Effects of specific rhythmic arm cycling parameters on the amplitude modulation of the Soleus H-reflex

by

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Abstract

Rhythmic locomotor activity involving the arms or the legs results in task and phase specific Hoffmann (H)-reflex modulation between the two arms or between the two legs. As well, specific ipsilateral and contralateral movement effects are observed. Recently it has been found that there is also interlimb (between arms and legs) task modulation of the H-reflex, using a rhythmic arm cycling paradigm. That is, the stationary Soleus H-reflex amplitude during arm cycling was attenuated when compared to a static condition (Frigon et al. 2004). The specific parameters of the arm cycling movement which may contribute to this attenuation however are unknown. The purpose of this research was to examine whether the interlimb Soleus H-reflex suppression is specific to: the phase of the arm movement; the movement of both arms; arm excursion; and, rate of arm cycling. Participants sat in a custom designed chair to prevent leg and trunk movement and performed bilateral arm cycling at frequencies of 1 and 2 Hz and with short and long crank lengths (to alter arm range of motion; ROM). As well, ipsilateral (relative to leg stimulated) and contralateral single arm cycling were performed at 1Hz with a long crank length. The Tibial nerve at the popliteal fossa was stimulated psuedorandomly at four phases of the arm cycle and changes in the Soleus H-reflex were recorded while maintaining a small, but stable motor (M)-wave for all trials. EMG was recorded from the Soleus, Tibialis Anterior, Vastus Lateralis and the Anterior Deltoid muscles. Peak to peak amplitudes of the H-reflex from each participant were determined off line and normalized to the M-max determined from individual M-H recruitment curves. Results indicate comparable suppressive effects in all phases of the arm movement, and with bilateral or unilateral cycling. The large ROM and the 2 Hz frequency of movement resulted in a stronger inhibition than with the small ROM and the 1 Hz arm cycling. This suggests that neural processes associated with generating both the rhythmic arm cycling pattern and the peripheral feedback from the arms, have an effect on the H-reflex modulation in the legs. We conclude that a general, rather than a specific, signal related to rhythmic arm muscle activity mediates the suppression of Soleus H-reflex during arm cycling.

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Dedication

This thesis is dedicated to my Mom and Dad who have inspired me to challenge my beliefs, my knowledge and my abilities.

Chapter 1: Introduction and Literature Review

Understanding human locomotion has been a fundamental goal of motor control research throughout the last century. A specific research focus has been to examine the neural control of the rhythmic and coordinated patterns of arm and leg movement involved in locomotor activities. These patterns are well studied at a cellular level in animal models with the benefit of invasive methodologies. Interlimb neural networks capable of maintaining rhythmic, spontaneous outputs between fore and hind limbs, even when isolated from the brain and sensory input, have been found consistently in invertebrates and in vertebrate spinal cords (see reviews from Grillner & Wallen, 1985; Grillner, Wallen, Hill, Cangiano, & el Manira, 2001) These networks – coupled oscillators - that control synchronous rhythmic patterns in animals and initiated by either voluntary or peripheral inputs are termed Central Pattern Generators (CPGs) and exist to control rhythmic activities such as breathing, chewing, gastrointestinal function as well as locomotion (Grillner, 1985). In contrast to animal studies, indirect methodologies must be used in humans to determine the neural pathways responsible for the control of coordinated limb movements during rhythmic forms of locomotion. Spinal reflexes evoked through activation of cutaneous or muscle afferents are commonly used as an indirect probe of neural mechanisms. The modulation of these reflexes allows postulation on the neural pathways responsible for the changes in motor output associated with movement. Knowledge of the neural control of human locomotion at a spinal cord level is important in the study of human movement. It provides influence to the study of rehabilitation when developing strategies to improve locomotion in people who have deficits of descending motor control such as in spinal cord injury, stroke or other brain injury.

Interlimb Coordination of the Fore and Hindlimbs of Animals During Locomotion

Coordination of the fore and the hind limbs (interlimb coordination) in quadruped vertebrates is evident during walking, running and swimming activities. Interlimb movements have been studied since the early 1900's when in 1911 Graham Brown noted that by electrically stimulating a section of the spinal cord of decerebrate cats that "the act of progression (was) induced in muscles de-afferented by cutting of their appropriate posterior spinal roots" and stated that "the rhythmic sequence of the act of progression is determined by phasic changes innate in the local centers and these phases are not essentially caused by peripheral stimuli"(Brown, 1911). Reciprocally organized movements between flexion and extension in the limbs in the absence of efferent descending input as well as afferent input from limb movement, has been more recently termed "fictive locomotion" and is evidence that neural networks, or CPGs, exist in an isolated spinal cord (Duysens & Van de Crommert, 1998). Hultborn, H. (Hultborn, 2001) discusses these neural networks as *functional units* and argues that the same basic unit can be used for multiple functions depending on the input from afferent and supraspinal systems.

Evidence for Spinal Interlimb Neural Pathways for Locomotion in the Animal

Ongoing research in animal studies gives the basis for the current understanding of the locomotor pattern controlled by the CPG. Much of the conclusive work in this area is from anatomical and physiological studies that examine neural pathways in the spinal cord. Anatomical studies of animal spinal cords have found enlargements of the cervical and lumbosacral areas that are connected by long propriospinal neurons (Miller, Reitsma, & Meche, 1973; Miller, Van Der Burg, & Van Der Meche, 1975). These enlargements are areas of concentrated neural networks that when stimulated result in the production of a motor pattern resembling locomotion (Kiehn & Butt, 2003). Skinner, Adams, & Remmel (1980) specifically identified propriospinal neurons that join the cervical enlargement to an L2 segment of the spinal cord. These anatomical connections are thought to not only connect the neural networks of the fore and hind limbs, but also to mediate changes in reflex excitability (Miller et al., 1973).

Physiological studies of interlimb locomotion examine the functional outcomes that come from stimulation of these neural connections in the spinal cord. Miller et al. (1973) in their study of 41 cats found that monosynaptic reflexes of the nerves supplying the pectoralis major muscle and to the physiological flexors of the forelimb were strongly facilitated by the quadriceps and sartorius muscles' nerve stimulation in the hindlimbs. As well, an ipsilateral nerve was more effective than a contralateral nerve. Miller's group also found that polysynaptic reflexes to the same muscles were also strongly facilitated, but were followed by a prolonged depression. Again, the ipsilateral nerves of the hindlimb were more effective than the contralateral nerves. In the same study, Miller and colleagues recorded reflexes in the nerves of the Latissmus Dorsi (LD) muscle and stimulated the nerves from the ipsi and contralateral quadriceps muscle. The results from the LD muscle nerve showed a reciprocal pattern of facilitation from the hindlimb contralateral quadriceps nerves and a depression form the ipsilateral quadriceps nerves. These findings would allow for the potential of coordinated patterns of movement between the fore and hindlimbs during animal locomotion. Two other studies reinforced the premise of phase related motor patterning of locomotion. Schomburg, Meinck, Haustein, & Roesler (1978) found that intracellular afferent stimulation of mixed and cutaneous nerves in the forelimbs of 22 high spinal decerebrate cats led to a phase modulated response in the hind limbs' motoneurons. They postulated that the descending propriospinal neurons from the cervical segments mediate excitatory and inhibitory inputs onto the lumbar segments. In a similar study by Miller, Ruit, & Van Der Burg (1977) reflexes of the hindlimb nerves were found to be modulated by forelimb nerve stimulation in accordance with the step cycle.

The coupling of cervical and lumbar regions, specifically the CPG, has more recently been examined in isolated spinal cords of neonatal rats (Juvin, Simmers, & Morin, 2005). It was found that, although the cervical and lumbar regions had independently functioning CPG's during fictive locomotion, the phase modulation of interlimb EMG responses involved a caudorostral excitability gradient from the lumbar CPG to the cervical CPG via propriospinal neurons. Moreover, when the two spinal regions were decoupled, the cervical generators were unable to elicit lumbar, phase-related, locomotor activity. Thus it is likely, in rats, that the forelimbs and the hindlimbs are linked in their neural control of locomotion, but that the lumbar region mediates a powerful ascending phasic influence on the cervical region.

The evidence for interlimb coordination and coupling of the neural control in animals is robust. However, there is much less known about the control of human interlimb coordination.

Interlimb Coordination of the Arms and Legs of Humans During Locomotion

Coordination of the arms and legs in humans is evident during walking, running and crawling, but the locus of control is more difficult to ascertain than in animals due to indirect methodologies. Cervical and lumbosacral enlargements have been identified in the primate (Molenaar & Kuypers, 1978; Skinner, Coulter, Adams, & Remmel, 1979) that may represent a CPG, but it may be inappropriate to compare primates to humans, despite their many similarities, as the primate's locomotion remains mainly quadruped. From an evolutionary viewpoint, conceivably, human walking could be based on similar anatomy and neural control as in animals. The progression of the human to an upright stance and bipedal gait with skilled upper limb function, however, questions the similarities of human locomotion to mammalian quadruped locomotion. Dietz (2002) argues that the arms and legs coordination during human locomotion is indeed similar to the control of the quadruped, but is prevented or uncoupled when skilled upper limb movements are required. Deitz (2003) also suggests that a supraspinal inhibitory pathway may be present to suppress the arms when needed during locomotion. Jackson (1983) postulated that the arm swing observed in human walking is an evolutionary retention of forelimb movement in the quadruped. He further postulated that human arm movement during locomotion functions only to prevent a jerky uncoordinated gait that would be present without the arm's muscular control. Alternatively, movement of the arms during walking was shown by Fernandez-Ballesteros, Buchtal, & Rosenfalck (1965) to have an active and coordinated pattern of activity that exists even when the arms were bound, restricting them from movement – suggesting a more functional role during locomotion. Webb, D. Tuttle, R.H. & Baksh, M. (1994) studied the phasic movement of human arm swing in relation to the speed of walking and found that there was an active transition from double arm swing during very slow walking to a single, alternating arm swing with normal and fast walking. This has been more recently examined by Donker, Beek, Wagenaar, & Mulder (2001) who found that antiphase arm and leg movement also shows less variation from the alternating pattern with increased speeds of walking. Thus it now appears that movement in the arms during locomotion is a coordinated response associated with movement in the legs.

