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Context-dependent soleus H-reflex modulation in humans

by

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Abstract

Balance corrective reactions to perturbations during walking are characterized by short-latency responses in leg muscles. After forward perturbation, a short-latency response occurs in soleus after ankle dorsiflexion. Stretch reflexes may contribute to soleus activation in balance corrective reactions. The soleus H-reflex is used as a tool to investigate changes in a spinal pathway when stability is threatened. H-reflexes were elicited across the step cycle while subjects walked in five conditions of increasing postural threat. H-reflexes were modulated with the walking context in a phase-specific manner. At heelstrike, the H-reflex amplitude increased with the level of instability: smallest when subjects held stable handles and largest when subjects experienced perturbations with their arms crossed. The modulation of this spinal pathway with changes in postural threat indicates that central influences may regulate the involvement of spinal circuitries in balance reactions, suggesting that these pathways contribute to the larger, global balance corrective strategy.

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CHAPTER 1 – Introduction and review of literature

Introduction

Balance maintenance in human walking is a task requiring constant adjustment. Given the instability of our bipedal gait and the ever-changing environment we move through, muscles from the torso and limbs of the body work in an integrated fashion to maintain balance while accomplishing tasks of various complexities that are essential for daily living. Sensory inputs contribute to balance maintenance by providing information about the environment so the body can adapt. Sensory information often arrives ahead of balance disturbances, and combined with experience, can be used to produce anticipatory adjustments to maintain stability before balance is threatened. However, the unpredictability of our environment often results in sudden disturbances to balance that cannot be anticipated. In these instances, we must use fast-acting reactions to maintain our balance. This is often called the feedback or reflex mode of balance maintenance, or simply reactive balance, because it depends on sensory feedback to initiate balance corrective reactions when the body is already experiencing instability (Deliagina et al. 2006). Reactive balance maintenance has been investigated in humans primarily in studies that perturb either a support surface or the body during a task. These studies investigate the compensatory balance adjustments made by leg, torso, and arm muscles to maintain upright posture and continue with the given task. Compensatory balance adjustments during walking have been investigated in a variety of experimental situations that attempt to replicate naturally occurring balance disturbances. Compensatory balance adjustments share common basic features regardless of their perturbation type, but are also modulated in a task-dependent and phase-dependent manner and with the walking context. Current research suggests that somatosensory inputs from the periphery, including proprioceptors and cutaneous sensations, may serve to release pre-programmed responses, and alter the features of these responses depending on the context (Deliagina et al. 2006). In this thesis I investigate the context-dependent nature of a spinal reflex arising from proprioceptor afferents and draw comparisons to the context-dependent modulation of balance corrective reactions during walking. The similarities suggest that this simple spinal pathway may be a component of the larger complex corrective response.

Features of balance corrective reactions

The detailed characteristics of compensatory balance adjustments depend on the nature of the perturbation, but the basic features are conserved across tasks. Balance corrective reactions during perturbed walking involve the whole body including muscles of the legs, torso, and arms yet often begin with the activation of ankle muscles, recruiting muscles in a distal to proximal temporal order. This pattern is preserved despite variation in perturbation method. In standing subjects, this pattern of muscle activity is termed the ankle strategy characterized by a temporal sequencing of muscle recruitment beginning around the ankle and radiating proximally, with leg and torso muscle activation at latencies of 73 to 110 ms reported in response to support surface translation (Horak & Nashner 1986).

When subjects walked while experiencing surface translation, Nashner (1980) reported similar adjustments that successfully corrected for changes in the ankle angle. Nashner (1980) reported that ankle dorsiflexion perturbations during walking produced a 200-300% increase in support leg gastrocnemius (G) activity. Adjustments had latencies between 95-110 ms. Ankle plantarflexion produced strong activation of the tibialis anterior (TA) of the support leg, and diminished the normal activity of the G to nearly zero. In general, perturbation of the ankle joint during either standing or walking elicited compensatory responses in the perturbed leg primarily around the ankle joint and were specific to the balance recovery demands of the perturbation.

Tang et al. (1998) found that muscles of the leg were recruited in a distal to proximal order in response to forward surface translation of the right leg during walking. Subjects relied on the consistently- activated large amplitude short latency (90-140 ms) responses in the anterior leg muscles and the anterior and posterior thigh muscles to maintain balance. Thigh muscles were activated after TA when subjects recovered from the forward slip. Tang et al. (1998) illustrated the importance of ankle muscle responses in the recovery from perturbations affecting ankle joint angle, and also emphasize that balance corrective responses are characterized by a distal to proximal activation of leg muscles during walking. When perturbations were applied to the torso Misiaszek (2003) reported a similar distal to proximal muscle activation order, showing early responses in the ankle muscles with later activation of thigh muscles. The distal to proximal temporal activation order is a basic feature of walking balance corrective reactions that is conserved across perturbation types investigated thus far.

Compensatory balance adjustments are whole-body reactions involving not only the muscles of the legs but also the muscles of the arms (McIlroy and Maki 1995, Dietz et al. 2001, Marigold et al. 2003). Dietz et al. (2001) found that arm muscles contribute to short latency automatic balance corrective strategies and are part of a coordinated response and not due to reflex activation by local sensory signals. Misiaszek (2003) found consistent short latency reactions in the shoulder muscles across the step cycle even though the lower limb muscle responses showed phase-dependent differences in response to backwards perturbations. These findings support a short-latency balance corrective strategy for walking that is centrally organized, involving the whole body and not only the perturbed limb. The short latency of balance corrective reactions is suggestive of a contribution by spinal or long loop pathways.

Task-dependency of corrective responses

Reactive balance during standing is characterized by common basic features in the muscle activation patterns, similar to walking. For instance, in both standing and walking the muscle activation generally begins around the ankle joint with proximal muscles being activated later, coined the ankle strategy in standing balance. In essence, the corrective response begins at the joints closest to the stable base of support (Nashner 1982), which appears to be true for walking balance regardless of whether the displacement is located at the support surface, as in a platform translation (Nashner 1980), or whether the perturbation is applied to the torso (Misiaszek 2000, Misiaszek 2003a, Misiaszek and Krauss 2005). However, the muscles activated in balance corrective reactions in standing appear to be adjusted appropriately for the environmental constraints, kind of perturbation and the nature of the limb displacement. While corrective reactions in standing balance show modulation dependent on the nature of the limb displacement induced by a perturbation, walking balance corrections show phase- and context-dependency. Each of these tasks illustrates the functionally relevant modulation of corrective responses in muscles to maintain balance.

In standing balance when there are environmental constraints affecting the balance corrective strategy, such as when the boundaries of the feet exceed the edges of the base of support (or platform), both limbs show a different muscle activation pattern than the ankle strategy (Horak and Nashner 1986). Instead of the distal to proximal muscle activation order seen in regular perturbed standing, Horak and Nashner (1986) reported a “hip strategy” characterized by activation of the trunk and bilateral thigh muscles first and later the ankle muscles in order to stabilize the centre of mass. In this case, the force produced around the ankle joint to maintain stability would be insufficient to maintain balance on the shortened platform. As a result the balance corrective strategy is adjusted to control the centre of mass without further disrupting stability around the base of support.

Corrective reactions to perturbations of standing subjects show bilateral specificity when either a single limb is perturbed or the two legs are displaced in opposite directions (Dietz et al. 1989). When a single limb is perturbed by horizontal translation, the activation of muscles in the perturbed limb has higher amplitude and shorter latency than the contralateral activity, consistent with a short latency stretch reflex response. Compared to bilateral displacement, the EMG responses were smaller in both limbs, suggesting that bilateral activation has a greater central component, whereas muscle activation of a unilaterally displaced limb may involve more reflex contribution. When both legs were displaced in opposite directions, the EMG responses in the legs were significantly smaller in both limbs and the muscle activation was specific to the perturbation direction of the limb. Dietz et al. (1989) reported a small amplitude G response in the backward-displaced limb, and a small bilateral response in TA that had an earlier onset in the forward-displaced limb. These findings suggest a role for stretch reflex involvement as a component of centrally organized balance corrective reactions in standing.

Nashner et al. (1979) investigated leg muscle responses to vertical platform displacement in standing subjects in what they described as "locomotor-like perturbations". The locomotor-like perturbations consisted of reciprocal vertical displacement of the feet by sudden platform raising on one limb and platform lowering of the other. The balance corrective responses to these reciprocal vertical displacements had a longer latency than synchronous displacements (110 ms compared to 98 ms respectively) and showed differences in the muscle activation patterns between the two displaced limbs. Platform lowering activated the G and quadriceps of the ipsilateral leg in a distal to proximal order, while platform raising activated TA and the hamstrings. These muscle activation patterns are consistent with normal muscle activation in locomotion, resembling the stance phase activation and swing phase activation respectively (Nashner et al. 1979). The responses seen in reciprocal vertical displacement of the feet in standing subjects reflect the phase-dependent modulation seen in locomotion. These findings suggest that some of the underlying neural mechanisms involved in locomotion may organize balance corrective reactions in standing subjects as well. This may explain some of the conserved features of balance corrective reactions between standing and walking.

Phase-dependency of balance corrective reactions during walking

Muscle responses to antero-posterior perturbations applied to points across the step cycle show that balance corrective reactions are phase-dependent in the muscle activation patterns and the amplitude of the responses. In general, the largest amplitude responses of lower limb muscles occur when perturbations are applied from late swing to midstance (Misiaszek and Krauss 2005). The phase-dependency of the muscle responses suggests that establishing ground contact and the early portion of the stance phase are particularly important in maintaining balance. These responses may serve to stiffen the supporting limb and prevent further perturbation to the movement, indicated by the large co-contraction of ankle and knee antagonist pairs in response to backward perturbations observed especially at heelstrike (Misiaszek and Krauss 2005). During swing phase muscle responses are generally smaller in amplitude if they are present at all. The swing phase muscle responses to perturbation may serve to reposition the swing limb, such as to adjust the step length and/or subsequent foot placement to regain stability for the next step cycle. The phase-dependency of muscle responses suggest that the specific muscle responses of the balance corrective strategy may be adapted by a central locomotor pattern generator, by descending influences, or in part by sensory inputs to be appropriate for the step cycle phase.

Although the basic features of compensatory balance adjustments during walking are conserved across perturbation types, the specific muscles that are activated during compensatory balance adjustments depend on the direction of the perturbation. More specifically, recovery responses from perturbations that induce rotation about the ankle produce muscle activation that is appropriate to counteract the displacement of the centre of mass. Berger et al. (1984) reported large amplitude short latency muscle activity in ankle muscles specific to the ankle rotation due to perturbation. In response to sudden accelerations or decelerations of the treadmill at heelstrike, subjects robustly activated either G or TA respectively at latencies of 65 ms. The activation of the ankle muscle counteracted the passive change in ankle angle, and restored the angle to a normal position within 350-600 ms (Berger et al. 1984).

Misiaszek (2003) investigated arm and leg muscle activation in response to backward pulls applied to the torso throughout the step cycle. Backward pulls at heelstrike resulted in ankle plantarflexion. Backward pulls at heelstrike elicited a distal to proximal temporal order of activation of leg muscles, with robust responses in TA at a latency of 85 ms and vastus lateralis (VL) at a latency of 108 ms. Misiaszek and Krauss (2005) investigated muscle activity in recovery from both forward and backward perturbations. When forward perturbations were applied to the torso, the most robust responses were in the soleus (SOL) muscle at a latency of 132 ms. The SOL responses were largest at heelstrike and occurred after ankle dorsiflexion (latency range of 80.8-98.5 ms after deviation in ankle motion). The lower leg muscle activation pattern shown by Misiaszek (2003) and Misiaszek and Krauss (2005) is similar to that seen during surface translation sharing the features of distal to proximal muscle activation pattern and that ankle rotation is counteracted by large amplitude activity around the ankle joint to restore the appropriate ankle joint motion.

