Relative Contributions from the Arms and Legs to Cutaneous Reflex Modulation in the Legs During a Combined Rhythmic Task

by

Jaclyn Elise Balter
B.Sc., Indiana University, 2003

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

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University of Victoria

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ABSTRACT

Evidence suggests that a flexible, task-dependent neuronal coupling of the upper and lower limbs exists, and this allows for coordinated rhythmic movement (e.g., locomotion). To further understand this coupling, muscle activity and reflex patterns can be examined by stimulating peripheral nerves during various tasks. In particular, cutaneous reflexes demonstrate task- and phase-dependent modulation, making them highly sensitive probes into neural activity during rhythmic movement. The purpose of this research was to use reflex modulation to probe the neuronal coupling between the arms and legs. This was done using a cycling paradigm that allowed for the separation of arm and leg movement, which is difficult to do in most forms of locomotion (i.e., walking). Participants (N=14) performed three cycling tasks: 1) arm cycling with stationary legs (ARM); 2) leg cycling with stationary arms (LEG); and 3) combined arm and leg cycling (ARM&LEG). The relative contributions from the arms and legs to reflex modulation in the legs were then determined throughout the movement cycle. It was hypothesized that the individual contributions from arm and leg movement to reflex amplitudes in the legs would summate during the combined arm and leg task. This hypothesis was tested explicitly by comparing the reflex amplitudes expressed during the combined arm and leg task to the algebraic summation of the reflex amplitudes expressed during the arm cycling and leg cycling tasks alone. Static trials were also collected at 4 positions within each task. Tasks were performed under two different cycling conditions: 1) Focused tibialis anterior (TA) contraction (FCC) (N=14); and 2) normal cycling (NC) (n=8). During all trials, stimulation was delivered pseudorandomly throughout the movement cycle to the superficial peroneal nerve at the ankle. EMG was recorded bilaterally from muscles in the arms and legs, and kinematic data were obtained from the elbow and knee joints. Results focused on the middle latency reflex amplitudes in TA (ipsilateral to the site of stimulation) during the FCC condition because the focused contraction did not significantly alter EMG or reflex activity in the other leg muscles studied. This also allowed for comparisons among tasks at comparable EMG levels. The main finding from this study was that reflex amplitudes expressed during the ARM&LEG task agreed with the predicted algebraic summation of reflex amplitudes expressed during
the ARM and LEG tasks separately. Examination of the relative contributions from the arms and legs to the reflexes expressed during the combined task revealed that across all movement phases the legs accounted for 33% (p < .05) of the variance observed during the ARM&LEG task, while the arms accounted for an additional 5% (p < .05). The relative contributions from the arms and legs were also found to be phase dependent. That is, the relative contribution from the arms was dominant during the power phase of leg cycling while the leg contribution was dominant during the recovery phase. More specifically, the greatest contribution from the arms accounted for 57% of the variance in the ARM&LEG task when the leg was at 11 o’clock (p < .05) and the greatest contribution from the legs was 71% of the variance accounted for when the legs were at 9 o’clock (p < .05). Additionally, characteristic patterns of reflex amplitude modulation (i.e., phase- and task-dependent modulation) were observed during most of the cycling tasks. In conclusion, these findings suggest evidence for a neuronal coupling between the rhythm generators responsible for arm and leg movement which is functionally gated throughout the movement cycle of a combined arm and leg task.
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DEDICATION

I would like to dedicate this thesis to my family, with love.
CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

Locomotor tasks such as walking, running, and swimming require a coordinated movement of the arms and legs for the individual to move effectively and maintain balance. Evidence suggests that a flexible, task-dependent neuronal coupling of the upper and lower limbs exists (Dietz, Fouad, & Bastiaanse, 2001). This coupling can be defined as measurable effects of movement of one limb upon background or reflex muscle activity in another limb. For example, the effect of arm movement upon reflex activity in the legs. However, the relative contributions from the arms and legs to the reflex patterns and neural control expressed during a combined rhythmic task have yet to be determined.

Since few studies have examined this neuronal coupling directly during coordinated movement (e.g., locomotion), the specifics of the interaction between the arms and legs remains unclear. Burke (1999) suggests that reflex modulation patterns can be used as a neural probe into the nervous system during movement (Burke, 1999). In particular, cutaneous and Hoffmann (H-reflex) reflexes have been shown to demonstrate task- and phase-dependent modulation, making them highly sensitive probes into neural activity during movement.

This review of literature will focus on previous research that has examined muscle activity and reflex modulation patterns indirectly by the stimulation of peripheral nerves during various tasks to elucidate the interlimb pathways responsible for this neuronal coupling. Additionally, evidence for interlimb reflexes, defined as responses occurring in a limb where the stimulus was not directly applied, will be discussed in terms of their functional relevance to movement. The following sections address in turn: the pathways responsible for this coupling; reflex modulation in these pathways during arm, leg, and combined arm and leg movement; and the possible mechanisms that regulate transmission within these pathways during movement. The focus will be on human studies, although much of the groundwork comes from experiments on other animals.

Early Evidence for Interlimb Pathways

Animal Studies

Sherrington (Sherrington, 1910) was the first to examine interlimb reflexes in spinalized and decerebrate cats. These cats demonstrated fictive locomotion in the
absence of afferent feedback. Although, it was not until later that the interlimb pathways responsible for such coordination were investigated further.

Research in cats suggested a linkage between rhythmic hind- and forelimb movements resulting in coordinated locomotor movement (Miller, Van Der Burg, & Van Der Meche, 1975). Examination of spinalized cats found that stimulation of nerves innervating the hindlimbs evoked reflexes in the forelimbs. Within a stepping pattern during walking, it also appeared that flexors and extensors were reciprocally organized. This can be explained by spinal interneurons that traverse several segments and terminate within the spinal cord (i.e. propriospinal projections). Both ascending (Gernandt & Megirian, 1961) and descending (Skinner, Adams, & Remmel, 1980) pathways appear to link the cervical and lumbar regions of the spinal cord, and assist in this interlimb coordination in quadrupeds. Ascending long propriospinal paths facilitate flexion in the forelimbs while descending long propriospinal paths facilitate extension in hindlimbs (Lloyd & McIntyre, 1948). Further research conducted in the cat and monkey showed that neurons of the long descending propriospinal tract (LDPT) are ideally situated for conveying sensory information from the forelimb to elicit reflexes in the hindlimb, and for coordinating motor functions between the two pairs of limbs (Skinner, Coulter, Adams, & Remmel, 1979). It was later suggested that long ascending propriospinal neurons and the ventral spinothalamocerebellar tract provide a direct connection between the cervical and lumbosacral locomotion centers which allows for the coordinated fore- and hindlimb movements observed during stepping in the cat (English, 1989). In summary, it appears that stimulation of fore- and hindlimbs during locomotion causes reflex responses in the opposite homologous limbs. These interlimb reflexes are mediated by long propriospinal neurons connecting the thoracic and lumbar regions of the cat spinal cord.

Coordination of the fore- and hindlimb rhythmic activity appears to be a main characteristic of quadrupedal locomotion (Dietz, 2002). Specialized neural networks (central pattern generators [CPGs]) were suggested to be responsible for this interlimb coordination. The term CPG refers to a functional network of neurons that generate a rhythm and shapes the pattern of motor neuron bursting (Grillner & Wallen, 1985). While it is believed that the commands for initiation and termination of these rhythm generators
are coming from supraspinal levels, feedback from the movement acting directly on the CPG or on motor neurons via reflex pathways controlled by the CPG is crucial in phase transitions during the step cycle (Duysens & Van de Crommert, 1998). Specialized neural networks within the caudal spinal cord were found to organize hindlimb locomotor activity, whereas specialized networks in the rostral spinal cord were found to control forelimb movements. Long propriospinal neurons couple these networks within the spinal cord and allow for the coordination between the two networks (Miller et al., 1975).

Early work examining these spinal locomotor centers was conducted in cats with a transected spinal cord and severed dorsal roots. These cats still showed rhythmic alternating contractions in ankle flexors and extensors which became the basis of the spinal “half-center” model (Brown, 1911). Since then there have been many replications of these early experiments (reviewed by Rossignol, 1996). The most convincing evidence that neural networks in the spinal cord are capable of producing rhythmic output was demonstrated in fictive locomotion (Duysens & Van de Crommert, 1998). In these studies, rhythmic movement was still observed from the CPG in isolation since descending drive and sensory input were absent. More recent work (Juvin, Simmers, & Morin, 2005) was conducted in an isolated spinal cord preparation of neonatal rats. Fictive locomotion was observed and its coordination patterns corresponded to a normal walking gait observed in neurologically intact rats. Additionally, propriospinal connections were examined by decoupling the cervical and lumbar rhythm generators, and this revealed independent rhythmogenic capabilities in the two locomotor regions (Juvin et al., 2005). Furthermore, these authors suggested that a “caudorostral propriospinal excitability gradient” may mediate interlimb coordination between the lumbar and cervical generators (Juvin et al., 2005).