Comparisons of other forms of human locomotion have been examined in an attempt to elucidate if a simple pattern generator, or *functional unit* (Hultborn, 2001), plays a role in controlling basic forms of human rhythmic locomotor activity. Wannier, Bastiaanse, Columbo, & Dietz (2001) found that there was indeed similar coordination between the arms and the legs during walking, creeping and swimming although a locked

1/1 frequency relationship was involved with walking and creeping only. In swimming, there was coordinated movement between the arms and legs, and the frequency relationship (arms/legs) decreased as the rate of swimming increased. This coordinated pattern of the arms and legs during swimming was maintained even when the movements of just the legs were slowed by the use of fins. However, the frequency relationship changed. Wannier and colleagues suggest that their results are evidence of a coupling of arm and leg oscillators in the neural circuitry connected by long propriospinal neurons between the lumbar and cervical segments of the spinal cord.

Although there is convincing functional evidence of arm and leg coupling, the exact neural control of coordinated arm and leg movement during human locomotion has not yet been fully elucidated. This type of research relies on the examination of spinal reflex responses, during rhythmic activities.

Evidence for Interlimb Neural Pathways in Human Locomotion

Examination of the neural control of human locomotion is conducted mainly through the analysis of reflex responses. Reflex responses have been found to be similar during rhythmic activities such as walking, arm or leg cycling, and swimming and show patterns of phase (occurring at specific times within the cycle of activity) and task (changes in reflex with different tasks) dependency (Wannier et al., 2001; Dietz, Fouad, & Bastiaanse, 2001; Zehr, Collins, & Chua, 2001a; Zehr & Haridas, 2003; Haridas & Zehr, 2003). This is considered a hallmark of the CPG in other animals. Additionally, reflex responses are similar between the two upper limbs (Zehr & Kido, 2001; Zehr et al., 2001a) and the two lower limbs (Zehr et al., 2001a).

Cutaneous reflexes (stimulation of a cutaneous nerve yielding oligosynaptic responses) have been a recent area of study and have been consistently found to be phase and task modulated during walking and cycling activities. Cutaneous stimulation of a nerve mimics the input of a low threshold cutaneous stimulus, such as touch or pressure, in the nerves distribution. These inputs are highly active during locomotion and responses to the cutaneous stimuli are important in adaptation to the environment. Zehr, Collins, & Chua, (2001a) found that interlimb reflexes in the leg muscles were evoked with stimulation of a nerve (superficial radialis- SR) in the arm and that reflexes in the arms were evoked with a stimulation of a nerve (superficial peroneal – SP) in the leg. As well, Haridas & Zehr (2003) found that, during walking, cutaneous reflexes in the arms and the legs were both evoked by stimulation of nerves in the hand and the foot. These responses were modulated in relation to the phase and task giving important evidence for spinal neural connections that regulate the arms and legs and allow coordinated locomotor activity.

Hoffmann reflexes (stimulation of the 1a afferent in a mixed peripheral nerve yielding motor responses) have also been used to study spinal responses to rhythmic interlimb coordination during human locomotion and will be the focus of the rest of this paper.

The Hoffmann Reflex

The Hoffmann reflex (H-reflex), named after Paul Hoffmann in 1918 is an important tool used in research for measuring spinal reflex excitability and in clinical practice to assist with diagnosis of neurological disease. It is often referred to as the electrical analogue of the physiological stretch reflex but it does not involve the fusimotor system of the muscle spindle and thus is a more direct measurement of the excitability of the reflex arc within the spinal cord. Electrical stimulation of a mixed peripheral nerve results in a short latency direct motor response (M-wave), and a longer latency response (H-reflex) that will vary depending on the length of the nerve stimulated (Zehr, 2002; Misiaszek, 2003). The H-reflex has, in the past, been termed a monosynaptic reflex with only one synapse occurring in the spinal cord dorsal horn between the 1a afferent fibers and the alpha motor neuron efferents. This has been recently disputed though based on 1) the existence of an M wave - which means that neurons of similar diameter size to the alpha motoneuron may be recruited at the same intensity of stimulation (ie group Ib, II, and larger diameter cutaneous neurons) (Misiaszek, 2003); and 2) the rise time of the excitatory post synaptic potential (EPSP) - which is long enough to allow oligosynaptic input on to the H-reflex (Burke, Gandevia, & McKeon, 1983; Burke, Gandevia, & McKeon, 1984) and infers that only the rising edge, or the first 5 ms, of the reflex is monosynaptic.

Use of the H-reflex requires some vigilance when used for the study of movement. It is, however, a valid and reliable tool of spinal excitability when used with careful implementation. First, the H-reflex amplitude is influenced by the number of active motoneurons in the muscle being tested (Burke, Adams, & Skuse, 1989; Stein & Kearney, 1995). This is generally a positive linear relationship (an increase in H-reflex amplitude with an increase in the number of active motoneurons), although a nonlinear relationship has been shown in the triceps surae (Zehr, 2002). Thus, when comparing the H-reflex amplitude between multiple trials or conditions, it is important that participants maintain a similar level of muscle contraction while the reflex is being measured (Zehr, 2002; Misiaszek, 2003). Maintenance of a tonic muscle contraction during H-reflex testing also serves to decrease the variability of the H–reflex amplitude (Burke et al., 1989) and give a relative value to the state of the motoneuronal pool (Schieppati, 1987; Burke et al., 1989).

Second, the H-reflex amplitude will vary directly as the number of Ia afferents activated increases with increases in intensity of nerve stimulation (Zehr, 2002). It is important then, when comparing results from multiple trials, that the stimulation intensity is similar in all trials. One method to achieve this is by maintaining a consistent M-wave size which serves as a guide to maintain nerve stimulus constancy throughout the multiple trials (Swett & Bourassa, 1981; Abbruzzese, Berardelli, Rothwell, Day, & Marsden, 1985; Brooke et al., 1997b; Zehr, 2002). Third, post activation depression of the reflex may occur with repetitious stimulations as the amount of neurotransmitter at the alpha motoneurons is depleted (Hultborn et al., 1996). This is controlled for by having a time delay between stimulations of at least 3 seconds (Rossi-Durand, Jones, Adams, & Bawa, 1999). Overall, with careful experimental procedures, the H-reflex is a reliable tool for measuring the spinal reflex modulation.

Mechanisms of H-Reflex Modulation

The connections with spinal interneurons allow modulation within the spinal cord from cortical, subcortical, spinal and peripheral inputs. Modulation can be mediated under the influence of either presynaptic inhibition on the 1a afferent or postsynaptically on the alpha motoneuron.

The H-reflex can be suppressed by facilitation of presynaptic inhibition (PSI) with the neurotransmitter gamma aminobutyric acid (GABA); or potentiated by inhibition of PSI (Lundberg, Malmgren, & Schomburg, 1987; Stein, 1995). The implication of premotoneuronal mediation during locomotion comes, in part, from evidence that H-reflex modulation does not follow motoneuronal excitation when moving from standing to walking or walking to running (Capaday & Stein, 1987; Brooke et al., 1997a). The H-reflex and EMG are not inhibited proportionally with presynaptic inhibition as they are with post synaptic inhibition (Stein, 1995) and changes in the slope are, in fact, used as a measure of H-reflex gain (Stein, 1995). PSI can arise from sensory afferent feedback (ie stretch receptors) during active and during passive limb movements (Stein, 1995; Brooke et al., 1997b). As well, inhibition mediated through reciprocal inhibition of a heteronymous muscle (or nerve stimulation) can occur (Pierrot-Deseilligny, Morin, Katz, & Bussel, 1977; Iles & Roberts, 1987; Crone & Nielsen, 1994; Pierrot-Deseilligny & Mazevet, 2000). Animal studies of fictive locomotion have also given much evidence for CPG mediated inhibition during rhythmic movement (Gossard, Cabelguen, & Rossignol, 1991). Finally, supraspinal influences on PSI can not be ruled out during active movement (Meunier & Pierrot-Deseilligny, 1998), which is in contrast to passive movement (Stein, 1995; Brooke et al., 1997b) which also delimits contraction induced muscle spindle and golgi tendon organ involvement (Brooke et al., 1997b). Additionally, vestibular inputs, postural and state related changes (Schieppati, 1987) influence the H-reflex amplitude through PSI. These influences can be minimized in experimental methodologies by maintaining a similar *postural set* and *level of intent* for comparable experimental conditions.

Modulation of the H-reflex During Walking

Modulation of the H-reflex occurs in relation to the task (task dependence) and the phase (phase dependence) of rhythmic movement which implicates the CPG as one of the mediators of modulation. Over a number of walking studies, it has been suggested that the Soleus H-reflex is suppressed through the progression of the postures and gait: lying to standing and walking to running (Capaday & Stein, 1986; Capaday & Stein, 1987; Capaday, Lavoie, & Comeau, 1995), although a study by Simonsen & Dyhre-Poulsen (1999) found a facilitation of the Soleus H-reflex with high running speeds (12-15 km/hr). The latter authors, however, used unconventional methodology and analyzed change in the H-reflex by measuring peak amplitude during the step cycle, and not the change in H-reflex amplitude for a given level of EMG.

Further to these studies, Ferris, Aagaard, Simonsen, Farley, & Dyhre-Poulsen, (2001) more specifically measured the gain of the H-reflex across the range of EMG levels during human walking by simulating reduced gravity and thus reducing muscle activity. Findings from this study were that the slopes of H-reflex amplitude versus EMG were independent of gravity (and therefore muscle activity) for walking and running, and that the H-reflex thresholds (not the slopes of the linear regressions) were higher in running than in walking. This is contrary to the previous study by Capaday and Stein (1987) and may have been due to methodological differences in data analysis with respect to changes in the maximal M response (M-max) throughout the walking cycle. It clearly proposes, however, that for a given afferent signal from the Soleus muscle, a greater efferent response will occur during walking compared to running, and that the difference is not dependent on muscle recruitment levels. This then leads to the suggestion that similar to animals, GABAb receptors may facilitate tonic inhibition through PSI on the 1a afferent fiber during running compared to walking (Ferris et al., 2001). The exact mechanism of this neural control is unknown.

These studies give evidence of task dependence of H-reflexes during walking although phase dependence of the H-reflex during walking is also well documented (Capaday & Stein, 1987; Yang & Stein, 1990; Ferris et al., 2001; Zehr & Duysens, 2004; Zehr, 2005) and together give some credence to the suggestion of central neural pattern generators that are active during the gait cycle. The limitation to the walking paradigm, although it is the most functionally relevant, is that it is difficult to study specific effects of leg and arm movement during rhythmic locomotion on reflex modulation.