Context-dependency of balance corrective reactions during walking

Evidence from perturbed walking studies investigating both arm and lower limb muscle responses suggests that balance corrective reactions are a coordinated response to recover from instability. However, these coordinated responses are specifically adjusted to be appropriate to the walking context. For example, Misiaszek and Krauss (2005) found that the lower leg responses were robustly enhanced when postural threat was increased. Subjects were perturbed during walking when their arms were restricted from swinging by crossing them either in front of the chest or behind the back (Misiaszek and Krauss 2005). Subjects reported a feeling of being less stable during the perturbations when their arms were crossed. In response to backward perturbations at heelstrike, the amplitude of lower limb responses in the SOL, TA, and VL muscles were increased when the arms were crossed. Soleus activation was also robustly enhanced in response to forward perturbations when the arms were crossed. These results suggest that a change in walking context, produced by restricting arm use, leads to an adaptation in corrective strategy to increase the reliance on the reactions in the legs.

Conversely, lower limb muscle responses to perturbations of the torso were substantially reduced or essentially abolished when subjects walked while holding stable handles (Misiaszek & Krauss 2004). Subjects reported feeling more confident and relaxed in responding to perturbations when they held handles. Responses in the muscles of the arms and shoulders were robust and the pattern of muscle activation depended on the direction of the perturbation (Misiaszek & Krauss 2004). The compensatory balance strategy was shifted to depend more on arm muscle responses when an additional support surface (stable handles) was provided. Rietdyk and Patla (1998) illustrated the effect of reducing postural threat on compensatory balance adjustments when subjects were unexpectedly tripped during swing phase while lightly touching handrails. The stance limb EMG responses decreased in amplitude even though most subjects exerted minimal force (0.5-2N) on the handles suggesting that the balance strategy was not transferred to arm muscles but was altered by a sense of reduced postural threat. Light touch contact with a stable surface has also been shown to reduce postural sway in standing subjects despite minimal force exerted by the finger on the support surface (Jeka & Lackner, 1994). The availability of an additional stable support surface may alter the balance corrective strategy that is used to respond to a perturbation. Thus, the context in which a subject walks appears to influence the selection or amplitude of the corrective reactions.

Possible neural mechanisms contributing to balance corrective reactions

The lower limb muscle responses of compensatory balance adjustments occur at a short latency, suggesting that balance corrective reactions are automatic responses. This suggestion is further supported by the similarity in the basic features of balance corrective reactions regardless of perturbation type. It is unlikely that these responses are voluntary, given that the short-latency (70-100 ms) of balance corrective reactions is faster than the latency of volitional responses such as those recorded from complex reaction time tests during walking (Haridas et al. 2005). Instead, balance corrective reactions may be pre-selected automatic responses involving spinal and long loop pathways. However, the context-dependent changes in balance corrective reactions seen in cases such as recovering from perturbations when the arms are restricted imply that the automatic responses are altered to be appropriate to the context. One theory is that sensory inputs providing information about the environment can be weighted and combined within the CNS to coordinate limb movements in a task and phase-dependent manner (Prochazka 1996). For example, in the transition from stance phase to swing phase in walking, particular rules about the location of the limb in space, the force the limb is exerting in which direction, and the stretch of the muscles of the limb must be met in order for the transition to take place. These pieces of information are provided by sensory cues and integrated and evaluated within the CNS so appropriate movements can be made. A similar model for the organization and execution of balance reactions during walking may also be proposed (Misiaszek 2006). During walking when specific rules for continued locomotion are not met, as when a subject experiences a slip or a perturbation, an automatic balance corrective strategy is released to regain balance (Misiaszek 2006). In the case of reactive balance, particular sensory cues, such as cutaneous signals or muscle stretch, may serve as a trigger for the release of the balance corrective strategy. Evidence for the potential involvement of spinal reflexes in locomotor activity and the task-, phase-, and context-dependent changes in walking is provided in the subsequent section.

Cutaneous-evoked "stumbling corrective reactions"

Direct evidence for the involvement of spinal reflexes in walking balance comes from studies in cats. Forssberg (1979) characterized "stumbling corrective reactions" in response to surface mechanical and electrical stimulation of the paw in the intact walking cat. Involvement of a spinal cutaneous reflex in stumbling corrective reactions was inferred by comparing responses to mechanical perturbation to those from electrical stimulation of the skin surface. Non-noxious electrical stimulation of the dorsum of the foot resulted in activation of reflex pathways consistent with the pattern of short-latency muscle activation observed in response to mechanical perturbation applied to the dorsum (Forssberg 1979). This study implies that cutaneous reflexes may contribute to the functionally meaningful stumbling corrective reactions. The electrical stimulation data from the intact cat are also consistent with studies on spinal cats (Forssberg et al. 1975, 1977), supporting a role for spinal reflex pathways in balance in the normally behaving animal.

Prochazka et al. (1978) and Wand et al. (1980) determined that cutaneous afferent stimulation was responsible for producing the short latency stumbling corrective responses in some muscles. Prochazka et al. (1978) found that local anaesthesia of the dorsum of the foot abolished the short latency muscle responses in lateral gastrocnemius and biceps femoris in cats stepping over an obstacle during swing phase. Furthermore, they found that the locally anaesthetized cats failed to show the normal obstacle avoidance response, continuing to press against the obstacle instead of stepping over it.

Wand et al. (1980) compared the responses to both mechanical and electrical perturbations of the swing paw in normal walking cats. Wand et al. (1980) characterized EMG responses to electrical stimulation of the dorsum of the foot and reported that although many similarities exist between the mechanically and electrically induced responses, the mechanical responses are more complex and longer in duration than the responses to electrical stimulation of cutaneous afferents. Buford and Smith (1993) found that reflex response patterns to electrical stimulation in the cat were similar for backward and forward walking and did not depend on the location of stimulation. The small number of differences in the reflex pattern to electrical stimulation between backward and forward walking are in sharp contrast to the large differences in functional motor responses seen when mechanical taps obstructed the swing limb. The responses to mechanical taps varied with the direction of walking and the location of the mechanical tap. This suggests that cutaneous reflexes, although involved in stumbling corrective reactions, may be only one component of a more complex balance recovery strategy. Wand et al. (1980) suggest that stretch reflexes also play a role, especially in ankle extensor and flexor activity, and that the involvement of supraspinal structures cannot be ruled out.

Cutaneous reflex studies in human walking

Spinal circuit involvement in walking balance has also been investigated in humans. Cutaneous reflexes in humans are complex responses to electrical stimulation that often include multiple phases, typically described as early, middle and late components of the response. The latencies of these responses can be consistent with the short latency muscle responses of many corrective reactions to perturbations. Cutaneous reflex studies in walking humans suggest a functional role for these spinal circuits in maintaining limb trajectory. Yang and Stein (1990) found that non-noxious stimulation of the tibial nerve resulted in TA muscle excitation during swing phase, and inhibition during the swing to stance transition. The same reflex reversal was found in the TA from sural nerve stimulation (Yang & Stein, 1990). This study showed that the reflex response was appropriate to maintain the trajectory of the limb at the time of stimulation, and is finely tuned to be appropriate for the continuation of walking.

Zehr et al. (1997) provided further evidence of the functional role of cutaneous reflexes in walking balance. Zehr et al. (1997) found that muscle responses to cutaneous stimulation were large during the transition phases when maintaining stability is essential to preventing a fall. Furthermore, they reported that the responses to superficial peroneal nerve stimulation mimicked stumbling corrective responses, linking the behaviour of human reflexes to those reported by Forssberg (1979) in response to cutaneous stimulation in the cat. In a 1998 paper, Zehr et al. characterized the response to sural nerve stimulation during swing as a withdrawal of the foot from the source of the stimulus, suggesting nerve specificity in responses that are functionally appropriate to the area of innervation (Zehr et al. 1998, Van Wezel et al. 1997). Zehr et al. (1997) also reported a withdrawal response to tibial nerve stimulation during the stance to swing transition, and a placing reaction during late swing. These responses agree with the reflex behaviour of the EMG reported by Yang and Stein (1990) with tibial nerve stimulation. Collectively, these studies illustrate that cutaneous reflexes are modulated in a manner that would be consistent with a putative role in assisting balance recovery. However, balance corrective reactions are more complex and of longer duration in response to mechanical perturbation than to cutaneous nerve stimulation. Therefore, it is likely that cutaneous reflexes are only a component of the balance corrective reactions in response to mechanical perturbations. From this evidence, it is reasonable to hypothesize that other spinal reflexes, such as the stretch reflex, may also play a role in balance corrective reactions and are worthy of further investigation.

Stretch reflexes contribute to SOL EMG activity in walking

In the case of unexpected muscle stretch, as with sudden ankle rotation evoked by a perturbation, stretch reflexes may contribute to balance corrective reactions. Evidence from animal studies and from human stretch reflex studies suggest that the stretch reflex contributes substantially to the amplitude of EMG activity in steady walking. Studies investigating EMG amplitude in the mesencephalic cat suggest that although the basic rhythm of hindlimb muscle firing during walking is set by a spinally-located oscillating network (often described as a central pattern generator), stretch reflexes contribute to the EMG activity seen in the normal walking cat. Stein et al. (2000) investigated the effect of muscle stretch on the EMG amplitude in high decerebrate cats as they walked. The Achilles tendon of one leg was cut and attached to a muscle puller. They then compared the EMG amplitude when the muscle was held isometrically to the EMG amplitude when the cat walked while the triceps surae muscle was stretched by the puller, simulating the stretch that occurs during normal walking (Stein et al. 2000). During isometric stretch, the changes in EMG amplitude across the step cycle reflected the central influence on muscle contraction. They found that 50% more EMG was present in stance phase in the triceps surae when the muscle was stretched phasically (Stein et al. 2000). The muscle stretch elicited phasic stretch reflexes contributing to the EMG amplitude.

Human studies investigating perturbations of the ankle joint that rapidly stretch the soleus muscle conclude that the stretch reflex contributes to muscle activation. By applying small rapid stretches to the soleus muscle, Yang et al. (1991) concluded that the stretch reflex contributes 30-60% in the activation of the soleus muscle during human walking. Using a pneumatic device that lifted the forefoot off the ground, Yang et al. (1991) rapidly dorsiflexed the ankle during early stance, stretching the soleus muscle. They reported early excitatory responses in the soleus muscle. Using linear equations to predict the EMG responses from the muscle stretch, they found that most of the variation in soleus EMG was accounted for by the velocity of the perturbation to the ankle joint. Yang et al. (1991) concluded that the velocity sensitive elements of the stretch reflex (the Ia afferents) contribute significantly to soleus muscle activation.

Sinkjaer et al. (1996) mechanically perturbed the ankle joint throughout the step cycle using a stretch device attached to the subject's foot and calf. The device enabled rapid dorsiflexion and plantarflexion of the ankle joint at any phase of the step cycle. These changes in ankle joint angle elicited short-latency stretch reflex responses in soleus with a latency of approximately 42 ms with the peak response occurring at 56 ms (Sinkjaer et al. 1996). The amplitude of the stretch reflex response was modulated throughout the step cycle, slightly leading and in parallel with the phase modulation of background soleus EMG. The stretch reflex amplitude was largest in early swing and near zero at toe-off. The phase lead suggests that the stretch reflex contributes to soleus muscle activity in stance phase (Sinkjaer et al. 1996).