**Human Studies**

Although the extent to which these specific interlimb pathways are present in humans remains unclear, evidence for similar connections exists. Early work (Kearney & Chan, 1979, 1981) demonstrated interlimb reflexes in arm muscles following cutaneous stimulation or displacement of the foot. Displacement of the foot (plantar or dorsiflexion) produced significant reflex amplitudes with short latencies (40-110 milliseconds after displacements), depending upon the direction of the displacement. These findings
allowed the researchers to conclude that interlimb reflex connections of proprioceptive afferents are stronger and more direct than those of cutaneous origin. If this remains the case, then interlimb connections of proprioceptive afferents may play an important role in the coordination of movement. This early work can be compared to “anticipatory postural reflexes” measured in the opposite arm, trunk, and leg involved in supporting the body (Marsden, Merton, & Morton, 1978) and reflexes evoked in ankle muscles (Traub, Rothwell, & Marsden, 1980) following displacement of the arm. It can be concluded from the above studies that ascending reflexes linking arm muscle activity to ankle displacement are organized similarly to the descending reflexes linking the activity of ankle muscles to arm displacement. However, the shorter latencies observed in arm muscles following foot displacement indicate that these descending and ascending reflexes may utilize different pathways (Kearney & Chan, 1981).

Electrophysiological recording of descending lumbar spinal cord potentials (DLCP) following stimulation of the median nerve at the elbow served as the first direct evidence of interlimb reflex action between the arm and leg in man (Sarica & Ertekin, 1985). These researchers concluded that DLCP activity measured at the level of the lumbar spinal cord segments is likely due to the activity of propriospinal descending pathways ipsilateral to the stimulated arm. Furthermore, the observed fast transmission of sensory information from the arm to the lumbar spinal cord is functionally important in the interlimb reflex control of posture and locomotion. Additionally, early physiological evidence seen in animals suggesting that long projecting propriospinal neurons couple the cervical and lumbar enlargements of the spinal cord was later observed anatomically in humans (Nathan, Smith, & Deacon, 1996) although this research appears weak.

Further research examined interlimb reflexes in people with complete spinal cord injuries (Calancie, 1991; Calancie, Lutton, & Broton, 1996). Interlimb reflexes in arm muscles were observed following stimulation of cutaneous nerves in the lower limb in individuals with both acute and chronic motor complete spinal cord injuries. Interestingly, and in contrast to previous work (Kearney & Chan, 1981), no interlimb reflexes were observed in neurologically intact or uninjured persons. The authors suggested that the presence of such interlimb reflexes following spinal cord injury may be due to a release of inhibition from descending centers following the injury.
To clarify some discrepancies between previous interlimb research and these findings by Calancie et al. (1996), interlimb reflexes following stimulation of cutaneous nerves innervating the hand and foot were studied in neurologically intact individuals performing focused contraction (Zehr, Collins, & Chua, 2001). Results described in this paper supported earlier descriptions of interlimb reflexes and extended them to the specific nerves in study. An extensive pattern of interlimb reflex connections in the neurologically intact human was observed and the latencies of some responses were suggestive of a propriospinally mediated early interlimb reflex response, although the authors did not exclude contributions from subcortical brain regions (Zehr et al., 2001).

In summary, early animal and human studies demonstrated interlimb reflex control. Evidence exists that this interlimb coordination is housed within propriospinal connections between the cervical and lumbar spinal regions. Human research discussed to this point has focused on interlimb reflexes during static conditions. The following section will discuss locomotion and the nature and modulation of such interlimb reflexes within movement.

**Reflex Modulation and Interlimb Pathways during Movement**

Most early research examined interlimb reflexes in humans under static conditions using displacement of a limb and electrical stimulation to elicit reflex responses. More recent research has investigated interlimb reflexes during locomotion, which provides some insight into the possible functional role these interlimb reflexes may serve. Before examining the role of these interlimb reflexes during locomotion it is important to understand the specific control of the arms and legs individually.

**Tripartite System**

It has been suggested that a tripartite system is involved in the regulation of rhythmic locomotor activity (reviewed in Zehr & Duysens, 2004). This tripartite system consists of complex interactions between supraspinal input, spinal central pattern generating circuits (CPGs), and sensory feedback. Initiation of movement involves descending commands that, in turn, activates these CPGs. During locomotor movement, a flood of afferent feedback from the movement and the periphery is delivered to both the spinal and supraspinal levels. This afferent feedback is further connected to motor neurons through complex reflex pathways controlled by the CPG. Additionally, some of
this feedback acts directly on the CPG to aid in phase transitions during the step cycle of walking (Duysens & Van de Crommert, 1998). Furthermore, CPG activity could explain observations of phase- and task-dependency via premotor neuronal gating of afferent feedback during rhythmic movement (Duysens & Tax, 1994).

**Reflex Control of the Legs during Locomotor Movement**

Human research during locomotion has focused on responses to perturbations and limb loading during the gait cycle to investigate the influence of sensory feedback on the control of rhythmic movement. Similar to work done in decerebrate and spinal cats (Grillner & Rossignol, 1978), information about limb loading and hip position are powerful signals for regulating the stepping pattern in human infants (Yang, Stephens, & Vishram, 1998; Pang & Yang, 2001). Infants exhibit a stepping response at birth and allows for researchers to study human stepping before the cerebrum exerts its full control (Yang et al., 1998). In response to cutaneous input from the foot during walking, it appears that evoked reflexes are modulated depending on the phase of the gait cycle in which they were evoked (Yang & Stein, 1990; Tax, Van Wezel, & Dietz, 1995; Zehr, Komiyama, & Stein, 1997; Van Wezel, Ottenhoff, & Duysens, 1997). For example, electrical cutaneous stimulation of the superficial peroneal nerve during walking evokes inhibitory responses in the tibialis anterior and excitatory responses in the vastus lateralis during the swing phase (Zehr et al., 1997). These authors suggest that these responses contribute functionally to the “stumbling corrective response”, where a combination of plantar flexion and knee flexion are used to avoid a perturbation during the swing phase of the gait cycle.

Other research on the control of the legs was conducted using a leg cycling paradigm. This allowed rhythmic leg movement to be studied in isolation, something that is difficult to do in walking studies. The general observation was that the reflex amplitude is often not correlated with the locomotor EMG and is related instead to the phase of the movement cycle during which it is evoked (phase-dependent modulation) (Duysens & Tax, 1994; Brooke et al., 1997; Komiyama, Zehr, & Stein, 2000).

In addition to phase-dependency, cutaneous reflex control seen in the human leg during locomotion is task-dependent. That is, the amplitude and sign of a reflex changes during different motor tasks. This task-dependency has been demonstrated at similar
levels of muscle activity during standing vs. walking (Komiyama et al., 2000), standing vs. running (Duysens, Tax, Trippel, & Dietz, 1993), and cycling vs. static contraction (Zehr, Hesketh, & Chua, 2001). During static contractions, it appears that the descending inputs are minimally affected or unaffected by CPG modulation since there is no rhythmic movement involved. Therefore, as the descending inputs increase, the reflex responses occurring during static contractions are scaled with the background EMG (Burke, Dickson, & Skuse, 1991; Zehr et al., 1997; Zehr & Chua, 2000; Zehr & Kido, 2001; Haridas & Zehr, 2003).

Another feature of cutaneous reflexes in the lower limb is nerve-specificity. Stimulation of cutaneous nerves innervating different areas of the human foot (superficial peroneal, sural, and posterior tibial nerves) evoke reflexes with both nerve-specific and nerve-aspecific features (Zehr et al., 1997; Van Wezel et al., 1997; Zehr, Fujita, & Stein, 1998). Interestingly, sural nerve stimulation yielded facilitatory responses in tibialis anterior at the end of stance while this response was minimal or absent following stimulation of the other cutaneous nerves in the foot (superficial peroneal and distal tibial) (Yang & Stein, 1990; Zehr et al., 1997; Van Wezel et al., 1997). In contrast, suppressive responses were observed in tibialis anterior during end swing and early stance independent of the nerve stimulated. In addition to nerves in the foot, stimulation of the superficial radial nerve at the wrist during walking also yields this suppressive response in tibialis anterior (Haridas & Zehr, 2003). The presence of this consistent suppressive response at the end of the swing phase, independent of the nerve being stimulated, indicates that there is widespread convergence of suppressive pathways to tibialis anterior (reviewed in Zehr & Duysens, 2004).

