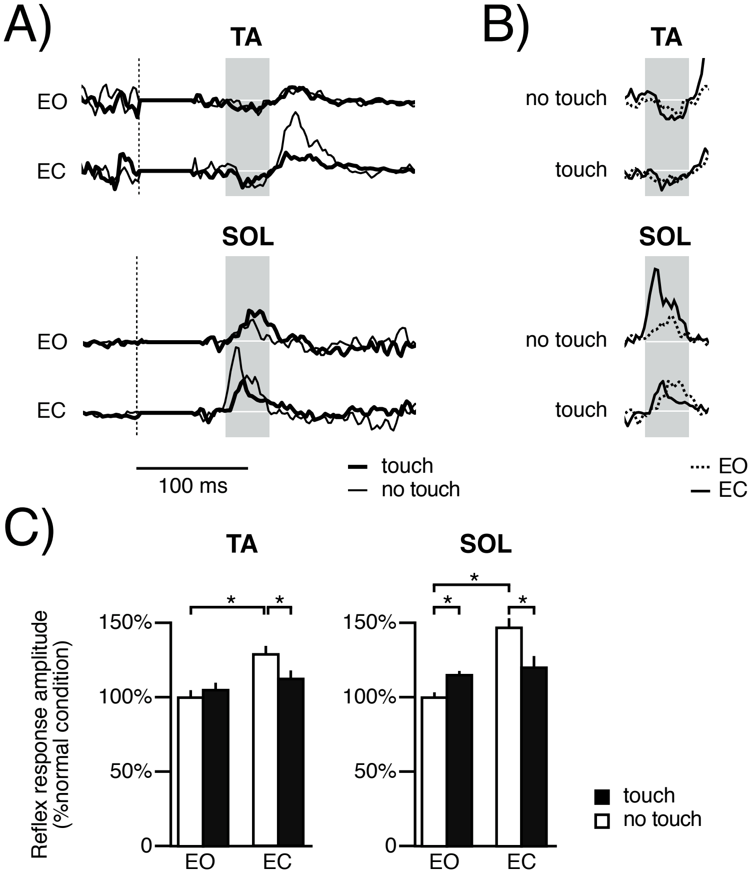

**Figure 5.1:** **A**, Subtracted electromyographic (EMG) traces for TA and SOL after median nerve stimulation for a single subject following electrical stimuli occurring at heel-strike. The top pair of traces in each grouping represents the response traces for the eyes open conditions and the bottom pair of traces represents the response traces for the eyes closed conditions. Thin traces represent average traces for the no-touch conditions and thick traces for the touch conditions. Rectangular boxes indicate the poststimulus time window in which the middle-latency reflex was analyzed. The vertical dashed line in each column is aligned to the onset of the stimulation. **B**, The data shown in A are rearranged and grouped according to the touch condition. The top pair of traces in each grouping represents the response traces for the no-touch conditions and the bottom pair of traces represents the response traces for the touch conditions. Dashed traces represent average traces for the eyes open conditions and solid traces for the eyes closed conditions. Rectangular boxes indicate the same poststimulus time window that is shown in A and in which the middle-latency reflex was analyzed. **C**, Means and standard errors of the middle-latency cutaneous reflexes arising from median nerve stimulation delivered at heel-strike for TA and SOL for each combination of the touch and vision conditions. The data were standardized to the normal condition for each subject. Open bars represent the data for the no-touch conditions. Solid bars represent the data for the touch conditions. The asterisks indicate average response amplitudes that are significantly different between conditions (TA: tibialis anterior, SOL: soleus).

latency reflex response amplitudes were measured. It can be seen from the data from the subject in Fig. 5-1A that the presence of touch affects the reflex response amplitudes in TA and SOL. In addition, the data in Fig. 5-1B shows a visible effect of vision on the reflex response in both muscles. These observations are further confirmed from the group data.

Middle latency reflex response amplitudes from stimulation of the MED are presented averaged across subjects in Fig. 5-1C. It can be observed from the data in Fig. 5-1C that the largest responses were found for the ECn condition while the smallest were found for the EOn condition. The ANOVA revealed a significant interaction effect between the touch and vision conditions for TA ($F=5.08$, $p=0.024$) and SOL ($F=15.10$, $p<0.001$). Post-hoc comparisons revealed that the amplitude of the reflex response in TA and SOL was significantly facilitated with the removal of vision compared to the normal condition (EOn → ECn). In addition, post-hoc comparisons showed that the provision of touch when subjects walked with the eyes closed (ECn → ECt) resulted in a significant suppression of the responses evoked in TA and SOL. However, the effect of touch observed when subjects walked with the eyes closed was not reproduced when they walked with the eyes open. For instance, the amplitude of the response in TA was not significantly affected by touch when vision was present. Moreover, when vision was present, the amplitude of the response in SOL increased significantly with the provision of touch. Hence, the responses in TA and SOL were inhibited with the provision of touch in the absence of vision, but unaffected in TA and facilitated in SOL with the provision of touch in the presence of vision. In summary, the reflexes evoked in TA and SOL from stimulation of the MED showed adaptation to the touch and vision conditions, and the effect of touch was influenced by the vision condition.

### 5.3.2 RAD stimulation protocol

Electrical stimulation of the RAD also resulted in middle latency responses in TA and SOL. The average response traces from the same subject presented in Fig. 5-1A and 5-1B are presented in Fig. 5-2A and 5-2B as an example of the reflexes evoked from the stimulation of the RAD. Each trace represents the average of 33 to 37 individual subtracted traces. The same convention used for the data presented in Fig. 5-1A and 5-1B was used for the data presented in Fig. 5-2A and 5-2B. Similar to the behavior depicted for the responses to stimulation of the MED, responses to stimulation of the RAD also presented adaptation to the touch and vision conditions. This observation is further confirmed from the group data.