Mazzaro et al. (2005) provide evidence to suggest that the Ia afferents contribute to stretch-induced muscle activation of the soleus muscle. Ankle dorsiflexion was slightly increased and decreased using a mechanical device attached to the ankle. The changes in ankle dorsiflexion were intended to enhance the normal changes in ankle angle during walking and were small amplitude and slow velocity stretches in order to resemble naturally occurring fluctuations in ankle angle. Mazzaro et al. (2005) found gradual increases and decreases in soleus EMG, corresponding to increases and decreases in ankle dorsiflexion and muscle stretch. The increases in soleus EMG were reduced in amplitude when the Ia afferents were blocked with ischemia to the leg. The Mazzaro et al. (2005) study provides evidence to support a role of the Ia afferents in enhancing soleus EMG in response to changes in joint angle that could occur naturally, for example in a sudden trip or in response to changes in walking surface.

The potential role of stretch reflexes in balance corrective reactions

In his investigation of the fixed patterns of muscle activity in balance correction in perturbed standing, Nashner (1977) found that direct ankle rotation elicited the same muscle activation pattern as antero-posterior translation of the support surface. The latency of muscle activation was the same for both perturbation methods, consistent with the latency of functional stretch responses reported previously. Nashner (1977) suggests that ankle stretch reflexes release the centrally-organized pre-programmed postural responses for balance recovery. During perturbed walking, Tang et al. (1998) found that TA activation in response to a forward slip at heelstrike occurred after ankle plantarflexion. They suggest that muscle stretch of the TA may have elicited a local stretch reflex, enhancing TA activation and inhibiting G activation to restore the ankle angle (Tang et al. 1998). Berger et al. (1984) reported EMG responses to perturbation with a latency of 65 ms. The responses occurred after ankle joint rotation suggesting that stretch reflexes may be involved in the responses. Misiaszek and Krauss (2005) showed large amplitude SOL responses to forward perturbation of the torso occurring after ankle dorsiflexion at heelstrike and midstance. We suggest that stretch of the SOL muscle by sudden ankle dorsiflexion may contribute to the short latency muscle responses to forward perturbation applied to the torso at heelstrike and midstance. Due to the short latency of compensatory balance adjustments in perturbed walking and their tendency to first occur in ankle muscles to control ankle joint motion regardless of perturbation type, we suggest that local spinally-mediated reflexes may be a component of the compensatory balance reactions observed during walking.

Stretch reflexes have been shown to contribute substantially to the SOL muscle EMG during walking. We suggest that a stretch reflex is a good candidate to contribute to the balance corrective reactions seen in perturbed walking. More specifically, Misiaszek and Krauss (2005) reported large amplitude SOL EMG in response to forward perturbations at heelstrike and midstance when subjects walked with their arms crossed. These responses occurred 80.8-89.5 ms after the peak ankle dorsiflexion induced by the perturbation (Misiaszek and Krauss 2005). Given that stretch reflexes have been shown to contribute to SOL EMG amplitude, and the burst of SOL EMG in response to forward perturbation occurs after SOL muscle stretch (inferred by the ankle dorsiflexion), we suggest that a stretch reflex may be responsible for the SOL EMG burst of the balance corrective strategy at heelstrike and midstance.

Furthermore, SOL EMG activation in response to forward perturbations at heelstrike and midstance had an increased amplitude when the arms were crossed than when they were freely swinging (Misiaszek and Krauss 2005). This enhancement of lower limb muscle responses may reflect an increase in postural threat. Prochazka et al. (1986) illustrated in cats performing difficult locomotor tasks that the stretch sensitivity of muscle spindles was adjusted through increased descending fusimotor drive, possibly to facilitate stability and completion of the task. They describe this task and context-dependent adjustment as a product of "behavioural or fusimotor set". When postural threat is increased in human walking, fusimotor drive may also be increased. However, it is also possible that the gain of proprioceptive signals may be scaled in a task-, phase-, and context-dependent manner to be evaluated within the CNS to produce appropriate adjustments to locomotor activity (Prochazka 1996). Changes in the gain of proprioceptive signals related to task, phase and context are often inferred from studies investigating the Hoffman reflex.

Using the H-reflex as a tool to investigate stretch reflex involvement in complex locomotor tasks

In humans, it is technically difficult to experimentally elicit muscle stretch during a locomotor task. As a result, stretch reflex modulation in humans has been inferred from the investigation of Hoffman (or H-) reflexes. The soleus (SOL) H-reflex is frequently investigated in locomotion. The H-reflex is elicited by electrical stimulation of the mixed nerve (tibial nerve in the case of the SOL H-reflex), and is the electrical analog of the monosynaptic stretch reflex. The H-reflex bypasses the muscle spindle sensory endings and reflects the influences of mainly the Ia afferent to α motoneuron synapse. The H-reflex provides clues in the modulation of the reflex at the spinal level, but does not reflect the influences of fusimotor drive on muscle spindle sensitivity, and does not represent the long loop (or M2 phase) of functional stretch reflexes. However, a study of H-reflex and stretch reflex modulation in the mesencephalic cat found that the pattern of H-reflex modulation essentially matched the pattern of stretch reflex modulation (Akazawa et al. 1982). Sinkjaer et al. (1996) found that the pattern of stretch reflex phase modulation in the SOL in human walking is similar to the pattern of SOL H-reflex modulation reported by others (Capaday and Stein 1986). Consequently, the H-reflex is a valuable tool for assessing changes in the reflex pathway at the spinal level. The modulation of the H-reflex has been studied in a variety of tasks, from walking to locomotor tasks of increased complexity (Zehr 2002).

H-reflex task-dependent modulation

H-reflexes during standing have higher amplitude and a lower sensitivity to EMG activation than H-reflexes obtained during walking for matched levels of SOL EMG activity. H-reflexes are substantially decreased in peak-to-peak amplitude during walking compared to standing at matched background EMG levels (Capaday and Stein 1986). Edamura et al. (1991) investigated the standing to walking transition. Edamura et al. (1991) presented an auditory tone as a go signal to initiate gait. For the first 100 ms after the auditory tone is presented, before the subject has initiated gait, the H-reflex is large in amplitude, comparable to the amplitude seen during standing. However, the rise in TA EMG signaling the start of gait initiation is coincident with a dramatic depression of the reflex. This depression of the reflex occurs within 200 ms of the tone. Furthermore, the H-reflexes in the first step of gait initiation are of similar amplitude to those in normal walking. These findings suggest that the depression in H-reflex from standing to walking is due to changes in the spinal circuitry initiated by the task, and not by the level of muscle output.

Running maintains the pattern of phase-dependent H-reflex modulation seen during walking despite differences in the duration of step cycle phases; however, the peak amplitude of the H-reflex across the step cycle is significantly smaller than during walking. For all points in the step cycle, on average there was a decrease in the peak amplitude of the H-reflex during running compared to walking (Capaday and Stein 1987). Capaday and Stein (1987) concluded that the reduction in peak H-reflex amplitude in running compared to walking is due to a tonic increase in presynaptic inhibition on the Ia afferent terminals.

Capaday and Stein (1987) reported a decrease in the gain of the reflex during running, meaning that higher levels of EMG activation are required to produce the H-reflex amplitude seen during walking. However, running is accompanied by higher EMG activation. Edamura et al. (1991) investigated the contribution of higher EMG activation in running and walking, which was also assessed later by Simonsen and Dyhre-Poulsen (1999) using different methodology. Edamura et al. (1991), employing the methods of Capaday and Stein (1987), found that for matched speeds of walking and running there was a significant decrease in the H-reflex amplitude during running. This decrease was preserved when looking at matched EMG levels and H-reflex amplitude. Edamura et al. (1991) concluded that the task of running was the most important factor in reducing the amplitude of the H-reflex, the reduction is not solely the effect of speed or increased EMG levels. A subsequent study by Ferris et al. (2001) compared walking H-reflex amplitude to running H-reflex amplitude when weight bearing was reduced in subjects. In this experiment, it was possible to compare reflex amplitudes for the two tasks at matched EMG activation. Ferris et al. (2001) reported that H-reflexes at every step cycle phase were of higher amplitude during walking than during running at matched SOL activation levels. The work of Ferris et al. (2001) reflects a task-dependent decrease in H-reflex amplitude across the step cycle during running compared to walking, but this decrease is of a small magnitude and not nearly as pronounced as the earlier studies suggest.

H-reflex amplitude is decreased during rhythmic locomotor-like tasks compared to stationary positions (Brooke et al. 1992, McIlroy et al. 1992). In both studies, subjects were either seated while maintaining particular joint positions or while passively pedaling. For H-reflexes stimulated at points across the rotation cycle, Brooke et al. (1992) found that the reflex amplitude was significantly decreased when subjects pedaled for matched joint angle positions. McIlroy et al. (1992) found that increasing the speed of passive pedaling further decreased the H-reflex amplitude across the rotation cycle. These studies illustrate a task-dependent modulation of H-reflex amplitude that is due to the locomotor nature of the task and not due to joint position. Furthermore, the decrease in H-reflex amplitude with faster pedaling is analogous to the decrease in H-reflex amplitude in running compared to walking.

Phase-dependent H-reflex modulation pattern during walking

During walking, the amplitude of the soleus H-reflex varies across the step cycle. Capaday and Stein (1986) reported a steady increase in H-reflex amplitude from the time of heel contact to maximum amplitude just prior to toe-off. Immediately after toe-off there was an abrupt and large decrease in amplitude persisting throughout the swing phase. Often the H-reflex is completely absent during swing phase. The relationship between H-reflex amplitude and peak-to-peak EMG amplitude is roughly linear, the largest amplitude of H-reflex loosely associated with higher EMG levels. However, the H-reflex modulation pattern throughout the step cycle is not closely related to the variations in the level of EMG activity in SOL, and thus cannot be explained solely by the excitation level of the α motoneurons. The reflex modulation is due in part to central influences on the Ia afferent to α motoneuron synapse. These findings support the conclusion of Akazawa et al. (1982) when they investigated stretch reflex modulation and H-reflex modulation in the mesencephalic cat. "Therefore, it is possible that the efficacy of the synaptic transmission between the Ia afferents and the motoneurons may be modulated by central neural mechanisms independently of the level of motoneuronal activity" (Akazawa et al. 1982 in Capaday and Stein 1986).

H-reflex amplitude is influenced by changes in the walking pattern

Larsen and Voigt (2004) caution investigators from attributing changes in H-reflex amplitude to context- or task-dependent difference, stating "as speed of movements and motor recruitment level influence the gain of the soleus H-reflex, it is significant that these two parameters are comparable before changes in H-reflexes are stated to be task-dependent." For example, the amplitude of the SOL H-reflex varies with the level of background EMG in the SOL muscle (Capaday and Stein 1986, Zehr 2002, Misiaszek 2003b). The level of EMG activation in antagonist muscles can also affect the H-reflex amplitude through reciprocal inhibitory mechanisms, such as the presence of distinct H-reflexes in late swing accompanying low TA activation reported in some subjects by Simonsen et al. (2002). Changes in joint angle, including the ankle, knee and hip joints, can also affect the amplitude of the H-reflex (Brooke et al. 1992). Adaptations in the walking pattern across conditions that affect joint angles would also affect the amplitude of the H-reflex. Therefore, it is essential that the level of background EMG and the features of the walking pattern are comparable across conditions when looking at context-dependent H-reflex modulation. Thus, only with proper controls can we determine that changes in the H-reflex amplitude are truly context-dependent and not due to overall adaptations in the walking pattern.