**Reflex Control of the Arms during Locomotor Movement**

It has been well-documented that reflexes in leg muscles during walking show extensive modulation (task-, phase-, and nerve-specific) during the locomotor cycle. However, the extent to which these characteristics apply to responses in the arms has remained less clear (reviewed in Zehr & Duysens, 2004). During locomotion, our upper limbs move in rhythmic patterns, although it is unclear if this coordinated arm movement is necessary in locomotion. Examination of arm swing reveals that movement of the arms during walking is due to muscular activity and not simply pendular movement (Jackson,
1983). Furthermore, when the upper limbs are restrained, the arm musculature still contracts rhythmically (Fernandez-Ballesteros, Buchtal, & Rosenfalck, 1965) suggesting that arm swing may function to counteract trunk rotation. Additionally, upper limbs move in cyclical patterns according to the cadence of locomotion (Jackson, Joseph, & Wyard, 1978). Recent work has examined natural arm swing during treadmill walking (Zehr & Haridas, 2003) and the control of rhythmic arm movement in isolation, using an arm cycling paradigm (Zehr & Chua, 2000; Zehr & Kido, 2001; Zehr, Collins, Frigon, & Hoogenboom, 2003). Zehr & Kido (2001) demonstrated evidence for nerve-specificity of cutaneous reflexes during rhythmic arm movement. Additionally, both cutaneous and H-reflexes in arm muscles were found to depend strongly on the portion of the movement in which they are evoked (phase-dependent) and upon the specific motor behavior performed (task-dependent) (i.e., arm cycling vs. static contraction) (Zehr & Chua, 2000; Zehr & Kido, 2001; Zehr et al., 2003). Furthermore, it is also well-documented that there is extensive modulation of cutaneous reflexes in arm muscles during the natural arm swing of walking (Zehr & Haridas, 2003). These authors demonstrated similar phase- and task-dependent modulation of early and middle latency cutaneous reflexes to those observed during arm cycling (Zehr & Chua, 2000; Zehr & Kido, 2001; Zehr et al., 2003). More recent research on arm cycling has suggested that reflex modulation during backward arm cycling is the approximate reversal of that observed during forward cycling (Zehr & Hundza, 2005). Based on these findings, it appears that the neural control of rhythmic arm movement is very similar to the control of rhythmic leg movement, because this control of reflex gain may also rely on the output of central pattern generating (CPG) networks (Duysens & Van de Crommert, 1998). During rhythmic tasks, reflex responses appear to be differentially modulated by the CPG and therefore these reflexes were not graded with the background EMG during these tasks.

Further research supports the flexible coupling of separate CPGs for each limb depending on the functional demands placed on the limbs. Reflexes demonstrating different phase-dependent modulation patterns in homologous muscles has been observed in the legs during treadmill running (Tax et al., 1995) and in the arms during various arm cycling tasks (Carroll, Zehr, & Collins, 2005). In the arms, it appeared as though the neural circuitry was common to both the cutaneous reflexes elicited in a particular muscle
and the functional context of the limb in which that muscle resides. Furthermore, this reflex modulation appears to be independent of the activity of the contralateral arm (Carroll et al., 2005) suggesting separate control of each arm.

In addition, these findings (Carroll et al., 2005) further suggest a weaker coupling between neural circuits (CPGs) for the arms as compared to those for the legs (Zehr & Duysens, 2004). These observations stem from research that examined the effects of contralateral arm movement (active or passive) on forearm H-reflex modulation (Zehr et al., 2003) and upper limb cutaneous reflex modulation (Carroll et al., 2005). Whereas contralateral passive leg movement has a strong effect on H-reflexes in the legs (Brooke et al., 1997), contralateral rhythmic arm movement does not have a significant effect on forearm H-reflex modulation, while movement of the ipsilateral arm does modulate the H-reflex (Zehr et al., 2003). Furthermore, this difference in the reflex linkages between the arms and legs may be functionally related to the fact that arms are more commonly used individually, which differs from the highly coordinated, simultaneous use of both legs during daily motor behaviors (reviewed in Zehr & Duysens, 2004).

**Coupling of the Arms and Legs during Locomotion**

During locomotor tasks that involve coordination of the arms and legs (walking, crawling, and swimming), the frequency relationship of the two pairs of limbs remains locked over a range of movement velocities. It was hypothesized that this coordination could be attributed to a system comprised of two coupled oscillators (CPGs), one each for the arms and legs (Wannier, Bastiaanse, Columbo, & Dietz, 2001). Additional research on the potential neural effects of coupling of the arms and legs has been studied in recumbent stepping (Huang & Ferris, 2004). The recumbent stepper was fixed with handles and foot plates that allowed for the coupling of the upper and lower limbs, thus allowing the users to drive the stepping motion with their upper and/or lower limbs. During stepping movements, neuromuscular recruitment was investigated during self and externally driven limb movement conditions. It was reported that active (self driven) upper limb movements led to an increase in lower limb neuromuscular activation when compared to passive (externally driven) upper limb movement. Furthermore, muscle activity amplitudes measured in the lower limbs increased as self driven upper limb exertion increased by either increasing the resistance (Huang & Ferris, 2004) or the
movement frequency (Kao & Ferris, 2005). These results demonstrate possible interlimb pathways that are responsible for the relay of information from active upper limbs onto passive lower limbs during cyclic stepping motions.

Evidence for this interlimb reflex coordination between the arms and legs has been extensively studied during walking. Distinct bilateral arm muscle responses with electrical stimulation of the distal tibial nerve and small leg displacements were observed during walking (Dietz et al., 2001). Interestingly, these interlimb responses are absent while swinging the arms during standing and during sitting. These observations suggest the existence of a flexible, task-dependent neuronal coupling between the arms and legs, and it is further suggested that a central pattern generator gates this pathway during walking (Dietz, 2002).

In an extension from earlier work examining interlimb reflexes evoked following electrical cutaneous stimulation of the foot and hand during static contraction (Zehr et al., 2001), these interlimb pathways were examined during treadmill walking (Haridas & Zehr, 2003). During walking it was shown that interlimb cutaneous reflexes in both the arms and legs evoked by stimulation at the hand (superficial radial nerve) and foot (superficial peroneal nerve) were task-dependent and phase-modulated during the walking cycle. Also, stimulation in both the upper and lower limbs evoked significant changes in lower limb kinematics which were able to be interpreted functionally. Additionally, a reciprocally organized pattern and coordination of reflex responses from hand to foot and from foot to hand was observed. Reflex responses observed in the upper and lower limb muscles on both sides of the body at the same portion of the step cycle suggests that a segmental CPG may be the mechanism allowing for the control of the cutaneous reflex responses observed (Haridas & Zehr, 2003).

During locomotion there is a possible interaction between rhythmic arm and leg activity which makes it difficult to determine the specific locus of the mechanisms regulating these interlimb reflexes (reviewed in Zehr & Duysens, 2004). Earlier research has investigated the remote effect of upper limb activity on reflex excitability in stationary legs (Delwaide, Figiel, & Richelle, 1973, 1977; Eke-Okoro, 1994; Hiraoka, 2001). For example, Hiraoka (2001) demonstrated a decrease in soleus H-reflex amplitude during rhythmic arm swing. More recently, the effects of rhythmic arm cycling
on stationary legs were studied (Frigon, Collins, & Zehr, 2004). In this study, remote rhythmic arm cycling was found to significantly inhibit the soleus H-reflex when compared to no arm movement, probably due to modulation of la presynaptic inhibition (Frigon et al., 2004). In an extension from this arm cycling study, cutaneous stimulation of the superficial radial nerve was found to increase the H-reflex during static conditions and countered the suppression of the H-reflex occurring during arm cycling (Zehr, Hoogenboom, Frigon, & Collins, 2004). These findings suggest that sensory feedback between the arms and legs is not suppressed during rhythmic movement. Thus, it is possible that sensory feedback could be used as a substrate for human interlimb coordination during locomotion, similar to findings in the cat (Miller et al., 1975).