Modulation of the Lower Limb H–Reflex During Leg Cycling

Leg cycling has been used to study the specific effects of rhythmic leg movement without the influence of the upper limb or trunk activity. The effect of leg cycling on the Soleus H-reflex is a well studied paradigm. Task modulation has been consistently found with bilateral leg cycling (McIlroy, Collins, & Brooke, 1992; Brooke, McIlroy, & Collins, 1992; Cheng, Brooke, Misiaszek, & Staines, 1998); when comparing H-reflex responses in static leg positions to those during active leg cycling. Specifically, there is an attenuation of the Soleus H-reflex during bilateral leg cycling compared to the static condition. Although the Soleus H-reflex during cycling has also been shown to scale with the background EMG levels of the homologous muscle (McIlroy et al., 1992; Zehr, Hesketh, & Chua, 2001b) during cycling, it is also scaled to background EMG during static contractions (Zehr et al., 2001b). This leads to the suggestion that the H-reflex modulation is mediated not only by homologous peripheral proprioceptive input, but also by mechanisms that may be converging centrally due to the cycling movement.

Further to this, Brooke and colleagues, in a series of experiments, have found that the Soleus H-reflex is modulated in active cycling conditions (Brooke et al., 1992) as well as passive cycling conditions (McIlroy et al., 1992; Cheng et al., 1998); ipsilateral as well as contralateral leg cycling; with the speed of leg cycling (McIlroy et al., 1992; Larsen & Voigt, 2004a); and with the phase of movement (McIlroy et al., 1992; Cheng et al., 1998).

Active/Passive leg cycling.

H-reflexes during active (Brooke et al., 1992; Brooke et al., 1997b) and passive (McIlroy et al., 1992) leg cycling are strongly attenuated although the passive condition exhibits less attenuation than the active condition. Supraspinal or spinal influences are likely sources of influence on the task dependent nature of the H-reflex during active and passive leg cycling (Brooke et al., 1997b), although the interaction from the muscle afferents is an important component of modulation via PSI during active movement (McIlroy et al., 1992; Brooke et al., 1997b). Changes in gain with passive leg movements eliminates the supraspinal effects of voluntary control onto segmental interneurons and removes the kinaesthetic discharge of the active muscle including the Golgi tendon organ and muscle spindle input (Brooke et al., 1997b). The attenuation of the H-reflex during passive leg cycling was thought by McIlroy et al. (1992) to be mediated through a source independent of the active muscle (i.e spindle stretch, skin stretch) or accounted for by a sub threshold change at the motoneuron. Modulation observed during passive movement may then provide insight into the possible gating mechanisms of peripheral feedback (Zehr et al., 2004).

Ipsilateral/Contralateral leg cycling.

One limb leg cycling was used by Brooke and colleagues to determine the effects of ipsilateral and possible *crossed* effects of contralateral leg movement on the Soleus H-reflex (McIlroy et al., 1992; Cheng et al., 1998). In an early experiment, active and passive ipsilateral leg cycling had a similar reflex gain to bilateral active leg cycling revealing that gain attenuation was not dependent on bilateral movement (McIlroy et al., 1992; Brooke et al., 1997b). Active and passive contralateral leg cycling, although significantly inhibited compared to the static condition, showed a specifically weaker effect than the ipsilateral and bilateral conditions (McIlroy et al., 1992). The authors suggest that because the H-reflex attenuation during contralateral leg cycling was greater than during the static condition, but less than during the ipsilateral and bilateral conditions (which were similar in gain) that there may be an additive effect with the ipsilateral leg having a greater weighting than the contralateral leg. The contralateral leg research paradigm thus can give evidence, then, that bilateral movement is not necessary for task modulation to be fully expressed and that there may be specific reflex modulation incurred with specific loci of control.

Speed of leg cycling.

An increase in the speed of leg cycling has resulted in a greater attenuation of the ipsilateral (McIlroy et al., 1992; Larsen & Voigt, 2004b) and contralateral (Cheng et al., 1998) Soleus H-reflex. The increased frequency of movement may be directly associated with an increase in the rate of spindle stretch with a subsequent increase in afferent discharge of the Ia fibres (Capaday & Stein, 1987; McIlroy et al., 1992). The change in the H-reflex gain with increased speed is thought to be a functional modification at the spinal level to prevent saturation of the motoneuron pool and allow for continued modification of the afferent peripheral feedback from the homologous muscles (Capaday & Stein, 1987; Edamura, Yang, & Stein, 1991; Larsen & Voigt, 2004c). Also, there may also be an increase in the central control with increased speeds of movement due to an increase in the physical and mental requirements of maintaining high speeds that then result in a greater H-reflex inhibition (Honore, Demaire, & Coquery, 1983; Grillon & Zarifian, 1985; Llewellyn, Yang, & Prochazka, 1990). As with the walking paradigm, the functional significance of a change in H-reflex modulation with changes in speed of movement is not clear. The most prevalent suggestion is that the decrease in H-reflex gain or the increase in the H-reflex threshold avoids saturation of the motoneuron pool during a greater output (Capaday & Stein, 1987).

Crank length of leg cycle ergometer.

The crank length of the cycle ergometer will alter the input from stretch and joint receptors of the leg. At small crank lengths, conceivably, there will be less stretch and associated firing of the group la and group ll fibers and less angular movement of the leg. It was found by Cheng, Brooke, Misiaszek, & Staines (1995) that attenuation of the Soleus H-reflex amplitude occurred with equivalent changes in crank length that affected the displacement of the vasti muscle group. It was concluded by the authors that the gain attenuation may arise from the spindle discharge in heteronymous extensor muscles occurring during movement.

There is no research that examines this phenomena using upper limb H-reflexes during arm cycling or using interlimb H-reflexes. The effect of upper limb changes in length or of muscle stretch on lower limb reflex modulation during arm cycling is yet to be determined.

Phase modulation during leg cycling.

The Soleus H-reflex is modulated with the phase of movement during bilateral leg cycling (McIlroy et al., 1992; Brooke et al., 1992; Brooke et al., 1997b; Cheng et al., 1998). It was found by McIlroy et al. (1992) that the modulation is most apparent when the hip and leg are in the fullest amount of flexion and the authors suggested that this may potentially be related to the role of the hip joint receptors to reset a central pattern generator. Because this has also been observed during passive cycling (McIlroy et al., 1992; Cheng et al., 1998), it is suggested that there is also a gating of the afferent feedback during movement (Brooke et al., 1997b; Zehr et al., 2004). Phase modulation is also present during active and passive ipsilateral leg cycling (McIlroy et al., 1992) which is suggestive that the same mechanisms may be used for ipsilateral cycling as for bilateral cycling. In contrast to the bilateral and ipsilateral cycling conditions, contralateral leg cycling is phase dependent during active, but not passive, leg cycling (Collins, McIlroy, & Brooke, 1993; Cheng et al., 1998). The reason for the lack of phase dependence observed during passive cycling of the contralateral leg is not clear, but may come from a more complex processing requirement than the one required for the ipsilateral leg (Brooke et al., 1997b).

Modulation of the Upper Limb H-reflex During Arm Cycling

The arm cycling paradigm has been used, like the leg cycling paradigm, to determine the effects of rhythmic arm movement conditioning on H-reflex modulation without interference from the legs or the trunk. The Flexor Carpi Radialis muscle (FCR) H reflex was measured during arm cycling in a study by Zehr and colleagues (Zehr, Collins, Frigon, & Hoogenboom, 2003) and it was found that the FCR H-reflexes were attenuated with bilateral, active ipsilateral and passive ipsilateral arm cycling which is similar to that found in the Soleus muscle by Brooke and colleagues (see 1997 review) during leg cycling. In contrast to the leg cycling experiments though, the FCR did not exhibit task or phase dependency with contralateral arm cycling (Zehr et al., 2003). The authors suggest that there is a stronger specification for each arm than for each leg associated with rhythmic movement. This may be related to the functional requirements of the arms as opposed to the legs to move independently of each other.

Experimental paradigms using arm and leg cycling separately have given insight into the separate neural control of arms and legs during rhythmic movement. Modulation of the H-reflex in the legs with respect to rhythmic arm movement may allow some insight into the neural connections between the arms and the legs during locomotion.

Interlimb Modulation of the H reflex During Locomotion

Modulation of the H-reflex from interlimb movement influences have been less studied. Postural effects of the arms have demonstrated changes in the H-reflex in stationary legs (Delwaide, Figiel, & Richelle, 1977; Eke-Okoro, 1994). These studies were used to examine if connections exist between cervical and the lumbar segments of the spine during static positions. Eke-Orkoro (1994) studied the effect of static arm swing positions on the Soleus H-reflex and combined this data with gait analysis and found that a relationship existed between the reflex responses and the upper limb position. Specifically, Eke-Okoro found that the maximum H-reflex amplitude was greater with the ipsilateral arm in the most flexed static swing position than when the contralateral arm was in the most flexed static swing position. Conversely, the maximum H-reflex amplitude was greater when the contralateral arm was in the most extended static arm swing position than when the ipsilateral arm was in the most extended static arm swing position. Interestingly, when both arms were positioned and the left tibial nerve was stimulated, the maximum H-reflex amplitude was greater when the contralateral arm was in the most flexed static position and the ipsilateral arm was in the most extended static position than when the ipsilateral arm was flexed and the contralateral arm was extended. This was not the case when the right tibial nerve was stimulated, and maximum H-reflex amplitudes were greater for all arm positions when the right tibial nerve was stimulated than when the left tibial nerve was stimulated. The author concluded that there may be at least a functional connection between the cervical and lumbar spinal segments, but because the arm positions did not alter the differences seen from right to left, that the lumbar spinal segments may have a dominant influence on the cervical spinal segments. The results of this study must be interpreted with caution however, as the experimental methodology (such as stimulus delivery and muscle activity) was not controlled. This study also does not examine the effect of rhythmical arm movement or arm swing which may be more related to functional walking.

The effect of rhythmic arm swing on the Soleus H-reflex in stationary legs has been studied. Hiraoka (2001) evoked the H-reflex in the Soleus muscle while participants performed arm swinging in a seated position. He also found suppression of the Soleus H-reflex associated with upper limb cyclic, rhythmic motion, but found the H-reflex amplitude was suppressed as the velocity of the swing increased. Reciprocal swing of both arms depressed the reflex at the shoulder extension position and thus it was concluded that phase dependency was evident. There are also methodological limitations of this study, however, and thus the findings are noted with this in mind. H-reflexes were taken as a percentage of the H-max which can vary significantly between trials; and different intensities of stimulation can elicit an H-reflex of the same size depending on which part of the M-wave:H-reflex (M-H) curve is tested (Zehr, 2002). As well, the participants did not maintain a constant level of Soleus muscle activation which controls for the effect of motoneuronal pool activation on the H-reflex (Schieppati, 1987; Burke et al., 1989). Therefore, it would be difficult to determine if the modulation is due to a change in the activation of the Soleus muscle during testing or if, in fact, it was due to the task of upper limb rhythmic motion.