Context-dependent H-reflex modulation in tasks with increased postural threat

The H-reflex amplitude increased during the first steps of an obstacle avoidance task under reduced vision (Hess et al. 2003). Subjects practiced stepping over an obstacle while treadmill walking as H-reflexes were elicited. Subjects' vision was later reduced and they performed the same task. During the first steps of the reduced vision condition, there was a significant increase in the amplitude of the H-reflex immediately before stepping over the obstacle. With repetition of the task, the H-reflex quickly decreased in amplitude to normal walking amplitudes. The reflex amplitude adaptation coincided with an increased confidence in performing the task as reported by subjects (Hess et al. 2003). In conditions of reduced vision when a difficult task that challenges balance is performed, the stretch reflex may be useful in responding to any disturbances of balance while the foot is clearing the height of the obstacle. However, as a subject becomes more comfortable with performing the task without the aid of vision, the task is performed more automatically and may pose less of a threat to balance.

Schneider and Capaday (2003) elicited H-reflexes during backward walking with various task constraints. In the first study, Schneider et al. (2000) reported a pronounced increase in H-reflex amplitude during late swing phase of backward walking. This finding is in stark contrast to forward walking where a strong suppression of the H-reflex is seen during swing phase. Schneider et al. (2000) hypothesized that the large H-reflex during late swing could be due to uncertainty of foot placement and subsequent balance disturbances when walking backwards. The increased H-reflex amplitude could indicate that the stretch reflex is important in responding to balance disturbances and task uncertainties.

Schneider and Capaday (2003) investigated the effects of backward walking training on the large amplitude H-reflex present in late swing phase. Within ten days of daily training at walking backwards, the peak swing phase H-reflex is delayed by 146 ms, coinciding more directly with the onset of the SOL EMG burst. The H-reflex amplitude during swing phase was also significantly decreased. After ten days of training, subjects reported that they were more confident and secure in backward walking because of the training.

Schneider and Capaday (2003) also found that increasing the security of the task in untrained subjects, by allowing subjects to hold stable handrails, delayed the peak H-reflex onset during swing phase and decreased the peak amplitude to values comparable to trained subjects. Conversely, when trained subjects were instructed to walk backwards with their eyes closed, the H-reflex amplitude again increased to the large pre-training value. Schneider and Capaday (2003) discussed the task-dependent H-reflex amplitude modulation as a response to the level of postural confidence. In tasks that feel unstable, including the initial trials of backward walking as well as backward walking with the eyes closed, spinal reflex sensitivity may be increased to respond quickly to balance disturbances. When postural confidence is increased, either through the use of handrails or with training, the high amplitude H-reflex may then disappear because the sense of threat to balance is reduced.

H-reflex modulation during beam walking

Llewellyn et al. (1990) also investigated H-reflexes in an environment with reduced postural confidence. H-reflexes were elicited in difficult beam walking. The width and height of the beam was set so that subjects found the task difficult. They reported a 40% decrease in the amplitude of the H-reflex compared to normal walking. The amplitude reduction was inferred to be due to presynaptic inhibition on the Ia afferent terminals from descending task-related inputs. The decreased H-reflex amplitude in beam walking contrasts with the increased amplitude reported in backward walking by Schneider et al. (2000). However, in beam walking the challenge to stability is mostly in the medio-lateral plane, compared to the antero-posterior balance disturbance that would result from inaccurate foot placement in backward walking. In beam walking foot placement must be closely controlled so the foot lands within the lateral bounds. Thus in this task it is possible that the need for accurate foot placement leads to suppression of automatic or reflexive actions. Alternatively, the H-reflex itself may be a destabilizing event (Trimble and Koceja 1994), which may be suppressed during beam walking to prevent subjects from being thrust off the beam.

Investigating spinal circuit modulation in walking tasks of increased postural threat

We have chosen to use the SOL H-reflex as a means to assess changes in the excitability of the central component of a spinal circuit related to the simple stretch reflex. We hypothesize that a stretch reflex may be a component of balance corrective reactions. However, this hypothesis may be counter-intuitive given the differences in latencies of the balance corrective reactions in comparison to the latencies of the stretch reflex and the H-reflex. Balance corrective reactions reported in perturbed walking studies generally occur at latencies ranging from 65 ms up to 140 ms after perturbation (Berger et al. 1984, Nashner 1980, Tang et al. 1998). We reported robust corrective responses in the SOL muscle 80-98 ms after ankle dorsiflexion from a forward perturbation at heelstrike (Misiaszek and Krauss 2005). These latencies are longer in duration than the expected latency of a simple stretch reflex. Sinkjaer et al. (1996) found that the latency of the stretch reflex was 42 ms following a mechanical displacement of the ankle joint. However, it is still possible that a simple stretch reflex may contribute to balance corrective reactions. First, a common feature of balance corrective reactions is that they occur after changes in joint angle that would produce muscle stretch (Berger et al. 1984, Misiaszek and Krauss 2005). Second, the characteristics of the imposed stretch influence the timing of the evoked response. For example, the peak velocity of ankle displacement imposed by Misiaszek and Krauss (2005) was 55°/s, whereas the peak velocity employed by Sinkjaer et al. (1996) was 250°/s. Thus, the peak stretch of SOL is substantially slower in the balance disturbance than following the mechanical perturbation applied at the ankle. This likely leads to differences in afferent recruitment (spatial summation) and in afferent firing (temporal summation) that then result in a delay in the summation to threshold at the SOL α-motoneurons. This delay would contribute to the longer latency of the balance corrective reactions compared with the latency reported for experimentally induced stretch reflexes.

The H-reflex also has a significantly shorter latency than both the simple stretch reflex and balance corrective reactions. The H-reflex has a latency of about 35 ms, far shorter than any balance corrective reactions reported. This short latency is due to the large synchronous volley of afferent inputs onto the α-motoneurons created by the large-voltage electrical stimulation. The H-reflex stimulation recruits multiple afferents synchronously, producing a large spatial summation arriving simultaneously at the spinal synapse. Although there are differences in some components of the circuitry (Burke et al. 1983) and amplitude modulation (Sinkjaer et al. 1996, Andersen and Sinkjaer 1999) between the two reflexes, the H-reflex is still a viable tool to test modulation of a spinal circuit in motor tasks. Given the H-reflex and simple stretch reflex share some common circuitry, changes in the amplitude of the H-reflex will provide clues about the central modulation of reflex transmission in motor tasks of some neural components of the stretch reflex. However, due to the differences in modulation between the two reflexes, any conclusions derived from H-reflex studies about stretch reflex involvement and modulation in motor tasks must be made with caution and subsequently tested in stretch reflex experiments to confirm.

Summary

Due to the short latency of many lower limb corrective balance adjustments in torso-perturbed walking (Misiaszek & Krauss, 2005), and previous evidence suggesting that spinal reflexes contribute to balance recovery, it is reasonable to suggest that the short latency stretch reflex may also contribute to balance recovery. The H-reflex can be used as a tool to investigate short latency stretch reflex involvement in an experimental paradigm assessing balance corrective reactions. Given that walking when perturbations are applied to the torso disturbs balance in the antero-posterior directions, similar to Schneider and Capaday's (2003) backward walking study, I hypothesize that the SOL H-reflex will have increased amplitude across the step cycle when postural threat is increased. Increased H-reflex amplitude infers increased stretch reflex sensitivity in order to facilitate the compensatory balance response to maintain stability in perturbed walking. I suggest that the amplitude of the SOL H-reflex will decrease when subjects hold stable handles, as previous findings suggest that holding handles reduces postural threat and redirects compensatory balance adjustments to depend more on arm muscle activation than leg responses (Misiaszek & Krauss, 2004). The behaviour of the H-reflex in contexts of varying levels of postural threat will provide insight into the neural adaptations that contribute to reactive balance recovery. It will also illustrate the interaction of peripheral sensory inputs with cognitive influences, namely the sense of instability or Prochazka's (1996) "behavioural set", to produce functionally meaningful motor outputs.

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CHAPTER 2 – Phase-specific modulation of the soleus H-reflex as a function of threat to stability during walking[1]

Introduction

In a recent study we observed that subjects who received a forward push while walking on a treadmill generated a burst of activity in the soleus (SOL) muscle of the stance leg (Misiaszek and Krauss 2005). This burst of activity in SOL was part of a larger whole-body corrective response to regain stability following the perturbation. Given that the burst of activity in SOL followed a dorsiflexion disturbance in the ankle joint motion, a stretch-related reflex may contribute to this balance corrective response in SOL, comparable to the reflexes observed with mechanical disturbances applied to the foot during walking (Sinkjaer et al. 1996). This would indicate that a portion of the corrective response evoked with a forward push at the torso is generated by reflexive mechanisms. In the same study, we also observed that the burst generated in SOL was substantially increased if the subjects walked with their arms voluntarily folded across the chest. The implication is that the corrective responses in the muscles of the legs are facilitated when postural threat is increased by the restriction of arm use. Consequently, if the burst of activity in SOL is derived from a stretch-related reflex then the expectation would be that SOL stretch reflexes would be facilitated when subjects walk with their arms restricted, compared to walking normally.

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[1] Paper currently submitted for publication in Experimental Brain Research. Original student contribution, authored by EM Krauss & JE Misiaszek.

The H-reflex, evoked in SOL by electrical stimulation of the tibial nerve, is the electrical analogue of the stretch reflex and a means by which the excitability of the stretch-evoked reflex can be assessed in humans (Misiaszek 2003). Although the modulation of the H-reflex has been shown to differ from that of the stretch reflex (Andersen and Sinkjaer 1999), the modulation pattern of the reflexes at heelstrike and early to midstance is conserved. The H-reflex is a means to test changes in reflex transmission in walking tasks. We suggest that changes in the H-reflex amplitude at heelstrike may indicate changes in stretch reflex transmission that may be relevant to the corrective responses to forward perturbation reported previously (Misiaszek and Krauss 2005). Consequently, we hypothesize that the SOL H-reflex will be facilitated during walking when there is an increased threat to postural stability, compared to normal walking. We also suggest that the amplitude of the SOL H-reflex should be scaled to the level of postural threat, showing higher amplitudes in the most unstable condition. Such an effect was noted by Schneider and Capaday (2003) who demonstrated that the SOL H-reflexes of subjects walking backward were substantially larger at midswing if the subjects walked without support. However, the H-reflex at midswing decreased immediately when subjects held safety handrails, suggesting the postural uncertainty of the novel task led to the facilitated reflex. In contrast, Llewellyn et al. (1990) demonstrated that the SOL H-reflex was suppressed at comparable SOL EMG activation when subjects walked on a narrow beam compared to walking on a treadmill, suggesting that increased postural threat decreases excitability of the monosynaptic component of the stretch reflex. In the present study we provide evidence to suggest that the SOL H-reflex is facilitated in a phase-specific manner when walking with increased postural threat. A portion of this work has been published as an abstract (Krauss and Misiaszek 2005).

Materials and Methods

Subjects and Protocol

A total of twenty subjects (age 20-34) participated in this study. Subjects reported no history of neurological, metabolic or cardiovascular disease, and had not experienced musculoskeletal injury, back pain, or concussion in the previous six months. All subjects provided written informed consent in a protocol approved by the University of Alberta Health Research Ethics Board.

In this study we compared the amplitude of the SOL H-reflex between five walking conditions. The intention of the H-reflex stimulation was to compare the reflex during periods of steady walking, but when the threat to stability was altered. It was not feasible to perform all five conditions in one experimental session due to the duration of each test condition. Consequently, the study was divided into two parts. Ten subjects participated in each part. For both parts, subjects walked on a motorized treadmill at a self-selected comfortable walking speed (range: 0.9-1.1 m/s). H-reflexes were elicited at four points of the step cycle: heelstrike, midstance, toe-off, and midswing of the right leg (Fig. 1c).