Middle latency reflex response amplitudes from stimulation of the RAD are presented averaged across subjects in Fig. 5-2C. It can be observed from the data in Fig. 5-2C that the largest responses were found for the ECn condition while the smallest were found for the EOt condition. The ANOVA revealed for TA a significant main effect of touch (F=9.66, p=0.001) and a significant main effect of

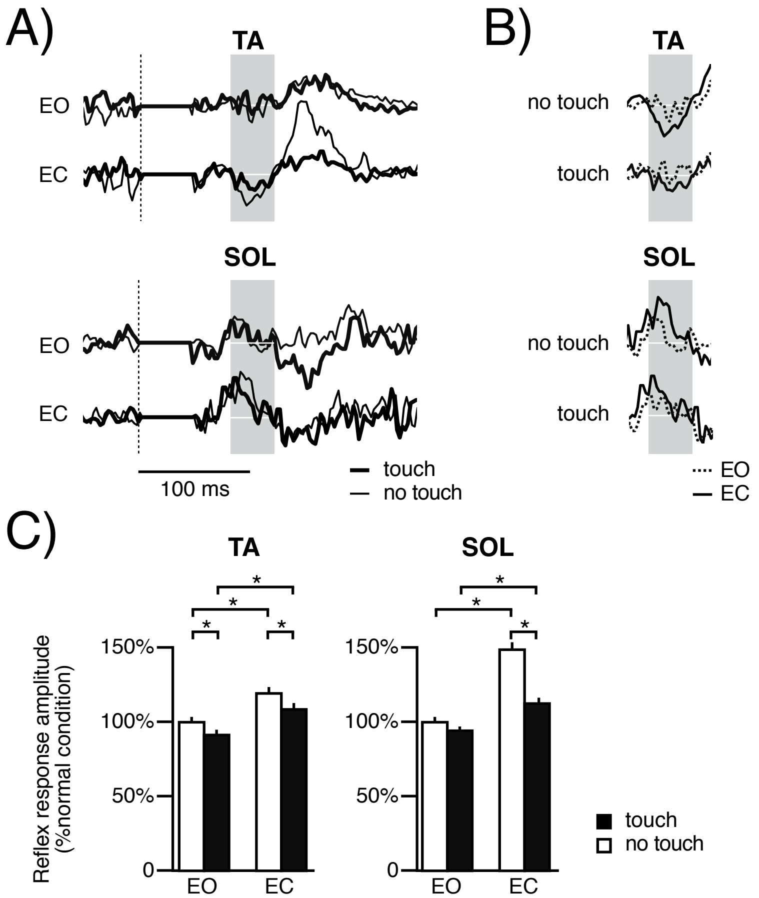

**Figure 5.2:** **A**, Subtracted electromyographic (EMG) traces for TA and SOL after radial nerve stimulation for a single subject following electrical stimuli occurring at heel-strike. The top pair of traces in each grouping represents the response traces for the eyes open conditions and the bottom pair of traces represents the response traces for the eyes closed conditions. Thin traces represent average traces for the no-touch conditions and thick traces for the touch conditions. Rectangular boxes indicate the poststimulus time window in which the middle-latency reflex was analyzed. The vertical dashed line in each column is aligned to the onset of the stimulation. **B**, The data shown in A are rearranged and grouped according to the touch condition. The top pair of traces in each grouping represents the response traces for the no-touch conditions and the bottom pair of traces represents the response traces for the touch conditions. Dashed traces represent average traces for the eyes open conditions and solid traces for the eyes closed conditions. Rectangular boxes indicate the same poststimulus time window that is shown in A and in which the middle-latency reflex was analyzed. **C**, Means and standard errors of the middle-latency cutaneous reflexes arising from median nerve stimulation delivered at heel-strike for TA and SOL for each combination of the touch and vision conditions. The data were standardized to the normal condition for each subject. Open bars represent the data for the no-touch conditions. Solid bars represent the data for the touch conditions. The asterisks indicate average response amplitudes that are significantly different between conditions.

vision (F=31.04, p<0.001) with no significant interaction between these two factors (F=0.18, p=0.670). Reflex responses in TA were of a larger amplitude when subjects walked with the eyes closed compared to when they walked with the eyes open. In addition, allowing the subjects to touch a stable surface while walking resulted in a reflex response that was smaller than when subjects were walking without touching the stable surface. The trend observed in TA was partly replicated in SOL. In particular, the provision of touch resulted in a reduction of the amplitude of the response in SOL when vision was absent but not when vision was present. This was clearly shown by the ANOVA, which revealed for SOL a significant interaction effect between the touch and vision conditions (F=29.83, p<0.001). Post-hoc comparisons revealed that the amplitude of the reflex responses in SOL was significantly larger when subjects walked with the eyes closed compared to when they walked with the eyes open, and, in the absence of vision the provision of touch resulted in a significant reduction in the amplitude of the response. Conversely, no significant differences were found between touch conditions when vision was present. It is important to note that, different from the results observed for TA, the mean amplitude of the responses in SOL showed a noticeable increase when vision was removed in the absence of touch (EOn → ECn), accompanied by a comparable reduction when touch was provided in the absence of vision (ECn → ECt). In summary, the reflexes evoked in TA and SOL from stimulation of the RAD showed adaptation to the touch and vision conditions. In general, while the removal of vision resulted in a facilitation of the responses, the provision of touch resulted in an inhibition of the responses.

### 5.3.3 Background activity

Background EMG was calculated from the control traces over the middle latency window (80 − 120 ms). In Fig. 5-3 the background EMG amplitude averaged across subjects for TA and SOL and normalized to the peak EMG amplitude recorded during unperturbed and unstimulated walking is shown. Visual inspection of the grouped data presented in Fig. 5-3 shows a general effect of both vision and touch on the background activity in both muscles. The ANOVA showed for TA and SOL a significant main effect of touch (F=13.63, p<0.001 and F=13.41, p<0.001) and vision (F=20.15, p<0.001 and F=40.27, p<0.001) with no

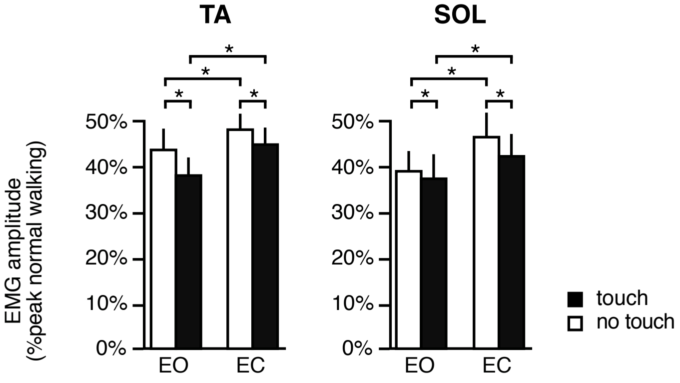

**Figure 5.3:** Means and standard errors of the background EMG for TA and SOL. The data were standardized to the maximum EMG amplitude observed during normal undisturbed walking. Open bars represent the data for the no-touch conditions. Solid bars represent the data for the touch conditions. The asterisks indicate average response amplitudes that are significantly different between conditions.

significant interaction between these two factors (F=0.85, p=0.354 and F=3.35, p=0.066). Hence, closing the eyes led to an increase in the background EMG of both TA and SOL, whereas the provision of light touch led to a reduction in the activity on both muscles. Moreover, the effect of touch was not affected by the vision condition.