In a study by Frigon, Collins, & Zehr (2004), the effect of the rhythmic arm cycling on the stationary Soleus H-reflex was compared to the effect of static arm positions on the stationary Soleus H-reflex. A significant suppression of the H-reflex during arm cycling was found (see Figure 1). This suppression was determined to be at a premotoneuronal level after finding that the H-reflex suppression during cycling was also altered significantly by conditioning (cutaneous sural nerve stimulation) known to presynaptically facilitate the Soleus H-reflex (Frigon et al., 2004). Additionally, the authors found that the arm cycling task had the largest effect when the ipsilateral arm was in a position of shoulder flexion. In contrast to the study by Hiraoka (2001), a constant input was ensured by Frigon et al. (2004) by maintaining a stable M wave and Soleus contraction level throughout the static and cycling trials. This important study gives evidence of interlimb task dependency. It does not however, give any specific evidence for phase dependency, or other modulating effects of arm cycling on the lower limb.

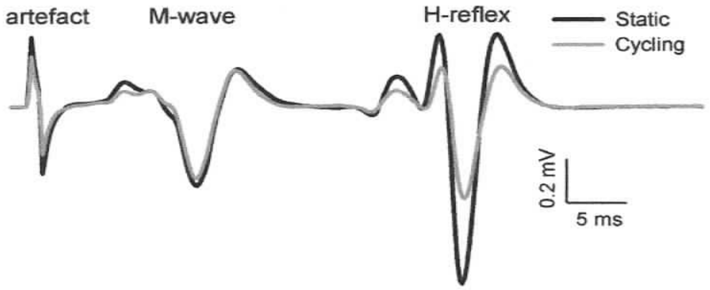

Figure 1. Task dependency of Soleus H-reflex during arm cycling. H-reflex amplitude is depressed during cycling compared to static trials. (from Frigon et al., 2004).

Zehr and colleagues (Zehr, Hoogenboom, Frigon, & Collins, 2004), found that the suppression of the H-reflex was countered by stimulating an ipsilateral cutaneous nerve (superficial radalis) in the hand. The authors suggested that the transmission of sensory feedback from the hand to the leg is not suppressed during rhythmic arm movement. This study gives evidence for interlimb pathways involving the integration of cutaneous feedback on the CPG during rhythmic movement.

Specific effects of upper limb rhythmic movement that may modulate the lower limb H-reflex have not been examined. It is of interest to determine whether ipsilateral and contralateral arm cycling, speed of arm cycling, and changes in crank lengths will have specific effects on the Soleus H-reflex suppression as has been already shown between the two arms and the two leg. This will be the focus of chapter 2 of this thesis.

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Chapter 2: Manuscript

Introduction

The arms and legs are both rhythmically active during human bipedal locomotion (Fernandez-Ballesteros, Buchtal, & Rosenfalck, 1965; Jackson, Joseph, & Wyard, 1983; Webb, Tuttle, & Baksh, 1994; Wannier, Bastiaanse, Columbo, & Dietz, 2001). In spite of an upright posture and the ability to use the arms for voluntary tasks during locomotion at slow speeds, it has been suggested that an interaction between the arms and legs (an "interlimb coupling") similar to that observed in quadrupedal animals is also present in the human (Dietz, 2002; Zehr & Duysens, 2004). Interlimb coordination during quadrupedal locomotion is associated with neural connections, or coupling, between the fore and hindlimbs (Miller, Van Der Burg, & Van Der Meche, 1975). More specifically, there is modulation of afferent feedback from the forelimbs to the hindlimbs during phases of the gait cycle (Miller, Ruit, & van der Meche, 1977; Schomburg, Meinck, Haustein, & Roesler, 1978). As well, *crossed* neural connections are present between the out of phase fore and hind limbs (Forssberg, Grillner, & Rossignol, 1977; Juvin, Simmers, & Morin, 2005). Crossed pathways and those responsible for phase dependent modulation, are thought to be influenced by afferent feedback (Miller, Reitsma, & Meche, 1973) and connected to spinal neural networks known as central pattern generators (CPGs) (Grillner & Wallen 1985). CPGs for the fore and hindlimbs are coupled through commissural neurons that cross the spinal cord (Butt & Kiehn, 2003) and propriospinal neurons that span the spinal cord between the cervical and lumbar segments (Miller et al., 1973; Skinner, Adams, & Remmel, 1980). Thus, the coordinated activity of the fore- and hindlimbs in spinalized animals is based upon the neural interaction between peripheral feedback and spinal pattern generation mechanisms. Functionally, this allows information from the local muscle and skin receptors of the forelimbs to be transmitted to the hindlimbs as well as maintenance of a coordinated gait pattern.

As mentioned, the mechanisms used in quadrupeds may have similar functions (as inferred by similarities in locomotor electromyography (EMG) and reflex responses) in humans (Dietz, 2002). Indeed, there is specific phase-dependent reflex modulation and the presence of crossed effects between the two legs during leg cycling that are further influenced by velocity of movement and changes in the range of leg movement (McIlroy, Collins, & Brooke, 1992; Brooke et al., 1997; Cheng, Brooke, Misiaszek, & Staines, 1998). This suggests a strong coupling between the two legs during locomotion which makes functional sense in order to maintain coordination and stability. Interactions between the two arms show some similar reflex responses in the moving arm, but responses are less specific which gives evidence for more functional independence between the two arms (Zehr, Collins, Frigon, & Hoogenboom, 2003). Interlimb muscular activity appears evident during locomotion as even when the arms are restricted during walking, there is rhythmic contraction of the arm musculature (Fernandez-Ballesteros et al., 1965). As well, coordinated arm and leg patterns occur and change with the speed of walking (Webb et al., 1994; Donker, Beek, Wagenaar, & Mulder, 2001; Donker, Daffertshofer, & Beek, 2005) in that there is an active transition from double arm swing during very slow walking to a single, alternating arm swing with normal and fast walking. The results of these experiments demonstrate an interaction is present between the arms and legs during rhythmic locomotor activity, but the specific effect of arm movement on the leg neuromuscular activity is less clear.

An experimental paradigm in which arm position changes while the legs remain stationary, allows specific analysis of arm position on the reflex responses in the legs. Delwaide et al. (Delwaide, Figiel, & Richelle, 1977) made an early attempt at this measure when they examined tendon reflexes in stationary leg muscles in response to changes in stationary arm positions associated with arm swing. Reciprocal positions of shoulder extension of ipsilateral and contralateral arms were found to have similar effects on the reflex amplitude. Further to this, Eke–Okoro (1994) reported that the position of the arms (related to arm swing) influenced the maximum Soleus H-reflex amplitude differently. However, the results from this study are difficult to interpret due to a lack of experimental control. A more relevant experimental paradigm to examine the influence of arm movement on leg movement during human locomotion has been to move the arms rhythmically and assess the change in EMG or reflex modulation in stationary legs. This eliminates the interaction of the arms and legs moving together and allows speculation on putative neural pathways that connect the arms and the legs. EMG measured in passive legs is augmented with the addition of fast, active, upper limb rhythmic movement using a recumbent stepping machine (Kao & Ferris, 2005).In addition, the Soleus H-reflex amplitude, in stationary legs, is suppressed during rhythmic arm cycling (Frigon, Collins, & Zehr, 2004). This suppression was determined to be at a premotoneuronal level after finding that the H-reflex suppression during cycling was also altered significantly by conditioning (cutaneous sural nerve stimulation) known to presynaptically facilitate the Soleus H-reflex (Frigon et al., 2004). Moreover, facilitatory cutaneous input from the hands (evoked by SR nerve simulation) interacts with the suppression of the H-reflex in the legs induced by arm cycling (Zehr, Hoogenboom, Frigon, & Collins, 2004). These studies give evidence that there are neural connections between the arms and the legs and that the neural connections are influenced by rhythmic arm movement. Our previous work with this paradigm suggested that the conditioning effects of rhythmic arm movement on the Soleus H-reflex may be a general rather than a specific one. For example, sampling at 2 phases of movement representing the extreme shoulder ranges of motion provided similar outcomes (Frigon et al., 2004). This led us to speculate a working hypothesis that a background of general suppression (i.e. "reflex bias") is created in the legs by rhythmic arm movement (Frigon et al., 2004). Alternatively, specific parameters of the arm movement may indeed be critical for the full expression of the interlimb coupling. For example, it may be that the suppression is phase modulated which would only be revealed by sampling more positions. However, as yet the possible effects of varying specific details of the parameters of arm cycling movement have not been examined. The conditioning effect of limb movement between the arms during arm cycling (Zehr et al., 2003) and between the legs during leg cycling (McIlroy et al., 1992; Cheng et al., 1998) has clearly been shown to result in specific changes in H-reflex amplitude. The outstanding question is: does a similar specificity exist for the interlimb effect of rhythmic arm movement on H-reflexes in the legs? In this study, we tested the experimental hypotheses that suppression of H-reflexes in the legs induced by rhythmic arm movement: 1) is dependent on the phase of the movement; 2) requires simultaneous movement of both arms; 3) is related to the excursion of the arm or the frequency of arm movement. Rejecting these experimental hypotheses would support the working hypothesis that general rather than specific movement features are key to the interlimb reflex suppression

Methods

Participants

Fifteen participants, aged 22 – 42, with no known peripheral or central neurological conditions or metabolic disease volunteered for this experiment. The participants gave written consent to a protocol approved under the Human Ethics and research Committee at the University of Victoria and performed in accordance with the Declaration of Helsinki. Participants were blind to the specific parameters and the hypotheses being studied in the experiment.

Protocol

Participants were seated in a custom fitted chair to minimize trunk or leg movement during arm cycling (see Figure 2). Hip and knee angles were approximately 90 and 120 degrees, respectively. The feet were secured to foot plates independent of the chair with the ankle angles set at approximately 90 degrees. Rhythmic forward arm cycling was performed on a hydraulic arm ergometer (Zehr & Hundza, 2005), with coupled cranks so that the right and the left arms were always 180 degrees in opposition. The ergometer was placed directly in front of the participant and the center (fulcrum) of the arm ergometer crank was directly in line with the shoulder joint. The cycle of movement was divided into four equal phases and named in accordance with the clock face from the right hand side of the ergometer (Zehr et al., 2004). Thus the arm was in the 3 o'clock position when the elbow was most extended and in the 9 o'clock position when the elbow was most flexed. Soleus H-reflex data were collected from the left leg (see H-reflex protocol below) for all conditions.