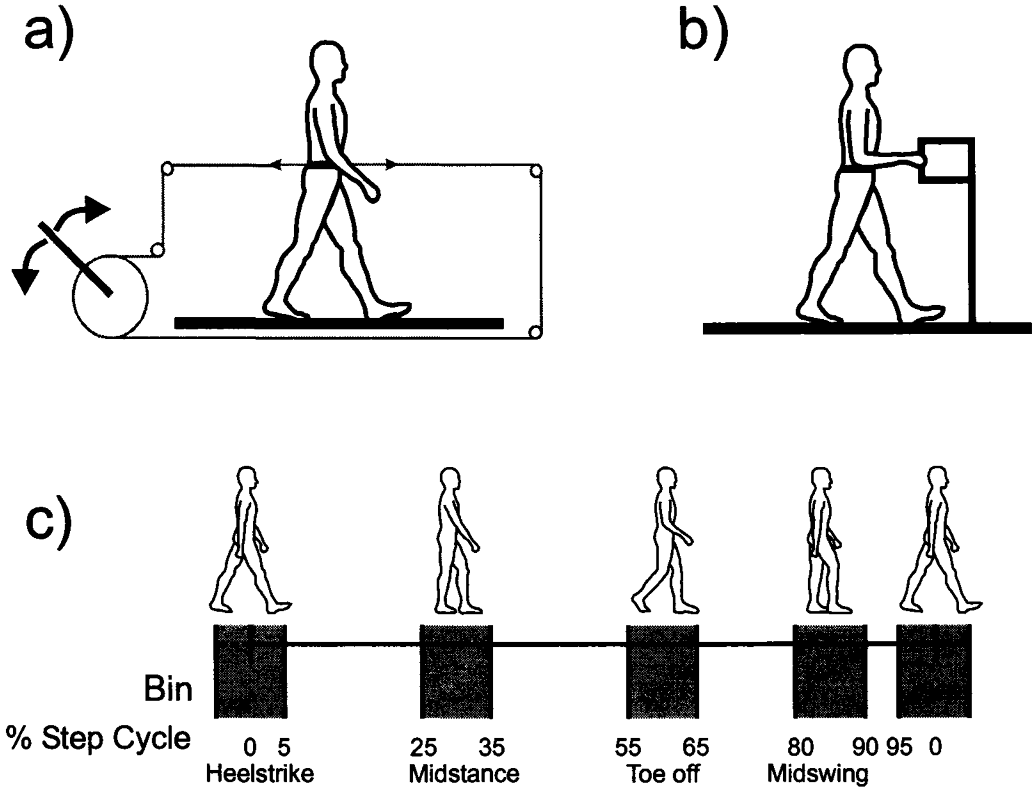

Figure 1. Schematic of the experimental set-up. a) Subjects walked on a motorized treadmill. Subjects walked either with their arms swinging freely or folded across their chest. In some conditions (AP, Arms Crossed AP) perturbations were applied to the torso using a continuous cable system attached to the subject's waist. The experimenter perturbed the subject either forward or backward by rotating the drum controlling the cable system forward or backward. b) In the Handles condition subjects held stable handles while they walked. The handles were mounted to the front of the treadmill frame, adjusted to a height forming a 90 degree angle at the subject's elbows. c) H-reflexes were elicited in blocks of stimuli at heelstrike, midstance, toe-off, and midswing of the step cycle for all walking conditions. The order of presentation was randomized across walking conditions and subjects.

In Part I, subjects walked in four conditions representing increasing levels of postural threat: (1) normally with the arms free (Normal), (2) with the arms voluntarily folded across the chest (Arms Crossed), (3) while receiving perturbations in the anterior and posterior directions applied to the torso (AP), and (4) while receiving perturbations to the torso and with their arms voluntarily folded across the chest (Arms Crossed AP). In the conditions with the arms crossed, subjects loosely held their arms across the chest, and were free to release their arms if it was necessary to recover from a perturbation. The order of presentation of the walking conditions was randomized across subjects. Subjects were informed before an AP or Arms Crossed AP trial that they could expect perturbations. Perturbations were manually applied in both the forward and backward directions using a continuous cable system that was attached to the subject at the waist using a padded belt (Fig. 1a). Perturbations occurred at a frequency of approximately 1 every 30 seconds throughout the step cycle, with a force ranging between 10-30% of the subject's body weight. Perturbation timing and direction were unpredictable to the subjects. The perturbations were utilized to create a sense of uncertainty and the responses to the perturbations were not analyzed (see Misiaszek and Krauss (2005) for analysis of responses to perturbations). We were investigating how the sense of postural threat affects the H-reflex amplitude and were not interested in H-reflex modulation during a perturbation. Therefore, H-reflexes were evoked in step cycles occurring at least 3 steps after a perturbation; hence, reflexes were elicited during periods of steady walking between perturbations. Safety railings mounted at the sides and front of the treadmill were available for subjects to use throughout all conditions; however, none of the subjects used the safety railings.

In Part II subjects walked (1) normally with the arms free (Normal) and (2) while holding stable handles (Handles) to reduce postural threat. The handles were mounted on the treadmill frame in front of their body. The height of the handles was adjusted so that subjects could maintain approximately a 90° angle at the elbow when holding onto the handles (Figure 1b). Perturbations were not applied in the Handles condition.

Nerve Stimulation

H-reflexes were evoked in SOL of the right leg by applying a 1 ms square wave pulse (Grass S88 stimulator) to the tibial nerve using a bipolar stimulating electrode placed on the skin over the popliteal fossa. To ensure that both increases and decreases in the amplitude of the H-reflex could be observed we used a stimulus intensity that produced an H-reflex on the ascending limb of the recruitment curve, while also producing a small, but stable M-wave (resulting from the direct activation of the α-motoneurons in the mixed nerve) of approximately 5% of the maximum M-wave amplitude (Mmax). Stimulus intensity (the amplitude of the M-wave) was monitored online throughout the experiment using an oscilloscope. The amplitude of Mmax has been shown to vary across the step cycle with a maximum amplitude at midstance (Simonsen et al. 1995). Consequently, Mmax was obtained for each point in the step cycle and the current required for achieving a 5% Mmax stimulus was appropriately adjusted. On average the smallest amplitude Mmax value in the step cycle was 26% less than the largest amplitude Mmax recorded at midstance. Therefore, the applied current was different for each point in the step cycle tested. As a result, H-reflex stimulation occurred in blocks with the stimulus delivered at one point of the step cycle at a time. Approximately twenty H-reflexes with M-waves of 5% Mmax were elicited for each point of the step cycle with an additional 10-15 H-reflexes randomly interspersed at other points in the step cycle to prevent predictability. Stimuli were manually triggered by the experimenter, and step cycle timing was monitored by viewing heel and toe contact data, obtained from custom-made sensors, displayed on an oscilloscope. Stimuli were elicited at least 5 seconds apart. The order of presentation of the stimulation points was randomized across walking conditions and across subjects.

Recording and Data Acquisition

Electromyographic (EMG) recordings were obtained for the SOL and tibialis anterior (TA) muscles of the right leg. Recordings were made using pairs of Ag/AgCl disposable surface electrodes (A10012, Vermed) placed over the bellies of the muscles. Ground electrodes were placed over the tibia. Signals were pre-amplified and bandpass filtered (30 Hz to 3 kHz, Grass Model P511). Electrogoniometers (Biometrics) were placed across the right knee and ankle joints to record joint angles during walking. Heel and toe contact data were measured using custom-made sensors affixed to the insole of the right shoe. All signals were digitized at 3000 Hz using a 12-bit analog-digital converter (PCI-

MIO-16E-4, National Instruments) and saved to computer using custom-written software (LabView 5.1, National Instruments) for later analysis.

Data Analysis

The twenty H-reflex stimuli evoked at each point in the step cycle for a walking condition were sorted post-hoc. Those stimuli that occurred within a 10% window of the step cycle phase with an M-wave of 4-6% Mmax for that step cycle phase were retained for further analysis. This typically resulted in 15-20 reflexes for each point in the step cycle, for each walking condition, being included in the analysis for each subject. Peak-to-peak amplitudes of the H-reflex and M-wave were measured from individual traces and were normalized to Mmax for that point in the step cycle. Normalized H-reflexes and M-waves were averaged for each subject and the average values were used for statistical analysis.

The SOL and TA EMG activities at the time H-reflexes were elicited were determined by calculating the mean activity for a 50 ms window prior to the stimulus artifact. To do this, the SOL and TA EMG signals were digitally full-wave rectified and then low-pass filtered at 50Hz with a 4th order dual-pass Butterworth filter. These values were then normalized to the maximum rectified and filtered EMG observed over the step cycle of 30 control steps (i.e. steps that did not receive a stimulus) taken from the Normal condition, for each subject. The normalized EMG values were then averaged for each subject and used in the subsequent statistical analysis. The average knee and ankle angles were calculated for the 50 ms window preceding the stimulus artifact for each subject and were used in the subsequent statistical analysis.

In this study we were interested in comparisons between walking conditions at each point in the step cycle, and not across different points in the cycle. Therefore, planned comparisons were used to test our hypotheses. The error term used in the planned comparisons was estimated from the residual error of a two-way repeated measures analysis of variance. Separate analyses were performed for each of the measured variables (M-wave amplitude, H-reflex amplitude, SOL EMG, TA EMG, ankle angle, knee angle). In addition, separate analyses were performed for Parts I and II of the study. Statistical significance was set at $P < 0.05$.

Results

The amplitude of the SOL H-reflex was modulated over a step cycle of treadmill locomotion (Fig. 2c), consistent with the phase-dependent modulation of reflex amplitude that has been noted previously (Capaday and Stein 1986). This general pattern of modulation (largest reflexes during stance and smallest during swing) was similar for all five walking conditions tested.