## 5.4 Discussion

The primary purpose of the current study was to investigate the effect of light touch on interlimb reflex responses evoked in muscles of the leg from stimulation of two nerves serving the hand, i. e. the median and radial nerves, during walking under an increased level of postural threat. The main findings were that 1) interlimb cutaneous reflexes were affected by touch and vision, 2) the effect of touch varies with the stimulated nerve and 3) background activity in both muscles was affected by touch and vision.

### 5.4.1 Nerve specific modulation of interlimb cutaneous reflexes

Cutaneous reflexes evoked in the legs by stimulating nerves serving the hand were used as probes to test the transmission along interlimb sensorimotor pathways originating from the area of the skin of the hand. Stimulation of the MED and RAD evoked clear interlimb reflex responses in muscles of the leg. It was found that the responses evoked in TA and SOL adapted to touch and vision. The removal of vision resulted in a general increase in the amplitude of the responses evoked by stimulating either the MED or the RAD. On the contrary, the effect of touch on the amplitude of the responses was different depending on the nerve being stimulated. For instance, in the presence of vision, the provision of touch resulted in a reduction in the amplitude of the response evoked from stimulation of the RAD. Conversely, the provision of touch in the presence of vision resulted in an increase in the amplitude of the response evoked from stimulation of the MED. Modulation of cutaneous reflexes in the upper limb (Zehr & Kido, 2001; Chapter 4) as well as in the lower limb (Zehr et al., 1997; Zehr et al., 1998) has been shown to be nerve-specific during walking. It has been argued that cutaneous reflexes from afferents serving different areas of the skin will be modulated according to the role the area of the skin plays for the task being performed. The results discussed in Chapter 4 showed that, when lightly touching a stable surface, cutaneous reflexes were facilitated if they transported sensory information from the skin in contact with the surface. The results observed in the current experiment might be explained in part with a similar approach. The facilitatory effect of touch on interlimb cutaneous pathways transporting information from the skin in contact with the surface was evident when subjects were asked to walk with the eyes open. Interlimb reflexes were facilitated with the provision of touch during the eyes open conditions only when evoked from stimulation of the MED but not the RAD. However, a facilitatory effect of touch during the eyes closed conditions is unlikely as the amplitude of the reflexes was clearly reduced with the provision of touch independently from the nerve being stimulated. The increase in amplitude observed in the reflexes evoked from stimulation of the MED in the presence of vision could be related to an increase in gain in the sensorimotor pathway.

### 5.4.2 Mechanisms of adaptation of interlimb cutaneous reflexes

It was pointed out in Chapters 3 and 4 that walking on a treadmill is a challenging task that gets harder when performed in the absence of vision. The fear of drifting backwards and falling off the back of the treadmill when walking with the eyes closed (Dickstein & Laufer, 2004) could result in a general increase in postural threat, hence resulting in a heightened level of anxiety. The link between anxiety and adaptation of postural control has been studied during standing (Adkin et al. 2000; Carpenter et al., 2001; Carpenter et al. 2004) and walking (Brown et al. 2002; Delbaere et al. 2009). For instance, Brown et al. (2002) found that environmental constraints that heightened anxiety were sufficient to modify gait patterns. In particular, they found that higher anxiety levels resulted in an increase in the activation levels of distal muscles in the leg (i.e. tibialis anterior and gastrocnemius) during walking. Accordingly, the data from the current experiment, together with the data presented in Chapter 3, showed that the removal of vision (increased anxiety) resulted in a significant increase in the level of activation in TA and SOL. Conversely, the provision of touch resulted in a significant reduction in the activity in TA and SOL. These results, along with those presented in Chapter 3, suggest that anxiety modifies muscle activity levels, and that touch assists in regulating this anxiety.

The changes in amplitude observed in the cutaneous reflexes evoked in TA and SOL by stimulating the MED and RAD can be related to changes in the level of postural anxiety. Changes in the level of postural threat during treadmill walking have been associated with changes in reflex responses before (Llewellyn et al., 1990; Haridas et al., 2005; 2006). However, a more likely explanation for the changes observed in the amplitude of the cutaneous reflexes measured in muscles of the legs could result from the changes in the excitability of the motoneuron pool (Matthews, 1986). In TA and SOL, the changes in amplitude observed for the reflexes evoked by stimulating the RAD mimic the changes in background EMG amplitude. This is, reflexes are facilitated with the removal of vision but inhibited with the provision of touch (Fig. 5-2C), directly paralleling the changes in background EMG activity (Fig. 5.3). Therefore, the changes in reflex responses evoked from stimulation of the RAD can be explained by changes in background activity. In contrast, the changes in reflex responses evoked from stimulation of the MED can only be partly explained from changes in the background activity. For instance, the amplitude measured for the reflex evoked in SOL by stimulating the RAD when touch was provided in the absence of vision (ECt) is not different from the amplitude measured during the normal condition (EOn) (Fig. 5-2C). It could be argued that the provision of touch completely reversed the loss of vision effect by lowering the high level of anxiety associated with walking in the absence of vision. However, the amplitude measured for the reflex evoked in SOL by stimulating the MED when touch was provided in the absence of vision is clearly larger than the amplitude measured during the normal condition (Fig. 5-1C). Arguably, when touch cues are not relevant (i.e. RAD) the reflexes are regulated by general anxiety, but when they are relevant (i.e. MED) the sensorimotor channel is facilitated relative to the normal condition (EOn), exemplified by the increase in MED reflex amplitude observed in the EOt condition in SOL, despite the decrease in background EMG. We suggest that the deviation in the regulation of the MED interlimb reflexes indicates that a level of control independent of that which is affecting the background EMG activity is also being expressed when touch is present. The implication is that when tactile feedback associated with the touch surface is available these interlimb sensorimotor pathways are facilitated, suggesting a functional integration within the ongoing locomotor activity of the legs.