Except where otherwise noted, arm cycling was with a long crank length (handle 18.5 cm from the fulcrum of the ergometer) and a cycling frequency of 1 Hz. Participants practiced cycling using an oscilloscope (Hameg 20MHz, HM 205-3, Frankfurt/Main, Germany) for visual feedback, but were encouraged to cycle with minimal use of the oscilloscope during the cycling experimental trials. Lastly, participants maintained, and visually monitored, a consistent low level tonic contraction of the Soleus muscle using a rectified and filtered EMG signal presented on a second channel of the oscilloscope.

For descriptive purposes, cycling conditions have been divided into three parts, but in actuality eight movement trials were randomly performed within the experiment. Static trials were used as controls.

Figure 2. Schematic diagram of the experimental paradigm showing the left arm in the 3 o'clock position. Note: sides of chair are omitted to show leg bolster and trunk supports placed to prevent leg and trunk movement respectively.

Static trials

Control (static) data were obtained at three different times during the experiment: 1) before the start of any movement trials (pre); 2) midway through the movement trials (mid); and 3) after the movement trials (post). This allowed us to monitor for stable stimulus input throughout the experiment. Static trials were performed with both hands on the ergometer, with the right hand at four positions in the cycle (3, 6, 9 & 12 o'clock) and a tonic Soleus contraction (see above) was maintained.

Movement trials

There were three main types of movement trials, all of which related to the hypotheses to be examined in the study. 1) *Arm position within the cycle*: Participants (*n* = 8) cycled bilaterally while data was collected at four arm positions (3, 6, 9 & 12 o'clock). 2) *Bilateral vs. unilateral arm cycling:* Participants (*n* = 10) used both arms simultaneously (bilateral), or each arm independently (ipsilateral and contralateral to the H-reflex) in three separate trials. During unilateral cycling, the inactive arm remained at rest in the lap of the participant. 3) *Interactions of Crank Length (CL) and Cycling*

Frequency: Participants (*n* =8) cycled using a long (18.5 cm) and a short (4 cm) crank length at two frequencies of movement (1 Hz, 2 Hz) during four separate trials.

Soleus H Reflexes

The Tibial nerve was stimulated at the left popliteal fossa using 1 ms square wave pulses to evoke the H-reflex using bipolar surface electrodes and a Digitmer (Medtel, NSW, Australia) constant current stimulator (model DS7A). Nerve stimulation was delivered pseudo randomly between 2 and 5 seconds apart during all trials. To examine the effect of arm position in the cycle, the Tibial nerve was stimulated and H-reflexes were sampled at four separate arm positions during static and arm cycling trials. Otherwise, the Tibial nerve was stimulated at the 3 o'clock position only as it has been demonstrated by Frigon et al. (2004) that there is a significant effect on the Soleus H-reflex amplitude at this position. Nerve stimulation at specific arm positions was attainable with the use of an optic encoder mounted on the internal frame of the arm ergometer. Voltage measured by the optic encoder at specific positions allowed for precise timing of the H-reflex stimulus at each arm position.

The stimulation intensity for all trials was sufficient to evoke a stable motor (M) wave. This stimulation evoked an H-reflex on the ascending limb of the M-wave–H-reflex (M-H) recruitment curve. Thus any change in the H-reflex amplitude was not due to a change in input to the Tibial nerve. M-waves were monitored on line and the stimulation intensity was adjusted to maintain consistency in amplitude. Current was measured using a mA-2000 Noncontact Milliammeter (Bell Technologies, Orlando, FL.) and amplified by 10.

M-H recruitment curves were constructed, using 50 sweeps, at the beginning and the end of each experiment. Both hands were on the ergometer with the left arm in the 3 o'clock position and the right arm in the 9 o'clock position. This data served to determine the maximal M-wave used to normalize the H-reflex and M-wave data, to determine the stimulus intensity required to obtain an M-wave with a corresponding H-reflex on the ascending limb of the of the M-H recruitment curve, and to examine the consistency of the maximum M-wave response (M-max) over the course of the experiment.

Kinematics

Joint range of motion (ROM) at the elbow ($n = 8$) was collected using light weight electro-goniometers (Biometrics Ltd., Gwent, U.K.) during all movement trials. Calibration data were collected at each speed with both large and small crank lengths.

EMG

EMG was recorded using Ag- AgCl bipolar configurations of surface electrodes (Thought Technologies Ltd.) from the left Soleus (SOL), Tibialis Anterior (TA), and Vastus Lateralis (VL) muscles. EMG was also recorded from the left Anterior Deltoid (AD) muscle during all experimental trials except during contralateral arm cycling when EMG from the right AD was recorded. Bipolar configurations of surface electrodes were used and the area over the muscle site was cleaned with rubbing alcohol prior to application. Individual ground electrodes were placed over bony landmarks near each muscle.

Data Acquisition and Analysis

Data were sampled at a rate of 2000 Hz with a 12- bit A/D converter controlled by a custom- written Lab-View (National Instruments, Austin, Tx. USA) computer program. For all conditions 15 sweeps (50-60 ms sweeps with a 20 ms prestimulus window) were collected. M-waves were also averaged and normalized to the M-max value. EMG signals were preamplified with a gain of 5000, band pass filtered at 100-300Hz (P511 Grass Instruments, AstroMed Inc.) and full wave rectified except for the Soleus muscle which was preamplified by 500 times and remained unrectified. Soleus H-reflex data were analyzed for peak to peak amplitudes and results were averaged and normalized to M-max of the individual data. The prestimulus EMG was used as a measure of muscle activity at the time of nerve stimulation. Maximum voluntary contractions (MVCs) were obtained for the SOL and TA and used for normalization of prestimulus SOL and TA EMG amplitudes. Kinematic data were calibrated to manually measured angles of joint movement during trials with large and small crank lengths.

Statistics

STATISTICA (StatSoft, Tulsa, OK., USA) was used to perform repeated measures analyses of variance (ANOVA) for all data to identify significant main effects and interactions of the independent variables on the amplitude of the Soleus H-reflexes, M waves, and prestimulus EMG levels. Separate analyses were conducted for each experimental hypothesis: 2 task (static, bilateral) x 4 condition (3, 6, 9, 12 o'clock positions); 4 condition (static, bilateral, ipsilateral, contralateral); and 2 task (1 Hz, 2 Hz) x 2 condition (short CL, long CL). Tukey's *HSD post hoc* tests were used to identify the significant main effects. Student's t tests were used to examine differences between the M-max values pre and post cycling trials as well as differences between the crank lengths and the movement frequencies. Additionally, the Students t test was used to examine differences between the static condition and the movement trials associated with frequency and arm excursion (crank length). Descriptive statistics included means ± standard error of the mean *(SEM)*. Statistical significance was set at $p < 0.05$.

Results

EMG

SOL, TA and VL EMG were not significantly different among conditions except during the 2 Hz cycling with a large crank length (see Table 1). In this condition, the TA and the VL EMG was larger than during the control or the other arm cycling trials (main effect for frequency of movement (TA: $F(1) = 9.33$, $p <.05$; VL: $F(1) = 9.24$, $p < .05$), and crank length (TA: $F(1) = 6.62$, $p < .04$; VL: $F(1) = 10.98$, $p < .05$). Interaction between frequency of movement and crank length (TA: $F(1) = 6.12$, $p < .05$; VL: $F(1) = 9.07$, $p < .02$)). Post hoc analysis showed significant differences for TA and VL between the bilateral arm cycling (large crank length) at 2 Hz and all other conditions ($p < .05$).

CONDITION	SOL (%MVC)	TA (%MVC)	VL (uV)
Static control	4.19 ± 0.59	0.46±0.11	1.67 ± 0.93
bilateral 1Hz large	3.99 ± 0.74	0.38±0.08	2.12 ± 1.35
bilateral 1 Hz small	4.39 ± 1.13	0.37±0.07	1.87 ± 1.32
bilateral 2 Hz large	4.45 ± 0.98	**1.50±0.43 ***	**7.85 ± 2.10 ***
bilateral 2Hz small	4.15 ± 0.71	0.46±0.08	2.38±1.32
ipsilateral 1 Hz large	4.07 ± 0.62	0.41±0.08	1.78± 0.92
contralateral 1 Hz large	4.01 ± 0.72	0.41±0.09	1.69±0.93

Table 1. SOL, TA and VL EMG during static and arm cycling conditions. Soleus and TA are measured as a percentage of MVC. VL is not normalized. * denotes significant differences among conditions.

Stationary/Static Control Trials

Analysis of the averaged pre, mid and post cycling static trials showed that there were no significant differences between the Soleus H–reflexes, M-waves or the prestimulus EMG amplitudes ($p > .05$). Thus, these three static trials were averaged and used as one control for the arm cycling movement trials. Analysis of the pre and post cycling recruitment curves showed that the M-max values did not change significantly ($p > .05$) over the experiment.

Rhythmic Arm Movement Trials

1) Effect of phase of arm movement

The effect of arm position on the Soleus H–reflex amplitude during static and arm cycling trials is shown in Figure 3. The bars show static (black) and arm cycling (grey) reflex amplitudes as a percentage of the M-max at four phases of the movement cycle. There was no significant effect of the arm position on the suppression of the H-reflex ($p > .05$). However, at each phase of movement reflex amplitudes were consistently lower during cycling compared to static conditions (main effect for task, $F(1) = 46.48$, $p < .05$). Post hoc significant differences ($p < .05$) are indicated by the asterisks in Figure 3. Both M-wave amplitudes and prestimulus EMG levels were not significantly different among phases of the cycle or among static and arm cycling conditions ($p > .05$).

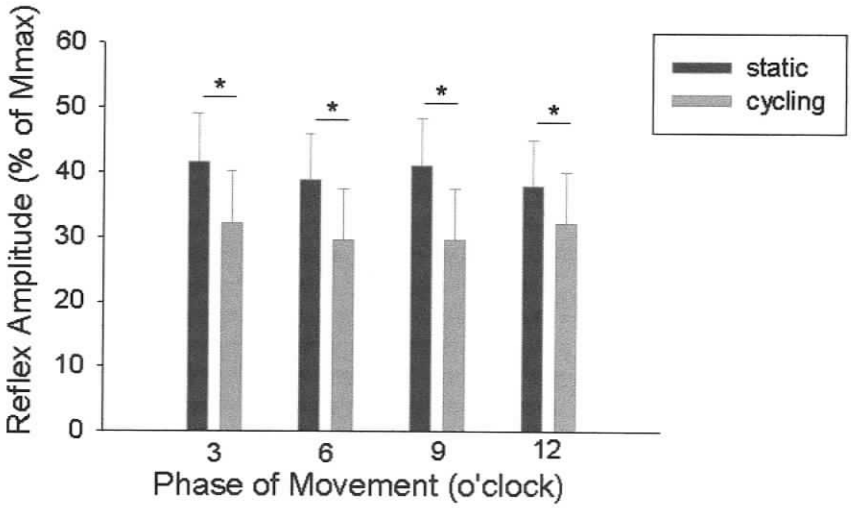

Figure 3. Soleus H-reflex peak to peak amplitudes at four phases of the movement cycle. Reflex amplitude is expressed as a percentage of the maximum M wave amplitude (M_{max}). Values are means across all participants (*n* = 8) ± *SEM.* Statistical differences (*) were found between the static and cycling tasks but not between phases of the movement.