H-reflex amplitude in unstable environments

In Part I, subjects were asked to walk on a treadmill in four conditions of increasing postural threat: Normal, Arms Crossed, AP, and Arms Crossed AP. The conditions represented various combinations of task constraints including

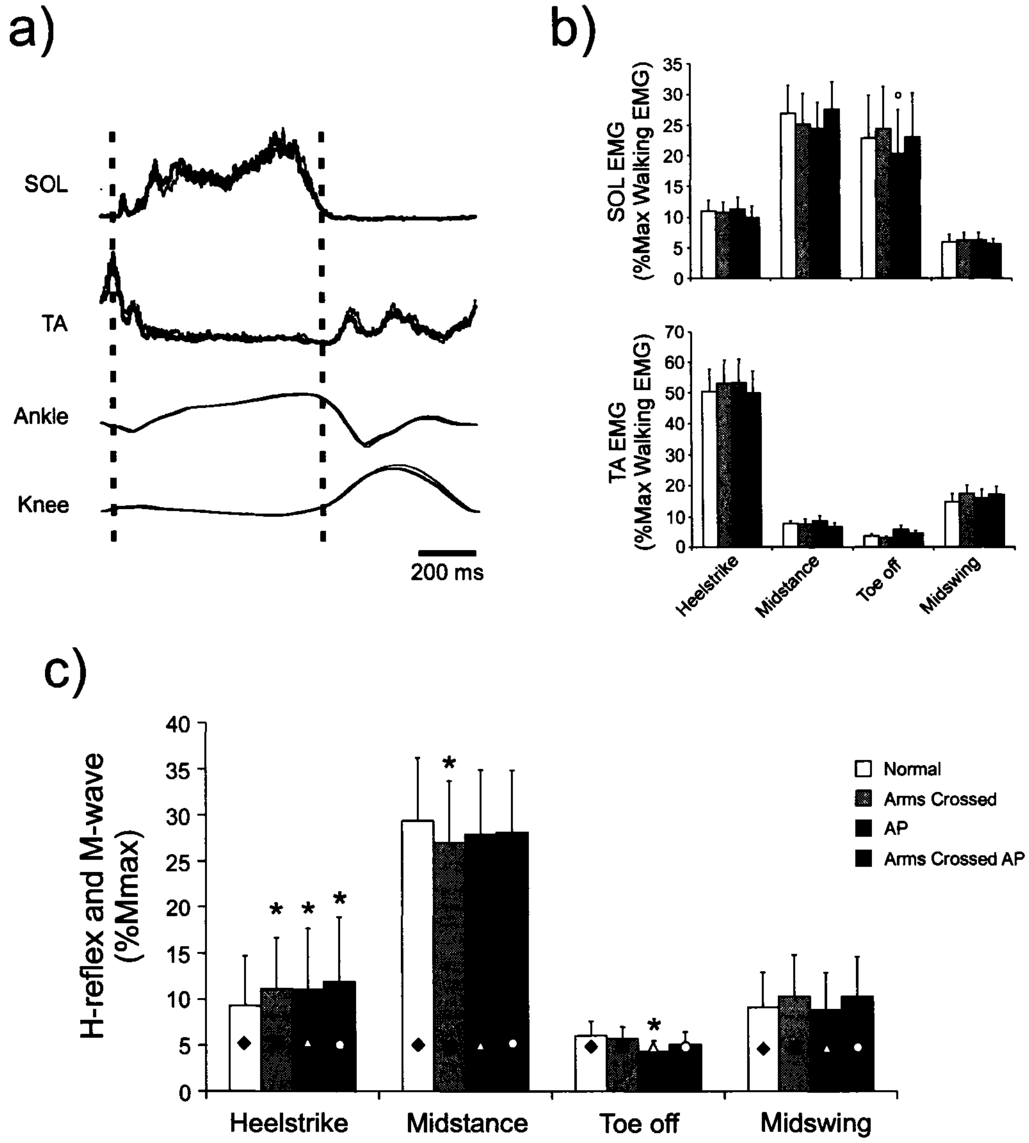

Figure 2. H-reflex amplitude and EMG activity across the step cycle for conditions with increased postural threat compared to Normal. a) Average (n=30) electromyography and goniometer traces from control steps during Arms Crossed AP (thick lines) and Normal walking (thin lines). Dotted lines represent heelstrike and toe-off respectively. b) Group averaged EMG amplitude in the SOL and TA muscles. Each bar represents the mean (N=10). Error bars represent one standard error. Circles indicate significant differences compared to the Arms Crossed condition for that point in the step cycle (planned comparison, $p<0.05$). c) Group averaged H-reflex amplitudes for the unstable walking conditions (Arms Crossed, AP, and Arms Crossed AP) are shown with the Normal condition for each point in the step cycle tested. Each bar represents the mean (N=10). Error bars represent one standard error. Group averaged M-wave amplitudes are shown by the symbols (closed diamond Normal; closed square Arms Crossed; open triangle AP; open circle Arms Crossed AP). Asterisks indicate significant difference compared to the Normal condition for that point in the step cycle (planned comparison, $p<0.05$).

restricting arm swing and/or experiencing periodic and unpredictable perturbations at the torso. Despite these changes in the task, the walking pattern of the legs was consistent across all four walking conditions. This is exemplified in Fig. 2a depicting average (n=30) data for two of the walking conditions for one subject; Normal is the thin trace which is generally obscured by the overlaid thicker trace representing the Arms Crossed AP condition. Specific analysis of the EMG levels in SOL and TA at the four points of the step cycle studied indicated no significant differences between tasks, with one exception (Fig. 2b). The SOL activity at toe-off was significantly lower during the AP condition than during the Arms Crossed condition ($p<0.05$). Ankle and knee angles were not different between tasks at any of the step cycle points studied. There were no apparent differences in step cycle duration or speed of movement across tasks.

The group averaged H-reflex amplitudes are shown in Fig. 2c for each of the points in the step cycle and the four walking conditions. The group averaged M-wave amplitudes are also plotted in Fig. 2c as the symbols. The average H-reflex amplitudes were compared between conditions for each point in the step cycle using planned comparisons. At heelstrike all conditions of decreased stability (Arms Crossed, AP, and Arms Crossed AP) resulted in significantly larger H-reflexes, as compared to the Normal condition. The H-reflex amplitude at heelstrike in the unstable conditions was 22% larger than during Normal walking. No differences were found between the three decreased stability conditions. At other points in the step cycle the H-reflex amplitude was relatively unaltered by the change in walking conditions, with only two additional differences detected. H-reflexes at midstance during the Arms Crossed condition were significantly decreased, compared to Normal. In addition, H-reflexes at toe-off during the AP condition were reduced, compared to Normal. No other significant differences were identified. The amplitude of the M-wave was specifically controlled to be 4-6% Mmax for all subjects and all points in the step cycle. Consequently, no differences were identified in the M-wave amplitudes.

H-reflex amplitude with increased stability

In Part II of these experiments subjects were asked to hold stable handles while walking. The muscle activity and movement patterns of the legs did not change significantly when subjects walked while holding stable handles placed in front of them. Average traces for the control step EMG and goniometer signals are shown in Fig. 3a for one subject, with the thin traces representing the Normal condition and the overlaid thick traces representing the Handles condition. The group averaged activity of SOL and TA at each point in the step cycle studied for both walking conditions are depicted in Fig. 3b. No differences were detected in the EMG amplitudes between conditions at any of the points of the step cycle. In addition, no differences in the ankle or knee angles were identified between walking conditions.

The amplitude of the H-reflex was reduced ($p<0.05$) during the Handles condition, compared with Normal, at both the heelstrike and midstance points of the step cycle (Fig. 3c). At heelstrike, the H-reflex amplitude was nearly 40%

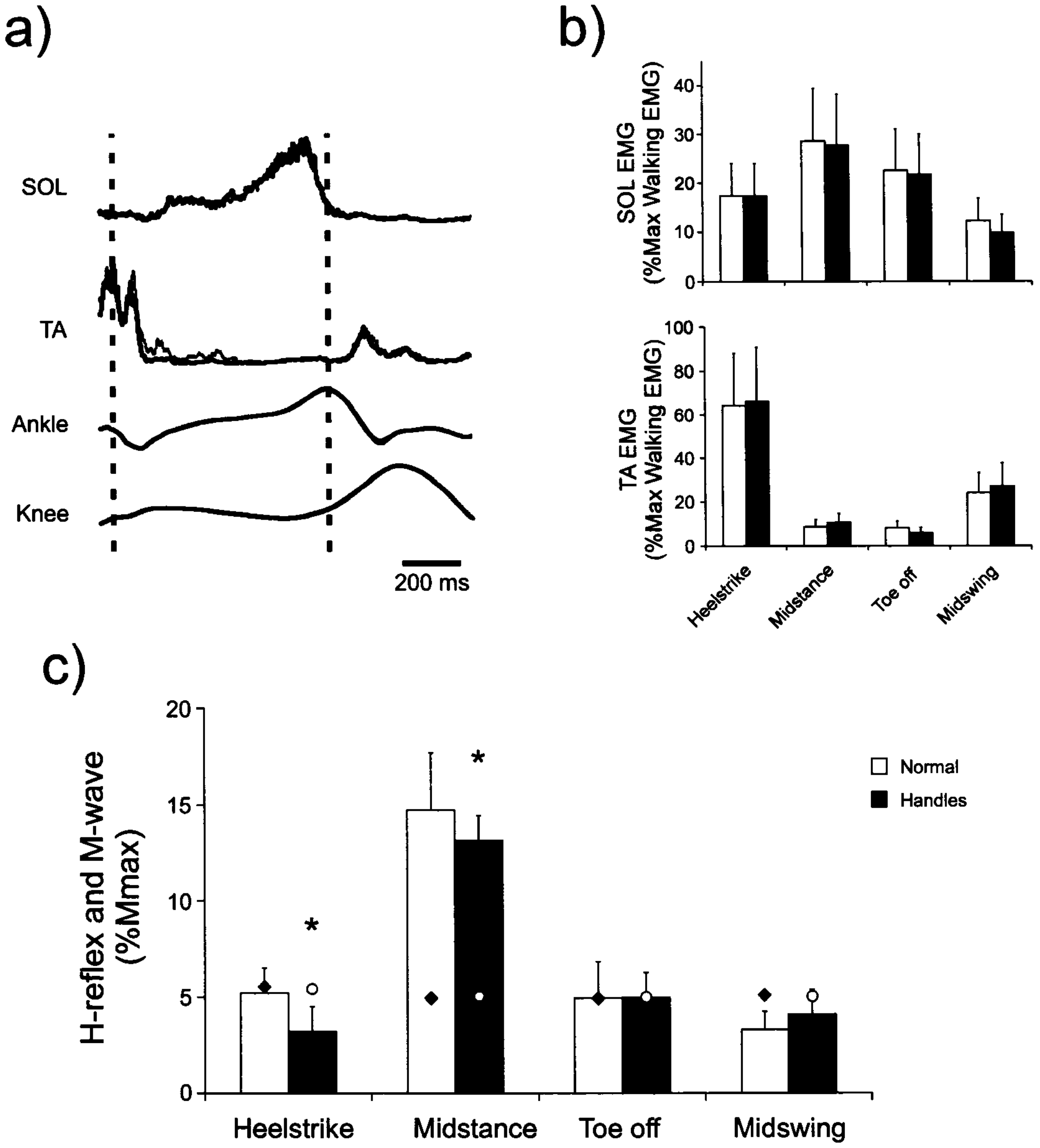

Figure 3. H-reflex amplitude and EMG activity across the step cycle for the Handles condition compared to Normal. a) Average (n=30) electromyography and goniometer traces from control steps during Handles (thick lines) and Normal walking (thin lines). Dotted lines represent heelstrike and toe-off respectively. b) Group averaged EMG amplitude in the SOL and TA muscles. Each bar represents the mean (N=10). Error bars represent one standard error. c) Group averaged H-reflex amplitudes for the Handles walking condition are shown with the Normal condition for each point in the step cycle tested. Each bar represents the mean (N=10). Error bars represent one standard error. Group averaged M-wave amplitudes are shown by the symbols (closed diamond Normal; open circle Handles). Asterisks indicate significant difference compared to the Normal condition for that point in the step cycle (planned comparison, $p<0.05$).

lower when subjects held Handles compared to Normal walking. The H-reflex amplitude in the Handles condition at midstance was 10% lower than in the Normal condition. No difference in reflex amplitude was observed between conditions at either the toe-off or midswing points in the step cycle. In addition, no differences were identified in the amplitudes of the M-waves as these were controlled throughout the experiment.

Discussion

In this study we showed that changing the context in which a person walked (by varying the level of postural threat) led to significant changes in the amplitude of the SOL H-reflex. However, the changes in H-reflex excitability were not generalized across the step cycle, but consisted of increases and decreases in amplitude specific to a few points of the step cycle. In particular, reflexes recorded at heelstrike appeared to be most susceptible to context-dependent adaptation. The H-reflex amplitude at heelstrike increased by 22% when subjects walked in less stable conditions and decreased by 40% when subjects walked in a more stable condition, compared to walking normally on the treadmill.