### 5.4.3 Functional considerations

There is ample evidence that light touch from the hands participates in balance control during standing (Jeka, 1997; Dickstein et al., 2001; Dickstein et al., 2003;

Johanssen et al., 2007; Wing et al., 2011), and now there is growing evidence that light touch also participates in balance control during walking (Dickstein & Laufer, 2004, Chapter 3). In particular, it was shown in Chapter 3 that light touch can lead to a scaling of balance corrective reactions during treadmill walking to aid in the restoration of balance after perturbations. The results from the current study show that interlimb reflexes are modulated according to touch and vision during walking. There is strong evidence that upper and lower limb movements are coordinated during walking (Dietz, 2002), and that interlimb cutaneous reflexes are functionally relevant in assisting with this coordination (Haridas & Zehr, 2003). In particular, Haridas & Zehr (2003) showed that functionally relevant reflex pathways exist from nerves in the arms onto muscles in the legs. Thus, the results from the current study suggest that sensory cues from light touch are integrated to coordinate and regulate the activity in the legs and participate in balance control during walking. Possibly, with the increase in spatial cues associated with the stable surface the central nervous system would be able to better estimate the location of the body in space. Such an enhancement in spatial orientation could allow for more efficient and better coordinated balance responses during walking. It could be argued that interlimb reflexes might be a rapid means of organizing and coordinating a whole body integrated corrective response. However, the functional benefit of light touch in stabilizing posture could also lead to problems under abnormal states. For instance, oscillation of the touch surface entrains postural sway during standing (Wing et al., 2011). Therefore, touch itself could be a source of disturbance, or cue for a disturbance if the arms are engaged in a balance functional task. For example, when using a walking assistive device, or holding an object that imparts a disturbance at the arms that needs correction, responses in the legs that are not directly related to a balance disturbance could be activated. The data presented in Chapter 2 showed that responses in the legs are activated in response to perturbations applied at the arms, even though these perturbations did not pose a substantial threat to balance. Whether the responses in the legs associated with an unstable touch surface could lead to instability in the control of posture is an open question that needs further study.

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# Chapter 6
# General Discussion

The results from this thesis confirm that tactile feedback from the hands has a strong influence in balance control during walking. This section summarizes the most relevant findings from this thesis and discusses the implications of the results in balance control and, particularly, its significance for rehabilitation.

## 6.1 The role of the arms and the hands in the regulation of balance

Balance corrective responses are not limited to activation of muscles in the legs but also involve activation of muscles in the arms (Marigold & Misiaszek, 2009). In particular, it has been shown that the responses evoked in the legs from slips (Marigold et al., 2003), trips (Eng et al., 1994), translation perturbations of the support surface (Dietz et al., 1987; Tang & Woollacott, 1998), sudden deceleration of the treadmill belt (Berger et al., 1984), or backward pulls applied at the waist (Misiaszek, 2003), share similar features independently from the locus of the disturbance. Based on the similarity of the responses, it was suggested that responses in the legs are most likely related to the balance disturbance per se, and not to the particular features of the perturbation (Misiaszek, 2003; Marigold &

Misiaszek, 2009). In Chapter 2, I showed that perturbations delivered at the arms also result in activation of muscles in the arms and the legs, and that the responses in the legs are comparable to those observed from other perturbation paradigms. Specifically, responses in the legs to perturbations applied at the hands share similar features to perturbations applied at the foot or waist. Similar to the results from other balance studies, responses in the arms and the legs were activated at comparable latencies when perturbations were delivered at the hands. This further supports the most likely explanation that balance corrective reactions involve the whole-body and are coordinated by a centrally mediated response (Misiaszek, 2003).

That corrective reactions involve whole-body responses is evidence that a link between the arms and legs exists and that it participates in the control of balance. For instance, balance corrective responses in the legs are strongly influenced by the task engaged by the arms. Restricting the movement of the arms by lightly folding them across the chest (Misiaszek & Krauss, 2005) or by holding on to stable handles (Misiaszek & Krauss, 2004) affects the amplitude of the responses in the legs to perturbations delivered at the waist. Similarly, the results presented in Chapter 2 show that the responses in the legs evoked from perturbation delivered at the arms are modulated by the demand to maintain stability at the arms. Thus, the task-dependent modulation of the responses in the legs does not only become apparent when the movement of the arms is restricted, but also when the arms are engaged in a support task while being perturbed. Misiaszek & Krauss (2005) suggested that the change in the amplitude of the corrective responses associated with the restriction of the movement of the arms indicated that balance corrective reactions during walking can be scaled according to the availability of the arms to assist in the recovery of balance. In addition, the results in Chapter 2 show that such scaling is also present when the arms are the source of the disturbance. If the task requires the position of the handles to remain stable then responses in the legs will be facilitated following disturbances at the arms. On the contrary, if stability of the handles is not part of the task then the responses in the legs will be inhibited. Thus, corrective responses are not only scaled according to the level of support the arms can provide in stabilizing balance following a perturbation, but are also modified to accommodate the task demands of the arms.

Further evidence of the participation of the arms in the regulation of balance is provided from the study of the influence of light touch on postural control. During standing, light touch participates in the regulation of body sway (Holden et al., 1994; Jeka & Lackner, 1994; Jeka et al., 1998; Clapp & Wing, 1999; Reginella et al., 1999; Rogers et al., 2001; Dickstein, 2005), and the modulation of responses to postural perturbations (Dickstein et al., 2003; Johannsen et al., 2007). Previously, only one study has evaluated the effect of light touch during walking (Dickstein & Laufer, 2004). However, in that study the effect of light touch on balance regulation during walking could not be fully addressed due to the limited number of steps subjects could walk on a treadmill with the eyes closed. I overcame the limitations of that study and showed in Chapter 3 that the effect of light touch in balance control during standing is also present during walking. Moreover, the provision of light touch reduces body sway and facilitates corrective responses to balance perturbations delivered during walking, as it does during standing (Dickstein et al., 2003; Johannsen et al., 2007). Thus, sensory input from the hands is incorporated by the central nervous system to regulate balance during walking similar to during standing.

However, balance control during walking imposes an additional challenge to the nervous system. In particular, in contrast to standing, during walking balance corrective responses have to be integrated within the locomotor activity in the legs and allow stepping to continue following a perturbation. Phase modulation of balance corrective responses has been demonstrated before (Patla, 2003). In particular, independent from the locus of the disturbance, responses to balance perturbations result in strong activation of muscles in the legs during the stance phase (Berger et al., 1984; Eng et al., 1994; Tang et al., 1998; Marigold et al., 2003; Misiaszek, 2003). Similarly, the data presented in Chapter 2 showed that perturbations applied during walking at the arms triggered strong and consistent responses in muscles of the leg during the stance but not the swing phase. Clearly, during walking, the position of the centre of mass will be immediately affected by the forces generated from the activation of muscles in the leg that is in contact with the ground. Therefore, that the effect of light touch hereby discussed during walking is comparable to the effect described before during standing informs our understanding of balance control providing further evidence that the mechanisms by which balance is regulated during standing and walking are essentially the same. The difference remains that during walking balance corrective responses are modulated to the step cycle to be integrated within the locomotor activity in the legs and allow stepping to continue following a perturbation.