**Summary**

Interlimb pathways and reflexes appear to play an integral role in coordinated movements such as locomotion. Pathways connecting regions of the spinal cord controlling fore- and hindlimbs are present in several species and have been shown to contribute to interlimb coordination. Rhythmic locomotor tasks appear to be controlled in part by central pattern generators (CPGs) which are heavily regulated by peripheral inputs. It appears that these CPGs are coupled between limbs and are instrumental in the effective coordination of the limbs. In contrast to direct evidence for such networks in animals, only indirect evidence has been observed in humans. Patterns of reflex modulation (task- and phase-dependency) likely represent activity of CPG networks associated with generating rhythmic patterns of both the arms and legs. Despite some differences in the strength of coupling between the arms compared with that between the legs, arm and leg movements appear to be regulated by CPG activity and both demonstrate similar reflex control during locomotion. Limited research has examined these interlimb pathways in isolation by increasing activity in a given pathway using electrical stimulation or rhythmic movement and measuring effects in opposing limbs (i.e. the effect of arm cycling on the soleus H-reflex (Frigon et al., 2004)). Further research is necessary during these isolated rhythmic conditions, and during more complicated activities where all limbs are active to better understand the control of the upper and lower limbs, individually and combined.
References


CHAPTER 2: MANUSCRIPT

Introduction

All locomotor tasks (e.g., walking, running, or swimming) require coordinated movement of the limbs for effective movement. Coordination between the fore- and hindlimbs (i.e., interlimb coordination) has been well documented during quadrupedal locomotion (Miller & Van Der Meche, 1975; Miller, Van Der Burg, & Van Der Meche, 1975) and has been attributed to neural linkages connecting cervical and lumbosacral networks in the spinal cord (Gernandt & Shimamura, 1961; Gernandt & Megirian, 1961). In fact, these neuronal linkages appear to be organized functionally since the ascending propriospinal system has been shown to promote limb flexion, while the descending system promotes limb extension (Lloyd & McIntyre, 1948). While direct evidence of this spinal circuitry is lacking in humans, indirect evidence demonstrates that this interlimb coordination is conserved during bipedal locomotion in humans (Dietz, 2002). Evidence suggests that rhythmic arm and leg movements (e.g., arm cycling, leg cycling, and walking) are regulated at least in part by central pattern generators (CPGs) (reviewed by Zehr & Duysens, 2004). However, some uncertainty remains as to the nature of the coordination between the arms and legs.

At the present time there are no direct ways to probe the human nervous system during movement, so more indirect measures are used (e.g., reflex modulation). That is, the change in reflex amplitude or sign during movement can be used as a tool to probe the activity in a given feedback pathway (Burke, 1999). It has been suggested that afferent feedback is modulated by CPGs and so CPG activity can be inferred by alterations in motor activity during rhythmic movement (reviewed by Zehr & Duysens, 2004). Thus, modulation of cutaneous and Hofmann reflexes (H-reflexes) in the arms and legs has been found to be dependent on the behavioral context (i.e., task-dependent modulation) and the specific phases of a motor task (i.e., phase-dependent modulation) during rhythmic movements such as walking, leg cycling, and arm cycling. These reflex modulation patterns are suggestive of CPG activity (Zehr & Duysens, 2004).

To further understand the nature of interlimb coordination, neural pathways have been studied using interlimb reflexes as probes. In this context, the term “interlimb” refers to widespread reflex responses occurring in limbs other than where the stimulus
was applied (Zehr, Collins, & Chua, 2001). Early research demonstrated these interlimb reflexes following the displacement of a limb or electrical stimulation during static conditions in healthy participants (Traub, Rothwell, & Marsden, 1980) and in participants with spinal cord injuries (Calancie, 1991; Calancie, Lutton, & Broton, 1996). More recent research has investigated interlimb reflexes during locomotion, which provides some insight on the neural connections between the rhythmic centers controlling arm and leg movement. For example, distinct bilateral arm muscle responses were observed during treadmill walking following electrical stimulation of the distal tibial nerve and small leg displacements (Dietz, Fouad, & Bastiaanse, 2001). Interestingly, at a similar level of background muscle activity, these interlimb responses were absent during voluntary arm swing while standing and during a seated writing task. These observations suggest the existence of a flexible, task-dependent neuronal coupling between the arms and legs during gait. Furthermore, this pathway appears to be gated by CPGs since it becomes rhythmically facilitated during walking and closed during the standing and sitting tasks (Dietz et al., 2001; Dietz, 2002). That is, throughout the gait cycle, changes in background muscle and reflex activity within these interlimb pathways reflects the opening and closing of alternate routes to motor neurons in all limbs (Duysens, Tax, Trippel, & Dietz, 1992).

To further examine the coupling between the upper and lower limbs, the effects of this coupling were studied during treadmill walking. Coupling effects are defined as a measurable effect of movement of one limb upon background or reflex muscle activity in another limb (e.g., the effect on arm swing on activity in the legs). During walking it was shown that that interlimb reflexes in both the arms and legs evoked by stimulation of cutaneous nerves at the hand (superficial radial (SR) nerve) and foot (superficial peroneal (SP) nerve) were task-dependent (i.e., static vs. walking) and phase-modulated during the walking cycle (Zehr & Haridas, 2003; Haridas & Zehr, 2003). Additionally, a reciprocally organized pattern and coordination of reflex responses from hand to foot and from foot to hand was demonstrated. For example, following SP nerve stimulation, inhibition was observed in the ipsilateral posterior deltoid muscle during stance, while facilitation was seen in the contralateral posterior deltoid muscle during contralateral stance. Reflex responses observed in the upper and lower limb muscles on both sides of
the body at the same portion of the step cycle suggests that a coupling between segmental CPGs regulating activity in the arms and legs may be the mechanisms giving rise to the cutaneous reflex modulation observed (Haridas & Zehr, 2003). However, during walking it has been suggested that there is an interaction between rhythmic arm and leg activity which makes it difficult to determine the specific locus of the mechanisms regulating these interlimb reflexes (Zehr & Duysens, 2004). That is, the dominant factor could be arm or leg movement but it is not possible to separate out these factors during walking when both the arms and legs are rhythmically active. Therefore, to understand the interaction between the arms and legs, research has focused on the remote effect of moving limbs on reflexes measured in limbs that are not moving. For example, early research demonstrated that upper limb movement could affect reflex excitability in stationary legs (Delwaide, Figiel, & Richelle, 1973, 1977; Eke-Okoro, 1994; Hiraoka, 2001). More recently, the effects of rhythmic arm cycling and somatosensory conditioning (i.e., local cutaneous nerve stimulation) on the soleus H-reflex amplitude in stationary legs was studied (Frigon, Collins, & Zehr, 2004). Rhythmic arm cycling was found to significantly inhibit the soleus H-reflex amplitude when compared to no arm movement. In addition, the H-reflex amplitudes were significantly altered by the local conditioning stimuli (i.e., sural and common peroneal nerves), suggesting that inputs arising from the somatosensory conditioning and arm cycling share a similar pathway. Furthermore, no task dependent differences were found in cutaneous reflex amplitudes in soleus when local cutaneous nerve stimulation was delivered alone. Thus the authors concluded that the task-dependent change in H-reflex amplitude was not due to changes in motor neuronal excitability (i.e., postsynaptic effects), but most likely due to modulation of Ia presynaptic inhibition (Frigon et al., 2004). These findings supported earlier work that demonstrated a decrease in soleus H-reflex amplitude during rhythmic arm swing (Hiraoka, 2001), showing that rhythmic arm movement affects reflex excitability in legs that are not moving.

In an extension from the Frigon (2004) study, cutaneous stimulation of the superficial radial (SR) nerve at the wrist was found to increase the H-reflex amplitude during static conditions and countered the suppression of the soleus H-reflex amplitude occurring during arm cycling (Zehr, Hoogenboom, Frigon, & Collins, 2004). In contrast
to the effects of local inputs from the legs (Frigon et al., 2004), these findings suggest that sensory feedback between the arms and legs is not suppressed during rhythmic arm movement. Thus, it is possible that sensory feedback could be used as a substrate for human interlimb coordination during locomotion, similar to findings in the cat (Miller et al., 1975).

This interaction between the upper and lower limbs during locomotion has also been examined through the neural coupling of the limbs during recumbent stepping (Huang & Ferris, 2004). It was reported that active (i.e., self driven) upper limb movements led to an increase in neuromuscular activation in passively moving lower limbs when compared to externally driven upper limb movement. That is, the activity state of the upper limbs is important in determining the amount of neuromuscular recruitment present in relaxed legs because a measurable increase in EMG was observed only when the arm muscles were actively used in the movement pattern (i.e., self driven arm movement). Furthermore, muscle activity amplitudes measured in the lower limbs increased as self driven upper limb exertion increased by either increasing the resistance (Huang & Ferris, 2004) or the movement frequency (Kao & Ferris, 2005). These results demonstrate interlimb coordination during stepping because information from active upper limbs was relayed to passive lower limbs during cyclic stepping motions and the patterns of muscle activation were similar to patterns observed during the active arms and legs condition.