2) Locus of arm movement: bilateral vs. unilateral arm cycling

The effect of bilateral and unilateral arm cycling on the amplitude of the Soleus H-reflex is shown in Figure 4 as a percentage of the static control amplitude. The Soleus H-reflex was suppressed compared to the static condition during the bilateral, ipsilateral and contralateral arm cycling conditions (main effect for task, F(3) = 14.19, $p < .05$). Post hoc differences ($p < .05$) are indicated by the asterisks in Figure 4. However, no significant differences were found among the three cycling conditions. That is, the suppression of the H-reflex amplitude was similar regardless of the type of arm movement. M-wave and prestimulus EMG amplitudes were not significantly among between cycling conditions.

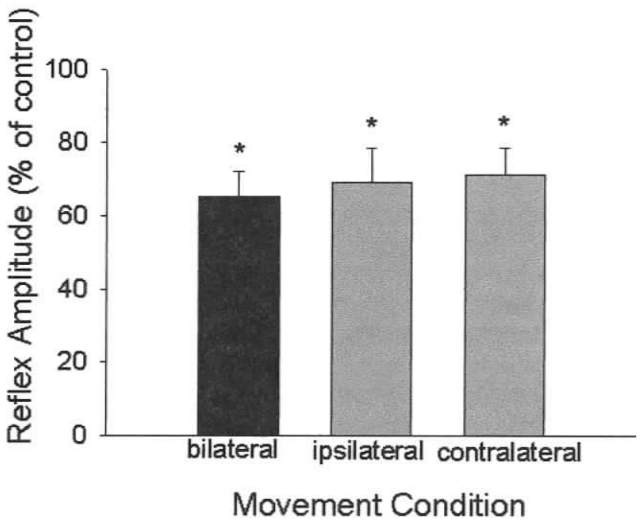

Figure 4. Soleus H–reflex peak to peak amplitude during bilateral and unilateral (ipsilateral and contralateral) arm cycling conditions. Reflex amplitude (bilateral – black bar; unilateral – grey bars) is expressed as a percentage of the static control condition and recorded at the 3 o'clock arm position during arm cycling. Values are means across all participants (n = 10) ± *SEM*. (*) denotes significant differences between the static control and arm cycling conditions.

3) Range of motion and frequency of movement

Figure 5A shows an example of the change in elbow joint angle across the movement cycle (starting at the 3 o'clock position) for the large (solid line) and small (broken line) crank lengths, and for 1 Hz (black line) and 2 Hz (grey line) frequencies of movement. At the 3 o'clock position, the elbow angle changed significantly ($p < .05$) by 28 ± 11(mean ± standard deviation (*SD*)) degrees between the large and small crank lengths at 1 Hz. There was no significant difference in this excursion between the 1 and 2 Hz cycling conditions ($p > .05$). The average change in the range of motion (ROM) of the elbow (3 o'clock to 9 o'clock) between the large and small crank lengths was 70 ± 5 (mean ± *SD*) degrees. There was also no significant difference between the frequencies of movement (1 or 2 Hz) at similar crank lengths ($p > .05$).

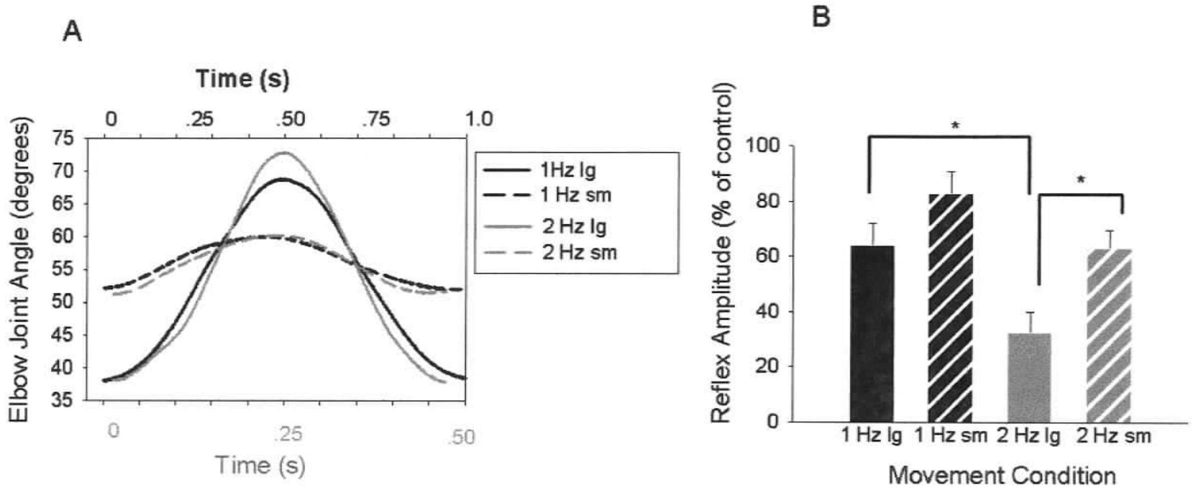

Figure 5. A) Single participant elbow joint kinematics for one cycle of movement during arm cycling at 1 Hz (black lines) and 2 Hz (grey lines) at large (lg) (solid lines) and small (sm) (dashed lines) crank lengths. The top scale represents time taken for 1 movement cycle at 1 Hz; the bottom scale represents time taken for 1 movement cycle at 2 Hz. **B) Soleus H–Reflex peak to peak amplitude due to changes in movement frequency and crank length.** Reflex amplitude is expressed as a percentage of the static control condition and recorded at the 3 o'clock arm position. 1 Hz (black bars) and 2 Hz (grey bars) conditions with large (lg) crank lengths (solid bar) and small (sm) crank lengths (diagonal line bar) are examined. Values are means across all participants ($n = 8$) ± *SEM.* (*) denotes the significant differences between cycling conditions.

The effect on the Soleus H-reflex amplitude from changes in crank length at two frequencies of movement can be seen in Figure 5B. The reflex amplitude at large (solid bars) and small (diagonal line bars) crank lengths and during 1 Hz (black bars) and 2 Hz (grey bars) cycling is shown as a percentage of the static control. Reflex amplitudes for all cycling conditions were lower than during static contraction ($p < .05$). A main effect among movement conditions ($F(3) = 7.32$, $p < .05$) was found. Post hoc analysis showed no difference between the reflex amplitude with the large and small crank lengths during 1 Hz cycling, but a significant difference was seen between the reflex amplitude with the large and small crank during 2 Hz cycling ($p < .05$). As well, there was no significant difference between the reflex amplitude with 1 and 2 Hz cycling with a small crank length, but a significant difference was seen at the large crank length ($p < .05$). This is highlighted in Figure 6 which shows single subject data. M-wave amplitude and Soleus prestimulus EMG were consistent between trials. However, the prestimulus EMG levels for TA and VL during the 2 Hz cycling with a large crank length condition was significantly different ($p < .05$) than during the other conditions (see Table 1 and EMG results above).

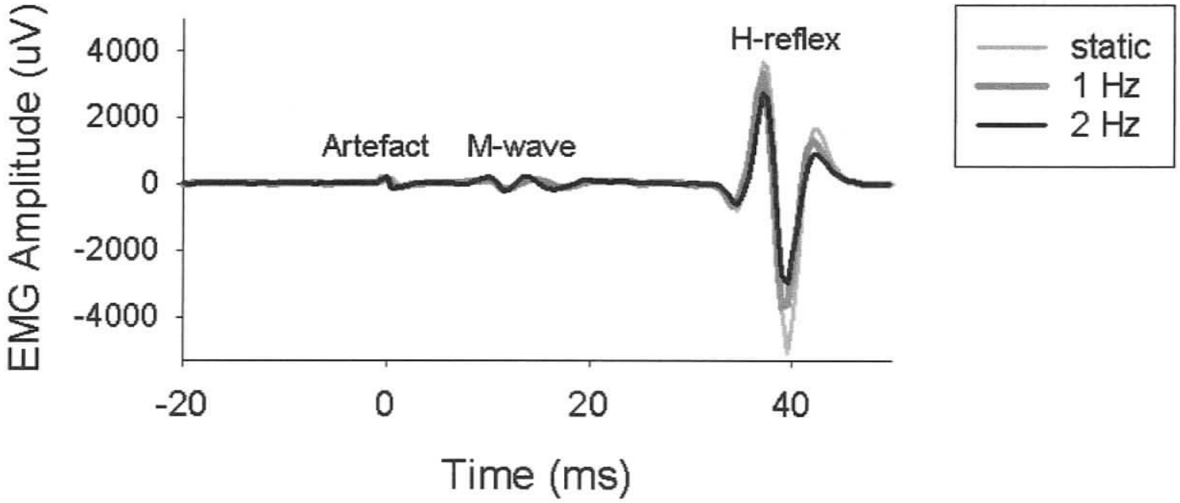

Figure 6. Suppression of the Soleus H-reflex amplitude with 1 Hz and 2 Hz arm cycling in a single participant. Average of 15 sweeps of data during static (grey line), 1 Hz arm cycling (dark grey line), and 2 Hz arm cycling (black line) recorded at the 3 o'clock arm position. The stimulus artefact, M-wave and the H-reflex is indicated.

Discussion

In the present study we found that specific features of arm cycling (phase of the cycle, locus of arm movement) do not produce specific modulation of the Soleus H-reflex. Instead, there is a general suppressive effect on the reflex related to the task of rhythmic arm movement. Additionally, the frequency and the range of the arm movement influence the modulation of the reflex suppression. The data support the working hypothesis that rhythmic arm movement creates a relatively non-specific signal of generalized activity that is then transferred to leg muscles.