## 6.2 Cutaneous sensory input from the hands and the regulation of balance

The effects of light touch on balance control presented in my thesis can be attributed to cutaneous feedback from the hands. Kouzaki & Masani (2008) suggested that the contribution of light touch from the hands to balance regulation is attributable to tactile feedback from the fingertip without mechanical support provided by the contact. The authors found that depriving finger tactile feedback by tourniquet ischemia resulted in a marked reduction of the effect of light touch on body sway during standing (Kouzaki & Masani, 2008). The results presented in my thesis present additional evidence for a specific role of cutaneous afferents from the skin in contact with the touch surface in the regulation of balance. For instance, the data in Chapter 2 can be explained in part by a contribution of cutaneous input in the organization of a corrective response to balance perturbations. More concrete evidence for the role of tactile feedback in the regulation of balance is exposed by the strong effect of light touch in the modulation of body sway, and its strong influence on the facilitation of corrective responses to balance perturbations, suggest a direct involvement of cutaneous afferents from the hand in the regulation of balance (Chapter 3). This observation is further supported by the fact that segmental (Chapter 4) and interlimb (Chapter 5) cutaneous pathways are selectively facilitated with the provision of light touch if they transport sensory information from the skin in contact with the touch surface. The results presented in Chapter 4 suggested that neural pathways to muscles in the arms are facilitated when touch is provided, and the results in Chapter 5 implied a functional integration of tactile feedback associated with the touch surface within the ongoing locomotor activity of the legs.

However, it is important to acknowledge that the effect of light touch on balance regulation as described in the previous paragraph can not be exclusively attributed to cutaneous feedback from the skin in the hands. Kouzaki & Massani (2008) recognized that tourniquet ischemia does not exclusively suppress feedback from tactile afferents in the skin of the hand but instead results in a general suppression of feedback from every sensory afferent in the hand including muscle spindles and golgi tendon organs. Thus, the effect observed in their results could be associated with the general loss of sensory feedback from the hand. Similarly, the results presented in Chapters 4 and 5 cannot be exclusively linked with feedback from cutaneous afferents from the hand. Both the medial and radial nerves are mixed-nerves. Although, distally from the wrist the radial nerve is composed of cutaneous afferents alone, this is not the case for the median nerve. In particular, muscle afferents to the first and second lumbricals of the hand and the thenar eminence are found in the median nerve at the level wrist. Therefore, the responses evoked from stimulation of the median nerve as described in Chapters 4 and 5 should not be exclusively associated with cutaneous afferents from the hand but might also include muscle afferents.

Although the effect of touch cannot be solely attributed to feedback from sensory afferents from the skin of the hand, these afferents most likely play an important role in the modulation of cutaneous reflex responses when light touch of a stable surface is provided at the tip of the index finger. It is well known that sensorimotor integration is necessary for the control of balance. In particular, based on information gathered from the internal and external worlds, the nervous system determines the appropriate motor patterns necessary for walking based on the interaction between the body and its surroundings (Latash et al., 1996). Although the arms do not provide mechanical support to help stabilizing balance when light touch is provided at the finger, cutaneous input from the skin in contact with the touch surface does provide relevant sensory information about the environment that can be used by the nervous system in the regulation of balance.

It might be argued that the influence on balance control from cutaneous feedback from the hands is similar to that from any other sensory input. Postural control is strongly modulated by sensory input from the vestibular, visual, and somatosensory systems. Subjects with no vestibular function standing on foam rubber with the eyes closed will fall over. But, if at least one source of sensory information is available then balance is maintained even though not reaching normal levels (Horak et al., 1990; Maurer et al., 2006; Mergner et al., 2009). The data in Chapter 3 of this thesis showed that light touch sensory cues can compensate for sensory loss affecting balance control. Compared to the normal condition (i.e. eyes open, no-touch), corrective responses to balance perturbations during walking were largely affected with the removal of vision. However, the provision of touch in the absence of vision allowed for balance control to be restored to near-to-normal levels. Additionally, Dickstein et al. (2001) showed that balance control deficits in patients with peripheral neuropathy was largely reduced with the provision of light touch to the tip of the index finger. Their data showed that providing patients with light touch stabilized postural control (i.e. angular trunk velocity) to a level comparable to the one observed in healthy subjects. These results suggest that fingertip touch provided sensory cues that were able to compensate for the deficiencies associated with the loss of sensory feedback from the feet associated with the neuropathy.

It could be argued that sensory input from the hands plays a role in balance regulation comparable to that of sensory input from the feet. The use of sensory feedback from cutaneous mechanoreceptors in the foot to regulate balance has been demonstrated in animal models. For instance, Ting & Macpherson (2004) compared the automatic postural responses during platform translations to those evoked during platform rotations in standing cats. Their results suggested that the ratio of shear to loading force plays an important role in the selection of the direction-specific response. The authors proposed that cutaneous receptors in the pads of the paws, that are capable of detecting direction specific shear forces, provide essential input for the selection of these direction-specific corrective responses. The relevance of cutaneous input from the paw of the cat has also been demonstrated during walking. Misiaszek & Bolton (2009) showed that the amplitude of corrective reactions in cats to lateral translations of the walkway were reduced when cutaneous innervation of the paws was surgically removed. These results imply first, a role for shear force sensation in the regulation of balance; and second, the direct involvement of cutaneous sensory input from the sole to provide such input.

The influence of cutaneous information from the foot in the regulation of balance has also been described from human studies. Sanes et al. (1985)

evaluated posture and voluntary control in patients with large-fiber sensory neuropathy associated with impaired position, vibration and cutaneous sensation. Among other motor control deficits, the authors found that postural control in these patients was largely affected in the absence of vision. Impaired postural control resulting from cutaneous sensory input deficits has also been studied in healthy humans. Mauritz & Dietz (1980) demonstrated an increase in body sway of standing subjects when sensory input from the feet were reduced following ischemic block. However, besides removing tactile sense this technique also impacts proprioceptive sensory feedback from the affected limb (Laszlo, 1966). The cooling of the foot results in a reduction of touch and pressure sensation without any associated impairment of proprioception, pain or motor function (Perry et al., 2000). Magnusson et al. (1990) found that body sway was largely affected following hypothermic anaesthesia, and Perry et al. (2000) found that compensatory stepping reactions evoked by large-magnitude perturbations in standing subjects were affected by the foot-cooling procedure. In addition, Meyer et al. (2004) demonstrated that anesthesia of the cutaneous soles of the foot induced by intradermal injections of local anesthetic resulted in balance deficits predominantly in the medio-lateral direction and only when vision was occluded during bipedal stance, but both in the medio-lateral and antero-posterior directions during unipedal stance with the eyes open. Thus, the role of cutaneous input from the hands in balance control is consistent with or reminiscent of the role of cutaneous feedback from the feet or paws.