In summary, evidence suggests the existence of a flexible neuronal coupling between the upper and lower limbs that is task-dependent. However, the specific interaction between the control of the arms and legs during locomotion has yet to be clearly determined. To better understand the coupling between the arms and legs, this study examined the effects of neuronal coupling on muscle and reflex modulation patterns during a combined rhythmic task (i.e., ARM&LEG cycling). Thus, a methodology that allowed for the separation of arm and leg movement, which is impossible to do during walking, was used to determine the individual contribution of the arms and legs during a combined arm and leg rhythmic task (ARM&LEG). The protocol used in this study parallels in some ways the general approach used by Juvin and colleagues to study the propriospinal circuitry underlying interlimb coordination in the
fictive neonatal rat preparation (Juvin, Simmers & Morin, 2005). In this study by Juvin et al. (2005) the cervical and lumbar rhythm generators were pharmacologically decoupled and the activity of these isolated cords was compared with patterns of interlimb coordination in the freely moving animal.

It was hypothesized that a measurable coupling between the control centers responsible for arm and leg movement would be observed. More specifically, significant coupling effects would be observed during the ARM&LEG task, and these effects would be the result of an algebraic summation of the effects observed during arm and leg movement in isolation. This hypothesis evolved from the simplest explanation for this predicted interaction between the arms and legs, which is that the reflexes would summate during the combined condition. To test this hypothesis explicitly, the coupling effects observed during the ARM&LEG task would be compared to the algebraic summation of the individual effects observed during the ARM and LEG tasks. Additionally, the relative contributions from each factor (i.e., arms and legs) to the coupling effects observed during the combined task would be determined throughout the movement cycle to elucidate any phase-dependent shifts in the neural control of this movement.

Methods

Participants

Fourteen participants (ages 24-44; 10 females and 4 males), free of any known history of neurological or metabolic disorders participated in this study. The participants provided informed written consent in a protocol approved by the Human Research Ethics Committee at the University of Victoria and performed in accordance with the Declaration of Helsinki.

Protocol

Experimental Protocol

The experimental methodology and protocol are similar to that described in previous experiments involving reflex modulation during arm (Zehr & Chua, 2000; Zehr & Kido, 2001; Zehr, Collins, Frigon, & Hoogenboom, 2003) and leg cycling (Zehr, Hesketh, & Chua, 2001). Participants completed three movement tasks: (1) arm cycling with legs stationary (ARM), (2) leg cycling with stationary arms at the side (LEG); and
(3) combined arm and leg cycling (ARM&LEG). Participants also held four static positions in each task for approximately one minute. This was done to determine if the stimulus intensity was adequate to elicit a reflex and to compare reflexes evoked at different phases within the movement cycle, with and without movement.

During all tasks a consistent EMG level was held in the tibialis anterior (TA) muscle, ipsilateral to the site of stimulation. To aid in maintaining this contraction, participants wore an ankle-foot orthosis (AFO) on their right side and were given visual feedback of this rectified EMG on an oscilloscope. In addition, maximum voluntary isometric contractions (MVICs) were recorded for TA in two different positions: foot in the pedal and foot on the floor. These were used to quantify contraction levels during the LEG and ARM&LEG tasks, and ARM task, respectively.

The experiment was conducted using an arm and leg ergometer (PRO II, SCIFIT Systems Inc., Tulsa OK) in which the arm and leg cranks were coupled and representative of normal interlimb phase relationships observed during walking. This allowed for the arms and legs to be 90 degrees out-of-phase with one another during the combined arm and leg cycling condition (see Figure 1). Also, the right and left limbs of the participant were 180 degrees out-of-phase from one another. Participants were seated on the ergometer with their backs supported in a custom adapted wheelchair and their feet were strapped into foot plates attached to the cranks. During arm cycling trials, participants gripped the handgrips firmly but comfortably with the forearms in a pronated position to ensure muscle activity in the arms. Additionally, during arm cycling trials the participant’s feet were removed from the pedals and fixed with a strap across their toes to the base of the ergometer at 90 degrees of knee flexion. Rhythmic cycling was performed in a clockwise direction at a comfortable pace (~60 rpm) for approximately eight minutes for each cycling task. This rate is similar to those used during leg cycling (Brown & Kukulka, 1993) and arm cycling (Zehr & Chua, 2000), and is considered to be equivalent to a typical walking cadence.
Figure 1. Schematic representing the arm and leg positions and corresponding functional phases of movement across the movement cycle. All positions and phases are in reference to the position of the right leg. Leg positions are labeled on the outside of the circle with 12 o’clock at the top center position. Note that the arm crank is 90 degrees ahead of the leg crank, meaning that when the leg is at 12 o’clock, the arm is at 3 o’clock (see arm positions labeled inside the circle). Also, the leg positions indicated by the ovals (i.e., 10, 12, 2, 3, 4, 6, 8, and 9 o’clock) correspond to the functional positions that were used for planned comparisons on bEMG and middle latency reflexes in all muscles except for iTA.
Finally, to address whether the contraction of TA during the focused contraction cycling (FCC) significantly altered the nature of the cycling, 8 of the 14 participants that performed the FCC also performed the same tasks with no focused contraction of TA (i.e., normal cycling (NC)). During the NC condition the AFO was removed and participants were asked to cycle normally.

**Cycle timing and kinematics.**

Positions of the cranks throughout the movement cycle were obtained from two optical encoders (i.e., one each for the arms and legs) that were mounted on the interior frame of the ergometer. This allowed for the division of the movement cycle into twelve phases, equivalent to a standard clock-face with 12 o’clock at the top center position (see Figure 1). During movement tasks, the positioning of the cranks is discussed in terms of the phase of movement (i.e., 12 o’clock refers to the limb approaching the top center position, and each subsequent phase is in 30 degree increments (i.e., one hour) from the previous one). Note that all phases of movement are with reference to the legs. These movement cycle phases were also defined in functional terms (e.g., power and recovery phases, see Figure 1 for details) to be comparable to other cycling studies. In addition, angular positions of the elbow (n = 12), and knee (n = 13) were measured using lightweight electro-goniometers (Twin Axis SG150 and SG110, Biometrics Ltd., Gwent, UK).

**Nerve stimulation.**

Cutaneous reflexes were evoked with pseudorandomly applied trains (5 x 1.0 ms pulses @ 300 Hz) of isolated constant current stimulation, utilizing a Grass S88 stimulator (Grass Instruments, AstroMed Inc.) connected in series with a SIU5 isolator and a CCU1 constant current unit. This electrical stimulation was applied to the superficial peroneal (SP) nerve using disposable bipolar Ag-AgCl electrodes placed on the anterior surface of the leg near the crease of the ankle joint. Stimulus intensity was set at 2.1 ± 0.18 (mean ± SD) x the threshold at which a clear radiating sensation (radiating threshold [RT]) spreads into the innervation area of the dorsum of the foot. Stimulation was delivered pseudo-randomly within the cycling phases, approximately once every two to three cycles; and between one and three seconds during static trials.
Electromyography (EMG).

Muscle activity was collected from ten muscles in total, including bilaterally from the posterior deltoid (PD), flexor carpi radialis (FCR), medial gastrocnemius (MG), and tibialis anterior (TA). Additionally, EMG was recorded unilaterally from vastus medialis (VM) and biceps femoris (BF) ipsilateral to the site of stimulation. Sites over the selected muscles were cleaned with rubbing alcohol and Ag-AgCl surface electrodes were then applied in a bipolar configuration with a 3 centimeter inter-electrode distance. Ground electrodes for EMG recordings were placed on bony landmarks near the selected muscles. EMG recordings were pre-amplified and band pass filtered at 100 - 300 Hz (P511 Grass Instruments, AstroMed Inc.) and signals were full-wave rectified offline during the analysis process.

Cutaneous Reflex Analysis

For each participant, subtracted EMG traces from each muscle were analyzed in terms of reflex amplitudes and latencies. These reflex traces were obtained by subtracting the average trace of nonstimulated cycles from the corresponding average trace of stimulated cycles. The stimulation artefact was removed and the EMG trace was low-pass filtered using a third order Butterworth dual pass filter set at 40Hz.