Methodological Considerations

As an indirect reflection or to gauge similar stimulus input to activate the Ia afferents, the M-wave amplitude (as a percentage of M-max) was kept constant between conditions. Thus, it is assumed that a change in the H-reflex motor response was not due to a change in the afferent volley which evokes the reflex output (Swett & Bourassa, 1981; Abbruzzese, Berardelli, Rothwell, Day, & Marsden, 1985; Brooke et al., 1997; Zehr, 2002) or the stimulus input. Additionally, because it had been suggested by Crone et al. (1990) that M-max may change over the course of an experiment, recruitment curves were gathered before and after each experiment and analyzed for stability of the maximum M-wave. As well, three static control trials were incorporated into the experiment (pre, mid and post) to monitor the stability of the control H-reflex amplitude. However, no significant changes were found between the pre and post experiment M-max amplitudes, or between control H–reflex amplitudes. Therefore, the changes observed in H-reflex amplitude were not likely due to a change in the stimulus input. Additionally, it is recognized that although reflex suppression during movement occurs similarly on the ascending limb, descending limb and at the maximum point of the H curve (Zehr, Hesketh, & Chua, 2001; Zehr et al., 2003), data were collected on the ascending limb only.

Although participants were seated in a chair that prevented movement of the trunk, legs, and ankle during arm cycling, EMG was collected from the TA and VL muscles during all experimental conditions to monitor possible heteronymous effects of local muscle activity (Pierrot-Deseilligny, Morin, Katz, & Bussel, 1977; Iles & Roberts, 1987; Crone & Nielsen, 1994; Pierrot-Deseilligny & Mazevet, 2000). No difference was seen in the EMG among trials except in the 2 Hz, large crank length condition. Here, the prestimulus EMG for TA and VL was significantly larger than that observed in the other movement or static conditions (refer to Table 1). Specifically, although the TA and VL EMG increased by almost 400% during the 2 Hz (large crank length) cycling condition, the actual contraction level was very low (1.5% of MVC and 7.9 uV respectively). As well, it has been shown that during walking the major factor in the suppression of the Soleus H-reflex observed is not the cocontraction of the ankle muscles (Yang & Whelan, 1993). It is not likely, then, that the TA contributed to the H-reflex change in amplitude. Further, H-reflex suppression was observed in spite of a potential heteronymous facilitation from the knee extensors (as suggested by elevated VL activity) (Hultborn, Meunier, Morin, & Pierrot-Deseilligny, 1987; Meunier, Pierrot-Deseilligny, & Simonetta, 1993). All reflexes were evoked during voluntary activation of the target muscle. Although facilitation of the H–reflex that occurs (due to reduced presynaptic inhibition) with a voluntary contraction of the test muscle (Pierrot-Deseilligny et al., 1977), tonic contraction of the test muscle also serves to decrease the variability of the H–reflex amplitude (Burke, Adams, & Skuse, 1989) and give a relative value to the state of the motoneuronal pool (Schieppati, 1987; Burke et al., 1989). In this experiment, a constant level of plantar flexion (average 4.18 ± .07 % MVC) was maintained for each experimental condition and there were no significant differences found between trials. Therefore any changes in reflex amplitude could not be directly related to the Soleus contraction level.

Supraspinal inputs, that may affect the Soleus H–reflex, act through spinal interneurons (McCrea, 1996) and modulate the level of presynaptic inhibition expressed at the Ia afferent. Vestibular inputs, postural and state related changes (Schieppati, 1987) were minimized by maintaining a similar *postural set* and *level of intent* for all static and cycling trials. As well, voluntary contraction of the test muscle, which lowers the Renshaw cell activity directed to the muscle motoneurons (Pierrot-Deseilligny et al., 1977), was kept constant through all experimental trials. Thus it is unlikely that supraspinal effects, apart from those possibly arising from the movement itself, confounded the results of this experiment.

Reduced neurotransmitter stores, due to repeated stimulation of the presynaptic terminal, may lead to depression of the H-reflex response (Hultborn et al., 1996). In fact it has been recommended to maintain at least 3 seconds (Rossi-Durand, Jones, Adams, & Bawa, 1999) between stimulations to the mixed nerve during H-reflex testing. Because of the relatively low number of stimuli (15 per trial), we maintained 2-5 seconds between stimuli, and had a 3-minute interval between trials. Thus, it is not likely that the suppression of the H-reflex seen in this study was due to effects of post activation depression.

In summary, we are confident that the effects discussed below are due to the task of rhythmic arm cycling only and are not due to confounding methodological factors.

Is There Phase–Dependent Modulation of Soleus H-reflex Amplitude Evoked by Rhythmic Arm Cycling?

We have shown that there were no significant differences in the Soleus H-reflex amplitude related to the phase of arm movement in which it is evoked (refer to Figure 3). This confirms and extends earlier work by Frigon et al. (2004) who also found no differences in the Soleus H-reflex amplitude measured at two phases of the cycle. Further, in static positioning across the movement cycle we found no alteration of H-reflex amplitude. The results are in opposition to those early studies which found significant Soleus H-reflex facilitation during shoulder flexion (comparable to our 3 o'clock position) and significant inhibition during shoulder extension (comparable to our 9 o'clock position) (Delwaide et al., 1977; Eke-Okoro, 1994). These previous studies had a lack of adequate experimental control related to stimulus delivery and muscle activity which may be the reason for the discrepancy.

Interestingly, the lack of interlimb phase dependency of the Soleus H-reflex during arm movement found in this experiment is different than results found during rhythmic movement studies in which the H-reflex is examined in the moving limb. There is strong evidence of phase modulation in the ipsilateral and contralateral Soleus H-reflex during leg cycling (Brooke et al., 1997) and in the ipsilateral FCR H-reflex during arm cycling (Zehr et al., 2003) which shows specificity in response of the moving limb. Phase modulated responses were also found in hindlimb muscles of cats, during walking, in response to intracellular afferent stimulation of mixed and cutaneous nerves in the forelimbs (Schomburg, Roesler, & Meinck, 1977; Miller & Scott, 1977; Schomburg et al., 1978). Human research has also demonstrated phase dependency in the TA muscle, during 1 Hz walking, in response to cutaneous nerve stimulation in the arm (Haridas & Zehr, 2003). However, although these studies give evidence for interlimb connections, cutaneous reflex pathways are not comparable to those of the H-reflex (Zehr et al., 2001) used in this study. Moreover, the walking studies do not isolate the specific effects of rhythmic arm movement on the reflex modulation in the legs and thus are not directly comparable to the current work. Possibly, the interaction of the arms and legs moving together may be required to observe interlimb phase dependency. We also acknowledge that, in this study, Soleus H-reflexes were only sampled at 4 phases in the cycle. Thus we cannot exclude the extremely small possibility that effects of phase modulation may be seen at phases other than those sampled here.

Does the Locus of Rhythmic Arm Movement Matter?

This study has shown that bilateral and unilateral arm cycling suppressed the Soleus H-reflex equivalently. That is, rhythmic activity of either or both arms evoked similar suppression of the H-reflex. This contrasts with observations between limb pairs (e.g. between the arms and legs), where specific effects of bilateral versus unilateral cycling have been found. During leg cycling, bilateral and ipsilateral cycling had a greater suppressive effect than contralateral cycling on the Soleus H-reflex (McIlroy et al., 1992; Brooke et al., 1997). This suppression was attributed to central mechanisms (CPG and supraspinal) that modulated the peripheral feedback from both legs (McIlroy et al., 1992; Brooke et al., 1997; Cheng et al., 1998; Schneider, Lavoie, & Capaday, 2000). This strong coupling between the two legs is thought to be important for stability and coordination during locomotion (Zehr & Stein, 1999b). In contrast, during arm cycling, only bilateral and ipsilateral movement resulted in Flexor Carpi Radialis (FCR) H-reflex modulation (Zehr et al., 2003). As well, the suppression of the reflex was less during ipsilateral cycling compared to bilateral arm cycling (Zehr et al., 2003). It was suggested by these authors that there is less gating of the reflexes between the arms in comparison to the legs, which would allow for the greater independence between arm movements. The result of task dependence in the current experiment gives evidence that both bilateral and unilateral arm cycling have a general effect of reflex suppression in the legs. The lack of any difference between bilateral or the unilateral arm cycling conditions confirms a lack of specificity in the neural coupling between the arms and the legs when the legs are not moving. Of note, however, is the suppressive effect of the contralateral arm movement on the stationary Soleus H-reflex which gives evidence of a crossed effect between opposite arms and legs. This may be expected during walking due to the antiphase coordination of the arms and legs observed during customary walking frequencies (Donker et al., 2001), and is found in both reduced cat and rat preparations (Forssberg et al., 1977; Juvin et al., 2005).

Is There an Effect of Range of Movement or Rate of Movement?

Effects on the Soleus H-reflex during arm cycling at 1 and 2 Hz with small and large crank lengths were analyzed to elucidate whether the frequency of movement or the range of movement from the arms was a more important contributor to the reflex suppression observed. It has been suggested that muscle spindle stretch of the local heteronymous and contralateral muscles of the moving limb during rhythmic locomotion is an important factor in H-reflex amplitude suppression (McIlroy et al., 1992; Cheng, Brooke, Misiaszek, & Staines, 1995; Brooke et al., 1997; Cheng et al., 1998; Zehr et al., 2003). In the current experiment, the change in elbow range of motion (ROM) due to the difference in the crank length was used as an indirect measure of the change in muscle length and subsequent muscle spindle stretch. Muscle spindle stretch is associated with firing of the group1a and II afferent fibres which are directly associated with the H-reflex pathway. Similarly, increased frequency of movement may be directly associated with an increase in the rate of spindle stretch with a subsequent increase in afferent discharge of the Ia fibres (Capaday & Stein, 1987; McIlroy et al., 1992). If the change in spindle fibre length was a dominating factor in the reflex suppression during arm cycling, it would follow that there would be significant differences between the large and small crank lengths at both frequencies of movement. However, the reflex amplitude was significantly different between the large and small crank lengths only when cycling at 2 Hz (see Figure 5B). Similarly, if the rate of spindle stretch was a dominating factor in the reflex suppression during arm cycling, it would follow that there would be significant differences between 1 and 2 Hz cycling conditions at both crank lengths. However, the reflex amplitude was only significantly different when the crank length was large (see Figure 5B). This suggests that both the amount of stretch and the rate of stretch of arm muscles are important in the Soleus H-reflex modulation. That is, at larger crank lengths (that result in greater change in ROM), and at higher frequencies of movement (that result in a greater rate of change of ROM) there is a greater suppression of the Soleus H-reflex. Suppression of the H-reflex pathway due to an increase in spindle stretch is well documented (see above). Suppression of the H-reflex during higher frequencies of movement may function to avoid saturation of the motoneuron pool during a greater output (Capaday & Stein, 1987), and allow continued modification of afferent feedback (McIlroy et al., 1992). The suppression at higher frequencies may also result from an increase in cortical control related to a putative increase in the physical and mental requirements of maintaining high speeds (Honore, Demaire, & Coquery, 1983; Grillon & Zarifian, 1985; Llewellyn, Yang, & Prochazka, 1990). Alternatively, the suppression at the higher frequency of movement may result from an increase in the spinal control of rhythm generation.