That arms and legs could play similar roles in the control of balance is not surprising. Arm and leg movements have been argued to be correlated during walking (Dietz et al., 2001). There is evidence of a neuronal linkage between upper and lower limbs. For example, cutaneous reflex responses are evoked in muscles throughout the body after stimulation of nerves serving the hands or feet of subjects maintaining tonic contractions (Zehr et al., 2001), or performing locomotor activities such as walking (Zehr & Haridas, 2003) and cycling (Sakamoto et al., 2006). Interlimb cutaneous reflexes evoked during locomotor activities show phase modulation of the reflex amplitude that is not directly related to the level of background EMG activity of the target muscle (Zehr & Haridas, 2003), suggesting that these reflexes might be relevant in assisting with movement coordination between the arms and legs during locomotor tasks (Zehr & Stein, 1999). The results from my thesis further support the existence of a neuronal linkage between arms and legs, and suggest that this linkage is not limited to serve in the coordination of their movement. The results presented in Chapter 5 suggested that, when the touch sensory cues were relevant to balance control, this feedback was integrated within the ongoing locomotor activity of the legs. This suggests that this interlimb cutaneous link could also then be important to functionally integrate tactile feedback from the hands into the control of balance during walking. Dietz (2002) suggested that the coordination between upper and lower limb movements during human gait might be a residual function of quadrupedal locomotion. Specialized networks capable of generating the basic spatiotemporal patterns characteristic of rhythmic movements (i.e locomotion, respiration) have been located at the lower levels of the motor control system (for review see Arshavsky et al., 1997). These central pattern generators (CPGs) have been largely studied across different species (for general reviews, see Marder & Calabrese, 1996; Stein et al., 1997), and their organization has been found to be genetically predetermined (Champagnat & Fortin, 1997). In the cat, CPGs have been located in the spinal cord (Grillner, 1985, for review see Dietz, 2003) and, nowadays, there is also data supporting the contribution of such networks in the generation of walking in humans (Barbeau & Rossignol, 1994; MacKay-Lyons, 2002). In addition, there are indications that similar networks are responsible for the control of rhythmic movements in the arms, and that these movements are regulated by sensory input much like leg movements (Zehr & Duysens, 2004). The results from my thesis suggest that sensory input from the hands can be integrated into the regulation of balance during walking in a similar way as sensory input from the foot, possibly an evolutionary preserved function of the cutaneous feedback from the hands. Taken together, these results suggest that dynamic stability during locomotion involves neural mechanisms consistent with a quadrupedal locomotor control system (Marigold & Misiaszek, 2009).

## 6.3 Functional relevance

There is a large collection of actions by which arms can assist to recover balance upon a perturbation. The arms can be used to protect the body by arresting a fall (Robinovitch et al. 2005; Feldman and Robinovitch 2007), to dissipate the centre of mass momentum induced by a perturbation (Oates et al. 2005; Roos et al. 2008), or to reach for nearby rails in order to increase support of the body (McIlroy and Maki 1995; Maki and McIlroy 2006). In addition, the arms can play a role in balance regulation that does not require their movement. Depending on the task at which the arms are engaged, different balance corrective strategies can be selected in response to a perturbation. Holding on to stable handles will result in a suppression of the responses in muscles of the legs to balance perturbations (Misiaszek & Krauss, 2004), and holding an object in the hands will suppress the reach-and-grasp response aimed at enhancing balance (Bateni et al., 2004).

The findings from this thesis expose the importance of tactile feedback from the hands in the regulation of balance during walking. Misiaszek (2006) presented a simple model based on finite state control theory (i.e. If-Then rules) to describe how the nervous system can rapidly select and execute an appropriate corrective response to a balance disturbance during walking. The key concept of the If-Then rules model thereby presented is that multiple sensory inputs are evaluated continuously to assess the state of the rules, and then the appropriate motor outputs can be generated based upon these sensory inputs. In this model any sensory input could be added, removed or scaled to the needs of the specific behavioural task being performed. The results from my thesis show that cutaneous information from the skin of the hand can be incorporated and utilized within the balance control mechanisms when the hands are engaged in a balance related task.

The nervous system regulates balance during walking by integrating information about the body and its surroundings within the ongoing activity of the legs. As evidenced in my thesis, tactile feedback from the hands can participate in the regulation of balance. On one side, the additional sensory input provided by the hands when engaged in a balance task can increase sensory feedback that would allow the nervous system to better discriminate the features of the surroundings. Sensory input supplied with light touch provides the nervous system with additional spatial orientation to reduce body sway during standing (Wing et al., 2011) or walking (Dickstein & Laufer, 2004) with the eyes open or closed. On another side, sensory input from the hands can compensate for the loss of other sensory inputs. It has been shown that sensory cues provided by light touch can improve balance in patients with peripheral neuropathy and compensate for the reduced somatosensory sensation in their feet (Dickstein et al., 2001; Dickstein et al., 2003). Also, the provision of light touch in the absence of vision allows for corrective responses to be restored to near-to-normal levels (i.e.

eyes open) (Chapter 3). In this context, it could be argued that tactile feedback from the hands can be used by the nervous system not only to enhance balance control, but also to compensate for the reduction, impairment or loss of feedback from other sources of sensory input.

Balance corrective responses are associated with different strategies depending on the context. It can be argued that, when the arms are engaged in balance, tactile feedback from the hands could contribute in the selection of a balance recovery strategy. For instance, the use of nearby handrails is a commonly used strategy to increase support and stabilize balance when challenged by rapid movement of the support-surface (Maki and McIlroy, 2006). Lamont & Zehr (2007) showed that neural pathways to specific muscles in the arm are gated to incorporate the rail into the automatic recovery strategy.