Peak reflex amplitudes were obtained by averaging a 10 millisecond window centered on the peak of each reflex response. Reflex amplitudes were analyzed at two distinct epochs: early (~50-75 ms to peak) and middle (~80-120 ms to peak), although the exact latency of these epochs was based on the overall pattern of responses from all participants and was not determined a priori. Reflex amplitudes were considered significant if at least one of the epochs exceeded a two standard deviation band calculated from recorded pre-stimulus activity subtraction error. Additionally, if the stimulus intensity was sufficient to evoke a significant reflex (i.e., early or middle latency) within each subject and muscle in at least one of the tasks performed, windows of muscle activity corresponding to these latencies for all tasks were selected. This allowed for an accurate gauge of the level of EMG when no reflexes were evoked and for comparison of these responses to tasks when significant reflexes were evoked. If no significant reflexes were observed in a given muscle during any of the tasks then no latency windows were selected. However, this was not the case in this study.
Cutaneous reflex amplitudes and background EMG for each subject were normalized to the peak value of the control (unstimulated) EMG for that muscle across the movement cycle. Activity in arm muscles were normalized to the peak value during the ARM task, while the peak value from the LEG task was used to normalize reflex amplitudes and background EMG in the leg muscles.

**Data Acquisition and Analysis**

Data were acquired at a sampling rate of 1000 Hz with a 12-bit A/D converter connected to a computer running custom-written Lab View software. Data were separated into twelve phases of the movement cycle, beginning with the top center position (12 o’clock) and were averaged throughout the movement cycle. During static contractions, averages of twenty sweeps were collected, while during cycling fifteen to twenty sweeps were averaged for each phase within the movement cycle.

**Statistical Analysis**

**Approach Common to All Data**

In all cases, analysis was conducted on averaged values for each subject from each phase in the movement cycle. STASTICA software (version 6.1, StatSoft Inc., Tulsa, OK) was used to perform repeated measures analyses of variance tests (RM ANOVAs).

A 2-way RM ANOVA was used to identify significant main effects for task and movement phase on background EMG (bEMG) levels and middle latency reflex amplitudes during static and cycling trials. The factors and their corresponding levels include the movement task (i.e., ARM, LEG, and ARM&LEG) and the movement phase (12 during cycling and 4 during static). Additionally, Tukey’s HSD post hoc test or planned comparisons were performed, dependent on the muscle. Descriptive statistics included means ± standard error of the mean (SEM) (except in table Table 1 where standard deviations (SD) are used). For all tests, statistical significance was based on an alpha level of p < .05.

Linear regression analysis using Pearson’s correlation coefficients (r) was used to determine relationships between reflex amplitudes and background EMG levels for each muscle during all tasks. For this regression analysis the critical r values were adjusted for each muscle depending on the number of participants for whom there were data for that
muscle within each task. The corresponding critical \( r \) values for a 2-tailed test at an alpha level of \( p < .05 \) were 0.62 (\( n = 11 \)), 0.591 (\( n = 12 \)), 0.568 (\( n = 13 \)), and 0.544 (\( n = 14 \)).

To ensure that reflexes were examined and compared among tasks in the same time window, a 2-way RM ANOVA was performed on the peak middle latencies for all muscles.

**Specific Details for Different Comparisons**

**Ipsilateral TA.**

Since ongoing muscle activity (bEMG) was experimentally controlled in ipsilateral tibialis anterior (iTA) during all three tasks, the statistical analysis for this muscle was different than the analysis performed for the other muscles. That is, 1-way RM ANOVAs were conducted for each task to determine whether middle latency reflexes were significantly modulated dependent on the phase of movement within that task. Additionally, planned comparisons were conducted at all phases within the cycle where bEMG was matched across tasks to determine if task-dependent differences in reflex amplitudes exist.

To test the hypotheses related to a simple algebraic summation, the following tests were performed on middle latency reflex amplitudes in iTA during all three tasks: 1) residual analysis; 2) algebraic summation; and 3) forward-stepwise multiple regression analysis. First, since we were interested primarily in the effects of movement, the consistent middle latency inhibition observed during all static trials was subtracted from the corresponding reflex amplitudes evoked during each cycling task for each individual. This calculation successfully removed a common factor from all tasks and provided a residual value for each task (e.g., rARM). This is similar in principle to calculating an H-reflex percentage change from control amplitude. Second, these residual values were then used in the predicted algebraic summation equation (rARM + rLEG) which was compared to the residual ARM&LEG task (rARM&LEG). A 2-way RM ANOVA was performed on all individual residual values to see whether the rARM&LEG task differed from the predicted summation (rARM + rLEG). Third, to gauge the relative contributions of arm and leg movement to the combined ARM&LEG task, a series of forward stepwise multiple regressions were performed. Multiple regression is a statistical technique that allows for the prediction of one variable (criterion variable) on the basis of
several other variables (predictor variables). In a forward stepwise regression each variable is entered into the model one at a time in an order determined by the strength of their correlation with the criterion variable and its value is accessed (Brace, Kemp & Snelgar, 2003). Across the entire movement cycle and within each specific phase, middle latency reflexes evoked during the ARM&LEG task were compared to two predictor variables: 1) middle latency reflexes evoked during the ARM task; and 2) middle latency reflexes evoked during the LEG task. Adjusted R² values reported represent the total amount of variance in the criterion variable (ARM&LEG) that is accounted for by the two predictor variables, while significant F-change values, beta coefficients, and R² change values were used to assess the relative contributions of each predictor variable. Additionally, a Hotellings t-test was used to assess the differences between the two dependent correlation coefficients.

**Comparison between focused TA contraction (FCC) and normal (NC) cycling.**

To determine whether the focused contraction had a significant effect on normal cycling patterns in the other leg muscles, the differences in bEMG and reflex modulation in the leg muscles ipsilateral to the site of stimulation (i.e., VM, BF, MG, and TA) were examined using a 3-way RM ANOVA (3 Task (ARM,LEG, and ARM&LEG) x 2 Cycling Conditions (NC and FCC) x 12 phases in the movement cycle).

**All other muscles.**

Muscle activation and reflex modulation patterns were further examined in the remaining muscles (i.e., i/cPD, i/cFCR, i/VM, i/BF, i/cmG, and cTA) during the FCC condition. Muscle activity and reflexes were collected in 13 participants for iPD, cPD, cFCR, and cTA; 12 participants for iFCR and cMG; and 11 participants for iVM, iBF, and iMG. Planned comparisons were performed at eight functionally important phases to determine whether differences among tasks exist at specific phases within the cycle. These functional movement phases were as follows: initial power (10 o’clock); mid power (12 o’clock); terminal power (2 o’clock); power to recovery transition (3 o’clock); initial recovery (4 o’clock); mid recovery (6 o’clock); terminal recovery (8 o’clock); and recovery to power transition (9 o’clock) (see Figure 1).
Results

Reflex Latencies

Reflex latencies as determined by time to peak response are shown in Table 1 for all muscles in each task (mean ± SD). Reflexes were examined at similar time windows among tasks within a muscle for a given individual since no significant differences were found among the reflex latencies for different tasks.

Table 1. Summary of average peak latencies for middle latency reflexes in all muscles during each task

<table>
<thead>
<tr>
<th>Muscle</th>
<th>ARM</th>
<th>LEG</th>
<th>ARM&amp;LEG</th>
</tr>
</thead>
<tbody>
<tr>
<td>iPd</td>
<td>99 ± 8</td>
<td>100 ± 15</td>
<td>107 ± 8</td>
</tr>
<tr>
<td>iFCR</td>
<td>101 ± 7</td>
<td>106 ± 6</td>
<td>104 ± 9</td>
</tr>
<tr>
<td>iVM</td>
<td>97 ± 11</td>
<td>99 ± 10</td>
<td>101 ± 12</td>
</tr>
<tr>
<td>iBF</td>
<td>100 ± 8</td>
<td>99 ± 6</td>
<td>97 ± 7</td>
</tr>
<tr>
<td>iMG</td>
<td>99 ± 13</td>
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<td>cPD</td>
<td>102 ± 6</td>
<td>100 ± 8</td>
<td>103 ± 5</td>
</tr>
<tr>
<td>cFCR</td>
<td>105 ± 7</td>
<td>105 ± 9</td>
<td>105 ± 6</td>
</tr>
<tr>
<td>cMG</td>
<td>104 ± 10</td>
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<td>103 ± 9</td>
<td>109 ± 10</td>
<td>105 ± 10</td>
</tr>
</tbody>
</table>

Note. Latencies are in milliseconds (ms) and values are combined from all participants and are represented by mean ± SD.
Ipsilateral TA (Focused contraction cycling (FCC))

Static Trials

During static trials within each task, a prominent middle latency inhibition was consistently observed. There was no significant effect for task or position on this middle latency inhibitory reflex in iTA. Therefore, all static tasks (ARM, LEG, and ARM&LEG) and positions (12, 3, 6, and 9 o'clock) were collapsed and averaged to give one static value for iTA (-20 ± 7.5 % bEMG (mean ± SEM, normalized to the peak EMG value from the unstimulated LEG task)). Note that all further discussions concerning static trials will refer to this collapsed static value (refer to the solid white bar at 12 o'clock on Figure 4).