It was not apparent from analysis of the data if the afferent input that resulted from a change in the muscle length or from the rate of change of muscle length affected the Soleus H-reflex, as we did not have a direct measure of spindle stretch. In an attempt to elucidate further these effects, we calculated the ratio of the change in ROM (from the kinematics data) to the time to complete 1 cycle of movement. This analysis can be seen in Figure 7 and, if compared to Figure 5B, shows a similar relationship to the pattern of suppression of the Soleus H-reflex. That is, in conditions where the ROM/s was larger (large crank lengths), the reflex suppression was similarly larger; and in conditions where the ROM/s was smaller (small crank lengths), the reflex suppression was smaller. Importantly, there is a significant difference between the ROM/s between the large and the small crank lengths at the same frequency of movement condition (i.e. 1 Hz large and 1 Hz small; 2 Hz large and 2 Hz small) which could suggest a difference in stretch is occurring between the large and small crank lengths. As well, there is no significant difference between the ratio of change in ROM to time in the 1 Hz small condition and the 2 Hz small conditions (which is in opposition to the large ROM conditions). This may be a reason for the lack of difference between the H-reflex suppression in the same two conditions, and give evidence for the importance of ROM, or muscle stretch in the modulation of interlimb H-reflexes.

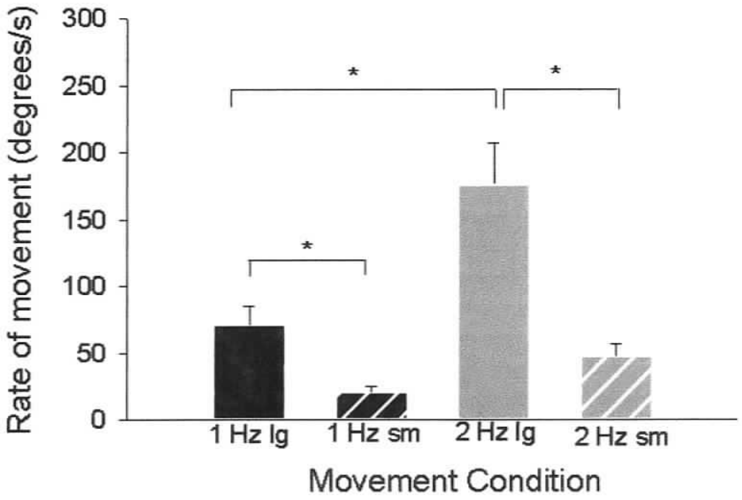

Figure 7. Ratio of change in elbow ROM (degrees) to time taken for 1 cycle of movement (seconds) during arm cycling conditions. Elbow ROM is from the 3 o'clock position to the 9 o'clock position and time is that taken to complete 1 cycle of movement. 1 Hz (black bars) and 2 Hz (grey bars) conditions are compared to large (lg) crank length (solid bar) and small (sm) crank length (diagonal line bar). Values are means across all participants ($n = 6$) ± *(SEM)*. (*) denotes the significant differences between cycling conditions.

Possible Sources of Reflex Suppression

Spinal, supraspinal and peripheral inputs may all have an influence on the modulation of the Soleus H-reflex pathway during arm cycling. It has been suggested that spinal mechanisms (e.g. the CPG) associated with coordination between the arms and between the legs are directed by peripheral and supraspinal inputs to insure coordinated and flexible motor responses during locomotion (Duysens & Van de Crommert, 1998; Dietz, 2003; Zehr & Duysens, 2004).This is evident in the cat model during fictive locomotion where PSI is evident in the absence of movement (Gossard, Cabelguen, & Rossignol, 1991). Long propriospinal neurons that run between cervical and lumbar segments have been found in humans (Nathan, Smith, & Deacon, 1996) and are thought to connect the rhythm generating mechanisms within the spinal cord (Duysens & Van de Crommert, 1998). Thus, it is plausible that the rhythm of arm cycling, as well as the afferent input from the arms, may use this pathway to modulate reflex responses in the legs. The greater effect on the Soleus H-reflex with 2 Hz cycling compared to 1 Hz cycling in this experiment implies a change in rhythm generation. However, the lack of phase modulation found in this experiment does not give implicit evidence for a CPG which would theoretically yield phasic changes. This result of interlimb observations is different to previous work that showed phase relationships and specific modulation of H-reflex responses due to movement of the bilateral and the ipsilateral arm(s) during arm cycling (Zehr et al., 2003) and leg(s) during leg cycling (Brooke et al., 1997). The coupling of cervical and lumbar regions, specifically the CPG, has recently been examined in isolated spinal cords of neonatal rats (Juvin et al., 2005) and may give some insight to our results. It was found that, although the cervical and lumbar regions had independently functioning CPG's, the phase modulation of interlimb EMG responses involved a caudorostral excitability gradient from the lumbar CPG to the cervical CPG via propriospinal neurons. Moreover, when the two spinal regions were decoupled, the cervical generators were unable to elicit lumbar, phase-related, locomotor activity. These results may help to explain the lack of specificity of reflex suppression found in the current experiment if indeed humans retain some of the circuitry found in the quadruped (Dietz, 2002; Zehr & Duysens, 2004). But, because an isolated spinal cord during fictive locomotion, as used by Juvin et al. (2005), is not influenced by peripheral input, the results are not fully transferable to this research. The current results infer that a general suppression of the Soleus H-reflex, in the stationary leg, is caused by rhythmic cycling of the arms. This influence most likely controls the motor output at a presynaptic level (Frigon et al., 2004) through excitatory or inhibitory interneurons.

Local peripheral inputs such as muscle spindle stretch are well known to synapse onto presynaptic pathways within the spinal cord and thus modulate the motoneuron response in the test muscle during rhythmic locomotion (Capaday & Stein, 1986; Misiaszek, Brooke, Lafferty, Cheng, & Staines, 1995; Brooke, Cheng, Misiaszek, & Lafferty, 1995). Results from the current experiment give support that there are strong effects of afferent input on the H-reflex modulation. Whether these remote muscle spindles act directly through PSI on the Soleus H-reflex pathway during arm cycling, or act indirectly via a spinal CPG is unknown. Changes in the range of the arm movement and the rate of the arm movement will affect muscle spindle length and rate of stretch and have been found to be a main contributor to the suppression of the H-reflex during locomotor-like movement of the canine leg (Misiaszek, Barclay, & Brooke, 1995). However, other peripheral inputs such as cutaneous, tendon and joint afferents associated with the arm movement cannot be ruled out as contributors to the change in PSI on the Soleus H-reflex pathway (Zehr, 2002; Misiaszek, 2003).

Finally, supraspinal pathways may have influenced the presynaptic inhibitory (PSI) pathway during the voluntary contractions of homologous (Valls-Sole, Alvarez, & Tolosa, 1994; Iles, 1996) and remote muscles (Zehr & Stein, 1999a). Homologous voluntary muscle activity in this experiment was kept at a constant level and thus changes in the Soleus H-reflex amplitude can not be attributed to this supraspinal source. There has been suggestion that suppression of the Soleus H-reflex during high rates of leg cycling may occur due to an increase in the central control in response to an increase in the physical and mental requirements of maintaining high speeds (Honore et al., 1983; Grillon & Zarifian, 1985). This can not be completely ruled out in this experiment although the mental requirement of cycling may have been minimized with the use of practice (Nelson, Brooke, McIlroy, Bishop, & Norrie, 2001). Recently, Carroll, Baldwin, Collins, & Zehr (2006) used sub threshold transcranial magnetic stimulation (TMS) to examine the supraspinal influence on the modulation of FCR H-reflexes during arm cycling and found that the TMS facilitated H-reflexes (at one position in the movement cycle) during tonic contractions but not during cycling. This gives evidence for a pathway, other than a corticospinal one, that is active during rhythmic locomotor activity of the arms. It does not rule out other potential pathways between the arms and legs (i.e. interlimb reflex pathways).

Functional Implications

The results of the current experiment suggest that there is a general suppression of the stationary Soleus H-reflex during arm cycling, irrespective of specific arm movement parameters. In contrast to suppression that occurs in the arm due to arm cycling, or in the leg due to leg cycling (Brooke et al., 1997; Zehr et al., 2003), both the contralateral and ipsilateral arm movement suppresses the Soleus H-reflex to the same extent. Although this gives evidence for a crossed effect, the lack of phase dependence suggests this may not reflect a connection between arm and leg coordination. Evidence of specific effects of arm conditioning on either leg EMG or reflex modulation is derived from experiments where the arms and legs are moving at the same time (Dietz, Fouad, & Bastiaanse, 2001; Haridas & Zehr, 2003; Huang & Ferris, 2004; Kao & Ferris, 2005). Thus, it is possible that a different result may be observed if the legs were cycling at the same time as were the arms. The robust effect of movement frequency observed in this experiment may be an indicator, as well, that at faster frequencies of movement more specific effects (phase dependency, crossed effects) would be apparent or may emerge. Certainly the coupling of antiphase arm and leg movement is less variable at higher walking speeds (Donker et al., 2001). This would make functional sense when comparing running to walking. The arms are not functionally a requirement for human locomotion at a slow frequency of movement. In fact, the arms are often used for activities other than arm swing during slow gait. This is not the case during running when it becomes more difficult for the arms to remain independent of the legs. It is dissimilar to the quadruped where specific afferent input is relayed from the fore to the hindlimbs in a phase related manner to control coordination and maintain stability during all locomotion (Miller et al., 1975; Grillner, 1975). A goal of further research may be to examine the Soleus H-reflex for phase dependence and crossed effects with respect to rhythmic arm movement 1) when the legs are moving and 2) at a high frequency of movement (e.g. 2 Hz).

The results of this experiment also give a basis for speculation on strategies used in rehabilitation. Rhythmic arm movement is likely an important mechanism to access the general neural circuitry between the arms and legs during locomotor retraining in a neurologically intact population. Specific interactions between the arms and legs, however, may not be accessible when the legs are stationary. As well as the goals for research mentioned above, examination of the Soleus H-reflex amplitude modulation during rhythmic arm cycling in a neurologically impaired population (e.g. stroke or spinal cord injured) will be important to further specify rehabilitation strategies.

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