It is also possible that disturbances to the contact surface itself could initiate balance corrections in the legs. It has been discussed before (Misiaszek, 2003), as well as in this thesis (Chapter 2), that balance corrective responses involve whole body reactions independently from the locus of the perturbation. The most likely point at which a disturbance to stability would be first detected is at the interface between a support surface and the body. Therefore, cutaneous feedback from the hands would seem a logical cue to initiate corrective reactions to a perturbation if the perturbation was applied through a contact with the hands. The data presented in Chapter 2 showed that perturbations delivered at the hands resulted in a change in force at the hands that preceded any change in position of the handles, by about 80 ms. Therefore, tactile feedback related to the applied force seems a logical cue for the detection of a balance disturbance applied at the hands. If so, then it would seem logical that this early detection of an impending disturbance can be used to initiate or trigger the appropriate reaction to maintain balance.

Although responses in the legs could be activated from cutaneous feedback from the hands, the task engaged by the arms would influence the expression of these responses. Misiaszek & Krauss (2004) showed that responses in the legs are inhibited when the arms position is stabilized by holding on to stable handles compared to when the arms were swinging normally. The data in Chapter 2 showed that holding onto unstable handles also resulted in inhibition of the responses in the legs, but only when the task did not require stability at the hands. On the contrary, responses in the legs were facilitated when the subjects were instructed to maintain the position of the handles (or resist the displacement). An example of how the task related expression of the evoked responses might serve a functional role would be to compare the demands of using a rolling walker or pushing a stroller. Hitting an obstacle with a walker would result in strong responses in the legs to assure stability of the device. Conversely, hitting an obstacle with a stroller would most likely result in compliance of the arms and a push strong enough only to overcome the obstacle. Although, in both cases the arms are involved in pushing a device while walking, only the walker is expected to provide additional support when balance is challenged (e.g. hitting an obstacle). Thus, the responses in the legs will be expressed differently whether the task is to secure stability of the device, or to ensure walking progression.

## 6.4 Limitations

Although the results from my thesis show the important relevance of tactile feedback from the hands in balance control, it is important to acknowledge that the interpretation of these results is restricted by the limitations of the experimental setup. Balance control during walking has been largely studied by having subjects walk on a treadmill. The advantage to studying locomotion during treadmill walking is the easiness in manipulating the environment. Although several studies have demonstrated the similarities between treadmill gait and overground gait (Riley et al., 2007; Mills et al., 2007; Damiano et al., 2011), it is important to acknowledge the most important differences between both paradigms. For instance, Dingwell et al. (2001) demonstrated that treadmill walking was associated with significant reductions in locomotor variability compared to overground walking. They concluded that changes in the neuromuscular control associated with the variability or stability of locomotion could be masked by having subjects walk on a treadmill. Certainly, walking on a treadmill is largely constrained compared to overground walking which results in an additional task for the nervous system. During treadmill walking the nervous system is not only challenged with the regulation of balance but also the maintenance of a safe gait within the limits of the treadmill belt. For instance, perturbations applied at the waist during treadmill walking result in rapid responses in muscles of the legs targeted at recovering balance and stabilizing walking on the treadmill within a few steps. Although pulls at the waist during overground walking might result in a similar response strategy, it is also possible that a person that is pulled at the waist can choose to simply stop walking to restore balance and avoid falling. Such a choice is not possible during treadmill walking. Thus, whether responses to perturbations applied during treadmill walking are intended to restore balance following the disturbance to maintain stability, or instead their purpose is to maintain the position on the treadmill remains uncertain. Moreover, it is also possible that both tasks cannot be dissociated one from another and to maintain a position on the treadmill stability will be regulated accordingly. Therefore, although the results from my thesis should translate to overground walking, it is possible that some aspects of the findings might be exaggerated because of the additional constraints imposed by the task of walking on a motorized treadmill.

To facilitate the measurements during the experiments we designed a repeated measures experiment. McIlroy & Maki (1995) showed that repeated exposure to the same postural perturbation results in adaptation of the responses. Although adaptation to the perturbations should occur within the first few repetitions, the characteristic of responses occurring in the unpredictable circumstances of everyday life can only be assessed based on the very first trial. Important information about the mechanisms involved in the activation of postural responses can be investigated from repeated measures designs, but it is important to note the importance of first trial responses (FTR) in balance control. Allum et al. (2011) presented an interesting review of the importance of first trial responses and how they are important sources of information about balance control. Specifically, responses to unexpected balance disturbances are often startling, while exposure to a constant perturbation results in adaptation of the responses. It is certain that due to the experimental design used in the studies in my thesis, the responses analyzed based on the collected data do not describe the true nature of a startling response to a balance perturbation. It could be argued that the results described in my thesis do not reflect a real life situation. However, because responses adapt to repeated perturbations and usually converge to minimize the use of the resources necessary to produce an optimal response, I would argue that similar results would be found for the effects described in my thesis if measured for the FTRs. Nevertheless, it is important to note that the limitation addressed in this paragraph would only be related to the data presented in Chapters 2 and 3. On the contrary, the data presented in Chapters 4 and 5 would be most likely not affected because balance reactions were not studied per se, but instead the gating of sensory channels was studied in a particular environment that was purposely and predictably unstable. Single trial studies would be very complicated due to the large number of subjects that would be needed. Also, the large inter-subject variability associated with the single measurement that can be obtained from each subject could confound the results. Nevertheless, it would be important, as suggested by Allum et al. (2011), that studies assessing balance performance routinely include FTRs in their analyses.

An important technique that was introduced in this thesis to study the effect of light touch during walking was the use of an auditory feedback that allowed subjects to walk safely with the eyes closed. Auditory feedback was first used by Chiari et al. (2005) who demonstrated that an audio-feedback system linked to trunk acceleration was capable of reducing postural sway of standing subjects. Based on their results, I translated this technique to allow subjects walking on a treadmill to get auditory feedback linked to their position on the treadmill (Chapters 3, 4 and 5). The success of this technique was demonstrated by the fact that subjects could walk on the treadmill with the eyes closed without drifting backwards, as would occur in the absence of any additional sensorimotor anchor that could be used in the absence of vision (Dickstein & Laufer, 2004). That auditory feedback allowed safe walking in the absence of touch and vision suggests that auditory cues were integrated by the central nervous system and used to provide a position reference on the treadmill. Although the auditory feedback was turned on for every tested condition, it is possible that auditory cues were integrated by the central nervous system differently depending on the availability of other more direct position cues such as touch and vision. In this sense, it is possible that varying cognitive loads were imposed on the nervous system during the different conditions, and possibly when vision and touch were both absent (i.e. EOn) the processing of the auditory cue into a position reference cue resulted in a high cognitive demand. Although it is not possible to evaluate from the data collected in the experiments defined in my thesis, it is important to acknowledge that the task of integrating auditory cues into meaningful position cues imposes an additional load on the central nervous system that could influence the observed results.