Background EMG

Control EMG amplitudes were calculated for each phase of the movement cycle on the data from unstimulated trials during each task. During the three tasks, participants maintained a focused TA contraction throughout the movement cycle at a level of 22 ± 3.2 % MVC (mean ± SEM) which was equivalent to 15.5 ± 10 % bEMG (mean ± SEM, normalized to the peak EMG value from the unstimulated LEG task). Statistical analysis showed that the participants were consistent in maintaining this level of bEMG in iTA among all three tasks at 10 out of the 12 phases of the movement cycle (the exceptions are 2 and 3 o'clock). Significant differences from post-hoc tests (p < .05) were found between the ARM task and LEG task at 3 o'clock; and the ARM task was different from the ARM&LEG task at 2 and 3 o'clock (indicated by the white box covering the data at these phases in Figure 3). Therefore, the following reflex analysis for iTA focus on these phases within the cycle where bEMG was matched across all three tasks (i.e., 12, 1, 4-11 o'clock). Note that bEMG and middle latency reflex data are not shown for 2 and 3 o'clock in Figures 3 and 4, respectively.

Reflex analysis

Phase-dependent reflex modulation.

Reflex traces in iTA muscle for a representative individual subject during each cycling task are shown in Figure 2. The phase of movement is noted by the numbers found to the left of each panel. Phase-modulation of the middle latency reflex (~ 85-110 ms after stimulation) can be seen within each task.
Figure 2. Subtracted reflex EMG traces in iTA muscle from one subject evoked during the ARM, LEG, and ARM&LEG tasks. In these traces the stimulus artefact has been removed and the phases (in a clockwise direction) are plotted vertically starting with the arm at 3 o’clock and/or the leg at 12 o’clock as the top plot. In addition to the visible middle latency reflex phase modulation, also note the decrease in inhibition observed at 12, 1, and 11 o’clock when comparing the middle latency reflex amplitudes during the LEG and ARM&LEG tasks to that of the ARM task. The vertical trace plotted to the right of each panel indicates the bEMG in iTA during that particular task, plotted on similar scales.
The most prominent phase dependent reflex amplitude modulation (refer to Figure 2) occurred during the LEG (middle panel) and ARM&LEG (last panel) tasks when compared to that seen during the ARM task (first panel). The corresponding bEMG traces across the entire movement cycle for each task are plotted vertically on the right side of each panel. Identical scales have been used for the subtracted reflex and bEMG traces to allow for comparison among the tasks.

Middle latency reflex amplitudes in iTA were found to be significantly phase modulated during the LEG and ARM&LEG tasks (significant main effect for the phase of movement (p < .05)). Figure 3 shows the average data across all participants for middle latency reflexes in iTA throughout the movement cycle during the ARM, LEG, and ARM&LEG tasks (top, middle, and bottom line plots, respectively). The corresponding bEMG plots are shown for each task (see top, middle, and bottom shaded plots in Figure 3 for ARM, LEG, and ARM&LEG tasks, respectively). Significant phase modulation of middle latency reflex amplitudes during the LEG and ARM&LEG tasks are indicated by “* PHASE”.

Additionally, results from a linear regression indicate that the modulation of bEMG and middle latency reflex amplitudes were not significantly correlated during each of these tasks (see Table 4 for Pearson r values).
Figure 3. Phase modulation of bEMG and middle latency reflexes in iTA during the three tasks averaged across all participants (N = 14). bEMG (shaded plots) and reflex amplitudes (line plots) have been normalized to the peak value of the background (unstimulated) EMG obtained in the movement cycle for the LEG task in each subject and are expressed as percentages. The white box covering the data at 2 and 3 o’clock indicate where the bEMG was found to be significantly different across the tasks. The "** PHASE" denotes the tasks in which significant phase modulation of middle latency reflex amplitudes was observed. Middle latency reflex amplitudes in iTA were phase modulated during the LEG and ARM&LEG tasks (p < .05) while no significant phase modulation was observed during the ARM task.
**Task-dependent reflex modulation.**

In addition to depicting phase-dependent reflex modulation, Figure 2 also shows task-dependent reflex modulation in iTA for a single subject. Examination of middle latency reflex amplitudes (highlighted by the shaded boxes) across the three tasks for this subject reveals a decrease in inhibitory amplitude during the LEG and ARM&LEG tasks (middle and last panel, respectively) when compared to the ARM task (first panel).

Middle latency reflex amplitudes in iTA across all participants are plotted in Figure 4 according to the phase within the cycle in which they were evoked. It can be seen that the pattern of reflex modulation is similar for the three tasks in most of the phases of movement. For example, reflexes during all three tasks are inhibitory and of similar amplitudes in the 4 through 10 o’clock phases. However, planned comparisons using the phases where bEMG was matched among tasks revealed that middle latency reflex amplitudes were task-dependent within certain phases of the movement cycle. Specifically, middle latency reflex inhibitory amplitudes during the ARM task were found to be significantly greater (indicated with asterisks in Figure 4) than those observed during the LEG and ARM&LEG tasks at 11, 12, and 1 o’clock.

When comparing middle latency reflex amplitudes evoked during static and cycling conditions, significant differences (p < .05) were found at only one position/phase (i.e., 12 o’clock), and this difference was only seen during the LEG and ARM&LEG tasks (see the double asterisks (**) at 12 o’clock on Figure 4). No significant differences were found between cycling and static conditions within the ARM task.
Figure 4. Middle latency reflexes in iTA averaged across all participants (N = 14) for ARM, LEG, and ARM&LEG tasks. Reflex amplitudes have been normalized to the peak value of the background (unstimulated) EMG obtained in the movement cycle for the LEG task in each subject and are expressed as percentages. Note that data is not shown for 2 and 3 o’clock since planned comparisons were not made within those movement phases. Since no significant phase modulation of middle latency reflex amplitudes was observed in iTA during static trials, reflex amplitudes from all 4 static positions were averaged (see the AVG static bar at 12 o’clock). Single asterisk (*) represent significant differences (p < .05) in reflex amplitude among tasks during each phase of movement, while double asterisks (**) denote where static trials were significantly different (p < .05) than cycling trials within a given task.
**Algebraic summation during the ARM&LEG task.**

Figure 5 shows group data comparing residual (i.e., cycling-static) middle latency reflex amplitudes in iTA during the ARM&LEG task (rARM&LEG represented by the white bars with black cross hatches) to the algebraic summation of rARM + rLEG (solid black bars) across the movement cycle. No significant differences were found between the two groups, suggesting that a simple algebraic summation of the individual effects from arm and leg movement is expressed during the ARM&LEG task. Figure 5 also shows the two components of this algebraic summation of residuals (i.e., rARM (dark grey line) and rLEG (light grey line)) compared to the rARM&LEG (white bars with black cross hatches) and rARM + rLEG (black bars). When comparing the amplitudes of these lines and bars at each phase, the dark grey line (rARM) is the smallest in amplitude. That is, there is less difference between the cycling and static trials within the ARM task, while a larger difference (or residual) can be seen for the LEG and ARM&LEG tasks (light grey line and black bars, respectively). In addition, examination of the reflex signs (i.e., negative or positive), demonstrates that ARM cycling reinforces the large inhibitory middle latency response observed during static conditions, whereas this inhibition is reduced during the LEG and ARM&LEG cycling tasks. This finding is similar to the task-dependent differences in iTA middle latency reflexes highlighted in Figures 3 and 4.
Figure 5. Middle latency reflexes in iTA during the ARM&LEG task compared to the predicted algebraic summation of reflexes evoked during the ARM and LEG task individually. All plotted values are residual values representing the difference between cycling and static trials within each individual in each task (i.e., residual ARM (rARM) = ARM – AVG static). Therefore, the algebraic summation is of the average residual ARM (dark grey line) plus the average residual LEG (light grey line). This summation (rARM + rLEG (black bars)) is compared to the average residual ARM&LEG (white bars with black cross hatches). That is, rARM + rLEG is the predicted summation observed during the ARM&LEG task. Reflex amplitudes have been normalized to the peak value of the background (unstimulated) EMG obtained in the movement cycle for the LEG task in each subject and are expressed as percentages.
Relative contributions from the arms and legs

In addition, the individual contribution, or weighting, of each factor (arms and legs) in this combined arm and leg cycling condition was determined using the original data (ARM, LEG, and ARM&LEG). Results from a forward stepwise multiple regression across the movement cycle (i.e., 12 phases of movement) for all fourteen participants indicated that the LEG task was the main contributor to middle latency reflex amplitudes expressed during the ARM&LEG task throughout the entire movement cycle. Specifically, the LEG predictor variable accounted for 33% (R² change = 0.33) of the total variance within the ARM&LEG condition (adjusted R² = 0.38; F₂,₁₆₅ = 50.87, p < 0.0001), while the ARM accounted for an additional 5% of the variance (R² change = 0.05, p < .05). Both LEG and ARM made statistically significant contributions to the ARM & LEG task (beta coefficients for each predictor variable were LEG β = 0.497; ARM β = 0.245 (p < .05)). Although, a Hotellings t-test (see the “entire cycle” at the bottom of Table 2) revealed that the two dependent correlation coefficients (r = 0.39 for ARM to ARM&LEG and r = 0.57 for LEG to ARM&LEG) were not significantly different from one another (t = -0.63) suggesting that the strength of correlation between each predictor variable with ARM&LEG were similar.