The modulation of the H-reflex at heelstrike supports our hypothesis. That is, H-reflexes were larger when walking in conditions that threatened stability. However, we did not find any difference in H-reflex amplitude between the AP and the Arms Crossed AP conditions. This is in direct contrast to our previous finding that the amplitude of the corrective response in SOL following perturbations was significantly increased when the subjects also crossed their arms (Misiaszek and Krauss 2005). In fact, in that study crossing the arms had the effect of more than doubling the amplitude of the evoked response in SOL at midstance. In this study the H-reflex amplitude at midstance was largely unchanged, showing mainly non-significant decreases in amplitude during walking conditions of increased postural threat. Consequently, the larger evoked response observed in SOL at midstance in our previous study is not related to changes that influence the H-reflex. Although we cannot exclude the possibility that changes in fusimotor drive acting on the simple stretch reflex might contribute to the larger corrective response in SOL, it is likely that other pathways, such as long-loop functional stretch reflexes or group II afferent pathways may be involved (Sinkjaer et al. 2000).

Nevertheless, the clear finding of this study was that the amplitude of the H-reflex was modified with the walking context. This was most apparent for reflexes evoked at heelstrike. However, there was also a significant decrease in H-reflex amplitude at toe-off during AP walking ($p<0.05$). We suggest this change in amplitude is related to changes in SOL EMG activation as the SOL EMG was also significantly reduced at this point in the step cycle for this condition (Fig 2b). In addition, H-reflexes were typically smaller at midstance during tasks of increased postural threat, and significantly reduced during the Arms Crossed condition (Fig. 2c). It is interesting that the H-reflex was also significantly reduced at midstance when subjects held stable handles ($p<0.05$). It is not clear why the H-reflex amplitude was decreased at midstance during conditions of both increased and decreased postural threat. However, at this point in the step cycle the H-reflex is relatively large during the Normal walking task and the ongoing EMG activity is substantial. A large H-reflex amplitude during the midstance phase may be further destabilizing to balance when subjects feel that their stability is threatened (see below, Trimble and Koceja 1994). As a result, the H-reflex may be suppressed at midstance in the unstable conditions to prevent further instability, and suppressed in the stable condition because the reflex may be of less functional relevance when the arms engaged in maintaining stability.

The changes in reflex amplitude we observed at heelstrike are reminiscent of the context-dependent changes in H-reflex amplitude described by Schneider and Capaday (2003). In that study, the authors noted that H-reflexes were substantially increased only during the swing phase of backward walking in subjects unaccustomed to the task. However, immediately upon grasping safety rails the H-reflexes during the swing phase were suppressed. The authors suggested that the increase in the H-reflex was related to the uncertainty of the task, associated with foot placement and stability. In our study, the H-reflex amplitude at midswing was unaltered between conditions. However, our subjects were walking forward and therefore likely had more confidence in the foot placement than the subjects in the Schneider and Capaday (2003) study. We suggest that in our study the larger H-reflexes at heelstrike during the unstable walking tasks and the smaller H-reflexes when subjects hold handles is similarly related to task uncertainties, in particular, the threat of losing balance. In this context, the increased H-reflex amplitude in less stable walking conditions may serve to assist in controlling ankle angle or joint stiffness at ground contact, when the new base of support is being established. It is also important to note that in our study we sampled only four points in the step cycle. Therefore, we cannot say that changes in the H-reflex between tasks are restricted to heelstrike per se. It is possible that changes in reflex amplitude also occurred in late swing or early stance.

Nielsen et al. (1993) reported significantly decreased SOL H-reflex amplitudes in trained ballet dancers, likely due to the daily training and performance of balance-demanding tasks that require co-contraction of the ankle antagonists. The H-reflex may be very finely tuned and is suppressed in situations when balance is not particularly threatening, such as normal standing for ballet dancers in Nielsen et al. (1993). This is similar to the decrease in H-reflex amplitude at mid- to late swing of backward walking reported by Schneider and Capaday (2003) when subjects were trained to walking backwards, compared to untrained subjects. These results are consistent with our study as the H-reflex was suppressed in situations when balance was less threatened (holding handles) and facilitated in conditions with increased threat.

Ours is not the first study to examine the influence of walking in an unstable environment on the amplitude of the SOL H-reflex. Llewellyn et al. (1990) found that subjects walking on a narrow beam suppressed the H-reflex by 40% at matched SOL EMG levels compared to walking on a treadmill. This suppression was most prominent for reflexes throughout stance phase from early stance to toe-off. Thus, it appears that the results of Llewellyn et al. (1990)

contrast with our current findings by showing a general reflex suppression that is large in magnitude. However, this difference is likely related to the very different environmental and task constraints imposed by the two studies. Beam walking consists of greater co-contraction of TA and SOL to stabilize the ankle joint and a longer double support phase than normal treadmill walking. Llewellyn et al. (1990) did not report the same phase-specific regulation of H-reflex amplitude as the current study, but rather a decrease persisting from early stance through to toe-off, and this may be due to differences in the walking pattern between beam walking and treadmill walking. In addition, the major threat to stability introduced by walking on a narrow beam is related to medial-lateral stability and the constraint imposed on medial-lateral placement of the feet. In this context, the electrically evoked H-reflex may itself be a source of instability (Earles et al. 2000, Trimble and Koceja 1994). Consequently, the suppression of the H-reflex during beam walking may have been an epiphenomenon of the technique. We cannot rule out the possibility that the instability evoked by the H-reflex in our study led to similar suppression to reduce the induced disturbance (which might account for the smaller H-reflex noted at midstance in the Arms Crossed condition). However, if this occurred then the facilitation of the reflex we observed at heelstrike occurred in spite of this competing influence.

Investigations of reflex modulation in seated (McIlroy et al. 2003) and standing (Chalmers and Knutzen 2002, Solopova et al. 2003) balance tasks found significant and consistent reductions in H-reflex amplitude with instability. Simultaneous investigation of H-reflexes with somatosensory evoked potentials

(McIlroy et al. 2003) or transcranial magnetic stimulation (TMS) – evoked motor responses (Solopova et al. 2003) suggest that spinal reflexes are reduced in amplitude to allow cortical inputs to play a greater role in maintaining stability during a skilled balance task and during unstable standing, respectively. McIlroy et al. (2003) found that the amplitude of somatosensory evoked potentials increased while the H-reflex amplitude decreased suggesting an increase in afferent inflow to the cortex. This may indicate that sensory inputs are facilitated to the cortex to enable greater cortical contribution to balance maintenance in this particular task. The balancing task during sitting required a high level of skill, similar to the skill demand of accurately placing the foot during beam walking (Llewellyn et al. 1990). It is likely that a large skill requirement in a task necessitates greater dependence on cortical influences than simple spinal mechanisms in balance threatened conditions. However, Koceja et al. (1995) reported that elderly subjects with large postural sway had increased H-reflex amplitudes when standing compared to lying prone. This is in contrast to young subjects and elderly subjects with minimal postural sway whose H-reflex amplitude decreased in simple standing compared to lying prone. It is likely that a spinal reflex is appropriate for maintaining stability in a simple task, such as simple standing, that was threatening to elderly subjects who had large natural postural sway. These findings support that the H-reflex may be increased with postural threat in some tasks, as a component of the balance maintenance strategy. Thus, the H-reflex is regulated in part with the sense of stability or postural threat, but the way in which it is regulated appears to be context-specific and may reflect the large numbers of postural strategies that can be employed in balance control. Taken together, the multiple investigations of H-reflexes in various tasks suggest that this context-specificity can be quite discrete adapting on a moment by moment basis across the step cycle, and can likely lead to either increases or decreases in H-reflex amplitude based on the context and the postural strategy employed.

An important finding in this study is the specificity of the influences of the walking task on the amplitude of the H-reflex. Recently, we demonstrated that the amplitudes of specific cutaneous reflexes in the legs were adapted at specific points in the step cycle when subjects walked in less stable or more stable conditions (Haridas et al. 2005). Together these findings suggest that spinal reflexes can be regulated in a very specific manner, according to the context of the task being performed. This context-dependent regulation of reflex excitability is likely achieved by cortical influences. Bretzner and Drew (2005) found that motor cortical influences on the excitability of cutaneous reflexes in the walking cat showed a high degree of specificity to the movement phase. These authors suggested that these cortical influences may be important to specifically regulate reflex excitability to stabilize movements. In addition, Pijnappels et al. (1998) demonstrated that cortical inputs can lead to phase-dependent influences on cutaneous reflex excitability. Thus, cortical influences are capable of producing phase-specific changes in reflex excitability, such as those observed here for the SOL H-reflex.

We have shown here and previously (Haridas et al. 2005) that spinal reflexes are specifically regulated as a function of threat to stability during walking. Many of these context-dependent adaptations in spinal reflexes complement the context-dependent adaptations of the corrective responses to balance disturbances during walking (Misiaszek et al. 2000; Misiaszek and Krauss 2005; Rietdyk and Patla 1998). We cannot state with certainty whether these spinal events are directly related to the balance corrective responses. However, Rietdyk and Patla (1998) noted that the magnitude of corrective response as a function of threat to stability was modulated in a complex manner, with specific adaptations occurring in different muscles. One possible means of accomplishing this complex modification of a functional response is by the cumulative integration of specific adaptations to a number of simpler responses. Thus, the specific adaptations observed in the amplitudes of the H-reflex, and cutaneous reflexes (Haridas et al. 2005), along with adaptations that likely occur in other reflexive responses (such as the functional stretch reflex, force feedback contributions and others) may occur to dynamically weight the expression of each of the related motor responses across the step cycle to meet the specific needs of the task constraints. This would be akin to adjusting 'motor membership functions' (Prochazka 1996) as a way to optimize balance corrective responses to meet the changing needs of a shifting environment (Misiaszek 2006).

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CHAPTER 3 - General discussion

When the level of postural threat is altered, there are corresponding changes in the H-reflex. These changes were most pronounced at or around heelstrike and may reflect the importance of establishing ground contact to maintain balance during walking. Our results from the behaviour of the H-reflex allow us to suggest that the sensitivity of reflex circuitry is altered at the level of the spinal cord through descending influences that reflect the level of postural threat.

We found that the H-reflex amplitude decreased at heelstrike and midstance in the most stable condition, when subjects held stable handles. We found that the H-reflex amplitude increased at heelstrike with increasing levels of postural threat. The most unstable condition, Arms Crossed AP, had the largest H-reflex amplitude at heelstrike. Previously we reported large amplitude responses at heelstrike and midstance in the SOL when subjects were perturbed forward with their arms crossed (Misiaszek and Krauss 2005). The context-dependent modulation of the H-reflex amplitude is comparable to the modulation in the amplitude of the corrective responses to balance perturbations at heelstrike, suggesting the two events may be related. Thus the spinal reflexes may be involved in the larger corrective responses following perturbations during walking.

In this study, we used the H-reflex to test the central modulation of a muscle afferent reflex loop in walking conditions of postural threat. Previous studies have inferred stretch reflex modulation from the behaviour of the H-reflex; however, the behaviour of the H-reflex can be misleading due to differences between the two reflexes. Firstly, the H-reflex and the stretch reflex involve recruitment of different muscle afferents. Due to the nature of electrical stimulation the H-reflex recruits primarily the large-diameter fibres of the Ia afferents, but at voltages required to elicit strong H-reflexes Ib inhibitory afferents and some group II afferents are also activated (Burke et al. 1983). Some local cutaneous afferents are evoked due to stimulation of the skin over the popliteal fossa from the electrode. The short-latency monosynaptic stretch reflex results from the activation of Ia afferents by muscles spindles, and the longer-latency functional stretch reflex results form the spindle activation of both Ia and group II muscle spindle afferents. Secondly, the H-reflex is not purely monosynaptic, but results in activation of interneurons in the spinal cord, resulting in a polysynaptic pathway in addition to monosynaptic excitation from the Ia afferents to the motoneurons (Burke et al. 1983). Thus, accurate comparisons between the H-reflex and the short latency stretch reflex (the monosynaptic component) cannot be made. Thirdly, the H-reflex technique bypasses the muscle spindles (Zehr 2001), and does not reflect changes in muscle spindle firing rates or changes in spindle sensitivity resulting from descending fusimotor influences.