## 6.5 Future directions

The main finding from this thesis is that tactile feedback from the hands is relevant for balance control during walking. An important observation was that cutaneous input from the hand might be important to initiate corrective reactions that would include activation of responses in the legs. The importance of mechanoreceptors in the sole of the foot in the control of balance has been assessed by cooling of the soles of the feet in ice-water during standing (Magnusson et al., 1990) and walking (Perry et al., 2000), as well as by anesthesizing the foot during standing (Meyer et al., 2004). Both techniques result in a significant reduction of plantar sensation that is reflected in a loss of pain, touch and temperature sensation. The use of either technique to desensitize cutaneous afferents from the hands could be used to better assess the role of cutaneous feedback from the hands in the initiation of corrective responses. The importance of tactile feedback from the hands in the initiation of corrective reactions to perturbations applied at the arms could be assessed from the effect of anesthesia on the responses evoked in arms and legs. According to the results from my thesis, it would be hypothesized that corrective responses to perturbations delivered at the arms would be delayed by the loss of sensory feedback from the skin of the hand induced with hypothermic anesthesia.

It is clear that balance is regulated from the integration of multiple sources of sensory input into an appropriate motor response. Stimulation of the visual (Berthoz et al., 1975), vestibular (Njiokiktjien & Folkerts, 1971), auditory (Dozza et al., 2007), and somatosensory (Jeka & Lackner, 1994) systems affects body sway during standing. In particular, it has been demonstrated that sensory information from touch of a stable surface affects balance control during standing and walking. In addition, it has been shown that oscillation of the touch surface will entrain body sway during standing (Jeka et al., 1997; Wing et al., 2011). In my thesis I demonstrated that the effect of light touch in the regulation of balance during standing is also present during walking. Therefore, it would be expected that movement of the touch surface would also induce balance instability during treadmill walking. Whether instability of the touch surface would also result in disruption of balance corrective responses is an open question. I showed in Chapter 3 that corrective responses are facilitated with the touching of a stable surface, which resulted in faster recovery of balance following a perturbation applied at the waist during walking. The effect of an unstable touch surface on balance corrective responses could be tested by applying perturbations at the waist and the touch surface simultaneously. It would then be hypothesized that corrective responses to perturbations delivered during walking would be affected by the stability of the touch surface. That is, compared to the no-touch condition, corrective responses will be facilitated with the provision of touch of a stable surface but impaired with the provision of touch of a moving surface.

A very important question was raised in the previous section. Allum et al. (2011) showed the importance of FTRs in the study of balance control. In this context, it would be important to evaluate the effect of tactile feedback on the very first response to a perturbation. First of all, it is important to acknowledge that single trial studies, such as the one needed to analyze FTRs, are complicated in that they require data from a large number of subjects in order to reduce the probability of a false negative (type II) error. However, the additional information that would become available about how tactile feedback from the hands participates in the regulation of balance based on the FTRs would help to better understand the link between arms and legs during balance control. One possibility is that the effect of tactile feedback on corrective responses to balance perturbations during walking is not affected by repeated exposure to the perturbations. This is, the very first response is not different from any subsequent response. Another possibility is that the effect of touch is a learned event that requires repeated exposure for the touch cues to be of benefit for balance regulation. In this sense, touch would not affect corrective responses during the very first trial. Subsequent exposure to the perturbations in the presence of touch would then result in rapid adaptation to the additional sensory cues and result in the effects hereby described. In my thesis I showed that the influence of tactile feedback is linked to the demands for the task the arms have to perform. Thus, depending on whether the touch surface is considered relevant for balance when the first response is activated would affect the use of tactile feedback in the modulation of the response. Changes in the amplitude of the responses with respect of the number of repetitions could be used as a measure for the adaptation to the influence of tactile feedback on the modulation of corrective responses to perturbations.

The contribution to walking balance control of cutaneous feedback from the hands could have important implications in the rehabilitation or treatment of individuals with balance impairments. If tactile feedback from the hands is capable of enhancing balance control performance, then it might be possible to apply this knowledge to assist patients with impaired balance. For example, walking aids are widely used to help patients with balance deficits in performing activities of daily living. The main role of walking aids such as walkers or canes is to provide additional support, and thereby increase the base of support to enhance balance. Based on the results presented in my thesis, it is possible that by enhancing tactile feedback at the hands, balance could be improved without the additional support provided by a walking aid. This hypothesis could be tested by developing different types of contact to be used with different types of walking aids. The different contact types could be associated with different textures, as well as with a vibrating surface such as the one suggested to be used in the feet to improve balance in patients with reduced somatosensory function (Priplata et al., 2006).

Additionally, the influence of tactile feedback from the hands in balance control could also be used to expand the understanding of how walking aids affect gait rehabilitation. For instance, altogether with the strong clinical evidence that the use of walking aids can improve balance in adults, there is also strong evidence that their use can increase the risk of falling (Bateni & Maki, 2005). One important factor for this is the mechanical and attentional demands associated with the use of a mobility aid. Thus, using walking aids during training in patients with impaired balance might impose additional demands that are not necessary for balance during walking. In other words, patients might be trained not to maintain balance while walking but instead to incorporate the use of the mobility aid within the walking activity. If the additional demands associated with the use of a mobility aid during training could be eliminated then training would be targeted to allow patients to regain the ability to maintain balance without the need of an additional device. The results presented in my thesis, together with previous work related to light touch and balance control, show that the hands participate in balance control even when mechanical support is unavailable. This hypothesis could be tested by studying adaptation to repeated exposure of balance training in the presence and absence of touch when mechanical support is available or not. If balance could be improved without the need of the mechanical support from the walking aid, possibly the risk of falling because of the use of such aids could be reduced.

## 6.6 Conclusion

The participation of the feet in the control of balance during walking is particularly clear given the feet are a direct interface between our bodies and the environment. The findings from my thesis show that the arms can be engaged as a similar interface. Forces applied at the arms can induce balance perturbations that will activate whole-body responses, thus making sensations from the hands especially well suited to detect these potential disturbances. Moreover, the hands will be often used to increase stability if possible. This ability is not limited to the provision of additional support, but also linked to the provision of additional sensory cues relevant for balance regulation. In summary, sensations from the hand participate in integrating additional information describing the interaction between the body and the environment, hence playing a strong role in the control of balance.

## 6.7 References

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