As a result of these differences, the H-reflex modulation pattern does not perfectly match stretch reflex modulation. Andersen and Sinkjaer (1999) reported differences in the phase-dependent modulation of H-reflexes and stretch reflexes elicited in the same subject. They found that stretch reflex amplitude was nearly zero in late stance, likely due to soleus muscle shortening at this step cycle phase. The H-reflex remained relatively large in late stance of walking, suggesting that the stretch reflex modulation pattern is influenced by unloading of the intrafusal muscle fibres and decreased spindle afferent firing at this point of the step cycle (Andersen and Sinkjaer 1999).

As well, stretch reflexes are not decreased in amplitude during walking as compared to standing (Sinkjaer et al. 1996), as seen with the H-reflex (Capaday and Stein 1986). Morita et al. (1998) determined that stretch reflexes were less susceptible to presynaptic inhibition than H-reflexes because of differences in the spatial and temporal firing characteristics of the electrically-elicited H-reflex and the naturally evoked stretch reflex. The H-reflex results from the synchronous activation of a large number of afferents arriving simultaneously at the motoneurons. Conversely, stretch reflexes increase in amplitude when the firing rate of a small number of afferents increases to allow for temporal summation and transmitter release. Changes in muscle spindle sensitivity, resulting from gamma motoneuron activity, would alter both the temporal and spatial firing characteristics of the stretch reflex. Thus, the influence of presynaptic inhibition on the stretch reflex modulation pattern may be reduced compared to H-reflexes because of the involvement of muscle spindle receptors and the fusimotor system in stretch reflexes.

Changes in H-reflexes reflect central modulation primarily of the Ia to alpha-motoneuron synapse due to changes in walking condition, in this case changes in postural threat. The modulation of the H-reflex and the stretch reflex do not need to match considering the stretch reflex involves more processing (gamma motoneuron firing, stretch sensitivity). However, the H-reflex is a valuable tool in assessing the central modulation of a primarily muscle afferent reflex. This central modulation reflects one component of the neural changes affecting stretch reflex circuitry during postural threat, but does not reflect the overall behaviour of the stretch reflex considering task-related changes in fusimotor drive (Prochazka et al. 1987) and muscle spindle sensitivity will impact the stretch reflex modulation pattern. The H-reflex has allowed us to assess one way in which the central nervous system modulates peripheral reflex inputs when balance in threatened.

Accurate foot placement at heelstrike is particularly important for establishing ground contact with the support surface when there is postural uncertainty (Pedotti 1977). The behaviour of the H-reflex suggests that the short-latency spinal reflex circuits may contribute to regulating stable contact at heelstrike when balance is threatened. Schneider and Capaday (2003) similarly found that H-reflexes had increased amplitude at late swing leading into ground contact in backward walking. They showed that the increased H-reflex amplitude was related to the sense of threat subjects felt when performing the task. Subjects trained in backward walking and who felt confident in the task had smaller H-reflexes in late swing than untrained subjects. A larger amplitude stretch reflex leading into ground contact may allow the limb to quickly adjust to instability when subjects are unsure of their foot placement. Ground contact is especially important during treadmill walking because subjects are prevented from pausing to adjust their walking pattern by the continuously moving treadmill belt. This characteristic of treadmill walking necessitates fast responses for balance recovery at heelstrike to recover stability, such as the short latency SOL responses to perturbations reported by Misiaszek and Krauss (2005). The behaviour of the H-reflex in environments of increased postural threat such as unfamiliar backward walking in Schneider and Capaday (2003) or the current perturbed walking task implies that a simple stretch reflex likely contributes to balance maintenance during walking.

Our findings also suggest specificity in the pattern of reflex modulation due to task. A monosynaptic stretch reflex may serve a very specific role in a particular context, such as heelstrike during instability, but does not appear to be a dominant or generalized mechanism of balance recovery across the step cycle. The H-reflex showed little task-related modulation at points other than heelstrike and midstance for the conditions of varying postural threat. Balance corrective reactions have been described for many points in the step cycle (Berger et al. 1984, Misiaszek and Krauss 2005), suggesting that multiple reflex mechanisms perhaps work in concert to contribute to balance recovery, and are weighted in a phase-specific manner.

In fact, context-specific differences in H-reflex amplitude modulation illustrate that there may be many postural strategies that consist of different reflex contributions. For instance, much of the previous work on H-reflexes in balancing tasks have shown decreases in amplitude, instead of the phase-specific increase we reported with increased postural threat. Decreased H-reflex amplitude in investigations of standing balance (Chalmers and Knutzen 2002, Solopova et al. 2003) and at stance phase in beam walking (Llewellyn et al. 1990) may suggest a hierarchical reorganization of reflex inputs for balance maintenance at midstance. Solopova et al. (2003) report increased motor-evoked potential amplitudes and lower-amplitude H-reflexes when subjects balance on a rotating platform. They suggest that cortical influences play a greater role than simple spinal mechanisms when balance is threatened during standing. However, the increased cortical influences for balance maintenance may be related to the task complexity. Koceja et al. (1995) found that elderly standing subjects who had large postural sway increased their H-reflex amplitude in a simple standing task compared to lying prone. The increased H-reflex amplitude may reflect a postural strategy including both simple reflexes and cortical inputs working in concert to maintain balance in the elderly unstable subjects. In contrast, the simple standing task was probably not destabilizing in the young subjects who had minimal postural sway, not necessitating heightened reflexes. Young subjects may use a different more sophisticated postural strategy in standing balance tasks when their stability is threatened.

The decrease in H-reflex amplitude during beam walking (Llewellyn et al. 1990) is likely due to the constraints of maintaining foot placement on a narrow beam when balance is threatened in the medio-lateral direction. McIlroy et al. (2003) suggest that an increase in the proprioceptive inputs to the cortex in a challenging balance task during sitting reflect an increased importance of cortical influence on maintaining stability and a reduced emphasis on simple spinal reflexes. Both beam walking (Llewellyn et al. 1990) and the seated balance task in McIlroy et al. (2003) have large skill requirements, perhaps necessitating greater cortical influence in performing the task. This may be reflected as a task-specific suppression of simple reflex mechanisms that are inappropriate for task demands in favour of cortical inputs for maintaining balance. The reflex contribution would thus be modulated with task and walking context, in line with the modulation of the balance maintenance strategy. Although spinal reflexes may play an important role in balance maintenance at heelstrike, the contribution of other more sophisticated reflexes and cortical inputs may be important for balance recovery at other points of the step cycle and in other balance-challenging tasks.

The characterization of compensatory balance reactions provides evidence for functional stretch reflex involvement in balance recovery. Berger et al. (1984) suggest that it is unlikely that monosynaptic stretch reflexes are responsible for muscle responses for balance recovery from treadmill accelerations and decelerations. They report muscle response latencies that are 25 ms longer than the latency of the H-reflex (the neural correlate of the monosynaptic stretch reflex). They also investigated the EMG responses to perturbation when ischemia was applied to the perturbed leg. Ischemia abolished the Achilles tendon jerk reflex, suggesting that many of the group I afferents were blocked. The amplitudes of the EMG responses were only slightly decreased with ischemia. Berger et al. (1984) state that although the short latency of the muscle responses suggest a stretch reflex mechanism, it is unlikely that the muscle responses are due solely to a monosynaptic stretch reflex, favouring group II afferent involvement.

Sinkjaer et al. (2000) suggested a role for the functional stretch reflex in contributing to SOL EMG activity, as opposed to a monosynaptic stretch reflex contribution. Unloading of the ankle extensors reduced the SOL background EMG during stance phase. This reduction was still present when the Ia afferent-mediated short latency stretch reflex was blocked with ischemia. These results, combined with previous perturbed walking experiments, point to a role of the stretch reflex in contributing to muscle activation during both normal unperturbed stance and also in response to balance perturbations. However, each study downplays the contribution of a monosynaptic stretch reflex, instead supporting a role for the functional stretch reflex including long loop and transcortical components.

Dietz et al. (1984) infer that balance corrective reactions during walking are triggered by long-loop reflexes when they compared muscle responses in perturbed standing and walking. The authors suggest that the latency and characteristics of the gastronemius response, such as duration of the burst, during perturbed walking match the characteristics of the second bursting response seen during perturbed stance. This response in standing is called the M2 response and represents multi-segment reflexes, or long loop spinal reflexes. The earlier M1 component, representing the monosynaptic stretch reflex, of balance corrective reactions seen in standing is thus absent in walking (Dietz et al. 1984). Long-loop stretch reflexes likely contribute to balance recovery responses during postural threat.

The suppression in H-reflex amplitude during the handles condition at heelstrike and midstance is likely due to reductions in the level of perceived postural threat. Previous studies have shown that stimulation of the superficial radial cutaneous nerve innervating the hands significantly increases the amplitude of the SOL H-reflex in sitting subjects (Zehr et al. 2004). This finding contributes to the body of evidence suggesting neural linkages between reflexes of the arms and legs. Frigon et al. (2004) showed that rhythmic arm movements significantly suppress SOL H-reflex amplitude in sitting subjects. These findings would suggest that conditions with rhythmic arm swing would have significantly lower H-reflex amplitudes than conditions with restricted arm swing. From these same studies it would be reasonable to hypothesize that the Handles condition, combining both restricted arm swing and cutaneous sensations at the hands, would have the largest amplitude H-reflex. However, these predictions are not consistent with the results of the current study, suggesting that the pattern of H-reflex context-dependent modulation is not simply due to the interaction of arm movements and arm sensory inputs with the lower limb circuitry, but due to a change in the overall perception of postural threat. In particular, the H-reflex was suppressed in amplitude during the Handles conditions, opposite to the predictions stemming from Zehr et al. (2004) and Frigon et al. (2004). When subjects walked while holding handles, cutaneous sensation from the hands likely contributes to the overall sensation of postural stability but does not directly influence the amplitude of the H-reflex in this particular condition. These results suggest that the amplitude of the H-reflex in conditions posing various levels of postural threat may be modulated by descending influences.

It is likely that multiple reflex pathways work in concert to produce balance corrective reactions that are functionally relevant to the task and the specific step cycle phase. It has been suggested that parallel reflex pathways are modulated in a complex manner and their contributions are "weighted" through cortical influence. This concept is described as "membership functions" in fuzzy logic models of locomotion (Prochazka 1996). Postural set is described as the "synaptic transmission of proprioceptive signals … modulated within the CNS according to task" (Prochazka 1996). The CNS influences may act pre- or post-synaptically to alter sensory transmission to the motoneuron pool. This potential influence on reflex transmission, in the case of the stretch reflex, is considered separate from the CNS-directed fusimotor influences on muscle spindle sensitivity. The behaviour of the H-reflex in the current project suggests that modulation may have occurred presynaptically because the excitability of the motoneuron pool was not altered with task, exemplified by the consistent background EMG levels between conditions. Based on the level of postural threat and the constraints of the walking task, various sensory afferent inputs may be weighted and combined to maintain stability. This allows a role for cutaneous reflexes to trigger corrective reactions after contact with an obstacle, and various stretch reflex mechanisms to contribute to muscle activation when appropriate.

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