To determine any phase dependent contributions from the arms and legs additional forward stepwise multiple regressions were performed on middle latency reflex amplitudes in iTA for all participants at each phase of movement. Significant adjusted R² values, beta coefficients, R² change, and F-change values for each predictor variable, according to the movement phase, are indicated by asterisks in Table 2 and Figure 6. Additionally, results from a Hotellings t-test revealed that the strength of the correlation between each predictor variable with the criterion variable was significantly greater for the LEG and ARM&LEG comparison at 4, 6, 7, 8, and 9 o’clock while the correlation between the ARM and ARM&LEG variable was significantly stronger at 11 o’clock (see double asterisks (***) indicating significant t-values in Table 2).

Figure 6 depicts the relative contributions from the arms and legs to reflex expression during the ARM&LEG task. While the legs (light grey bars) appear to account for the greatest amount of variance during the ARM&LEG task (see the black asterisks on Figure 6 at 4, 6, 7, 8, 9, and 11 o’clock), the arms (black bars) were also found to
make a significant contribution to the overall variance in ARM&LEG at certain phases of the movement cycle (see the white asterisks on Figure 6 at 2, 10, and 11 o’clock). Interestingly, expression of reflexes in the legs during the ARM&LEG task were found to be dominated by the arms during the power phase of leg movement, while the legs had a dominant role during the recovery phase of leg cycling (see Figure 1 for the functional positions that correspond to these phases of movement). More specifically, the greatest contribution from the arms was 57% at 11 o’clock ($R^2$ change = 0.57; beta = 0.63, p < .05; t = 0.85) and the greatest contribution from the legs was 71% at 9 o’clock ($R^2$ change = 0.71; beta = 0.84, p < .05; t = -1.41).
Table 2. Summary of forward step-wise multiple regression results and differences between two dependent correlation coefficients for middle latency reflex amplitudes at each phase of movement and across the entire movement phase.

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*Note: The predictor variables (ARM and LEG) were used to predict the variance within the criterion variable (ARM&LEG) and the order of these variables for each phase indicate the order determined by the forward stepwise multiple regression. Significant values (p < .05) are indicated with an
asterisk (*). Pearson r coefficients represent the strength of the relationship between each predictor variable with ARM&LEG. Hotellings t values represent the strength of the relationship between the r coefficients for each predictor variable and significant t-values are indicated by the double asterisks (**) if they exceed the critical t-value of 0.70 as determined by the degrees of freedom (v = n-3 or 11).

**Figure 6. Percent contribution from the arms and legs to middle latency reflexes expressed during the combined arm and leg task.** Relative contributions were determined by a series of step-wise multiple regression tests performed within each movement phase, and $R^2$ change values are plotted for each predictor variable (i.e., ARM and LEG). Significant contributors are designated by the single asterisk (*) denoting that a significant $R^2$ change value ($p < .05$) was found for that predictor variable that specific phase within the cycle. White asterisks denote a significant $R^2$ change value for the ARM variable, while black asterisks denote a significant contribution from the LEG variable.
Comparison between Normal Cycling (NC) and Focused TA Contraction Cycling (FCC)

Background EMG

The pattern of EMG activity (i.e., the amplitude relative to the movement phase) in leg muscles ipsilateral to the site of stimulation when comparing the two cycling conditions (FCC and NC) was generally similar in most muscles (see Figure 7). Group data for iMG (Figure 7, panel A) show that the lines representing the FCC condition (solid lines) and NC condition (dashed lines) appear to be superimposed on one another. In fact, statistics comparing the two cycling conditions revealed that for bEMG, significant effects of condition were observed only in VM and TA (p < .05). For TA, these results were expected because the muscle activity in TA was experimentally altered between these two cycling conditions. The bottom plot in Figure 7 (panel A) demonstrates the characteristic phasic EMG bursting in TA during normal cycling (dashed lines) and the more consistent level of EMG maintained during the FCC condition (solid lines). With the exception of VM, where bEMG was significantly altered by condition (p < .05) in three phases of the movement cycle (i.e., 2, 7, and 8 o’clock), the bEMG in the remaining leg muscles (i.e., BF and MG) were not significantly different between FCC and NC cycling conditions.

Middle Latency Reflex Amplitudes

Middle latency reflex amplitudes followed similar patterns of modulation during both cycling conditions (FCC and NC). That is, excitatory or inhibitory responses of similar amplitudes were seen in comparable phases of the movement cycle in both cycling conditions. An example of these similarities in middle latency reflexes between conditions is shown for iMG (top plot in panel B of Figure 7). Note how the solid (FCC) and dashed lines (NC) of corresponding shades of grey are superimposed, similar to the traces for bEMG (Figure 7, panel A). Therefore, middle latency reflex responses in iMG are similarly modulated throughout the movement cycle regardless of the cycling condition being performed. These data are representative of all other leg muscles with the exception of iTA, which was the only muscle where middle latency reflex amplitudes were significantly different in the LEG and ARM&LEG task depending on the cycling condition being performed (p < .05). See the bottom plot in Figure 7 (panel B) and notice
that the patterns of modulation for the LEG task (thick grey lines) and ARM&LEG task (black lines) are different when comparing the FCC (solid lines) and NC (dashed lines). More specifically, middle latency reflex responses in iTA differed within the LEG task between the NC and FCC conditions at 1, 4, and 7 o’clock (see the single asterisks on Figure 7 panel B denoting a significant difference between the solid and dashed grey lines and the asterisks between the bars with a grey border and those with grey diagonal lines on Figure 8). In addition, during the ARM&LEG task, NC was different than FCC at 3, 4, and 7 o’clock (see double asterisks on Figure 7, panel B between the solid and dashed black lines and asterisks on Figure 8 between the bars with a black border and those with black diagonal lines).

Of particular interest is the significant reflex reversal (p < .05) observed in iTA at 1 o’clock when comparing the middle latency reflexes evoked during each cycling condition within the LEG task (indicated by the solid grey arrow on Figure 8).
Figure 7. Comparison between Focused TA Contraction Cycling (FCC) and Normal Cycling (NC) averaged across all participants ($n = 8$). Background EMG (panel A) and middle latency reflex amplitudes (panel B) for ipsilateral medial gastrocnemius and tibialis anterior have been normalized to the peak value of the background (unstimulated) EMG obtained in the movement cycle for the LEG task in each subject within that cycling condition, and are expressed as percentages. Knee kinematics are represented by degrees range of motion. Significant main effects for condition in the LEG and ARM&LEG task are highlighted with the single and double asterisks, respectively.
Figure 8. Comparison of middle latency reflexes in iTA evoked during FCC and NC averaged across all participants ($n = 8$). Reflex amplitudes have been normalized to the peak value of the background (unstimulated) EMG obtained in the movement cycle for the LEG task for each subject, within each cycling condition, and are expressed as percentages. Significant main effects for cycling condition are labeled with #, while significant interactions between task, condition, and phase of movement are labeled with asterisks (*). Note the reflex sign reversal when comparing NC to FCC in the LEG task at 1 o’clock (indicated by the solid grey arrow).
**All Other Muscles**

As mentioned above, muscle activity and reflex modulation in the leg muscles were unaffected by the focused TA contraction during cycling tasks. As a result, bEMG and reflex modulation were examined further in all remaining muscles (i.e., i/cPD, i/cFCR, i/VM, i/BF, i/cMG, and cTA) during the FCC condition and are reported below. Significant results (p < .05) for additional planned comparisons at eight functionally important phases (see Figure 1) are discussed below, summarized in Table 3, and labeled on Figure 9 for ipsilateral muscles and Figure 10 for contralateral muscles. Also, on Figures 9 and 10 the left panel represents bEMG while the right panel shows middle latency reflex amplitudes across the movement phases.

**Background EMG Patterns**

It is important to note that the focused contraction was only maintained in iTA during the cycling tasks, so for the remaining muscles bEMG may not be matched when comparing certain tasks (e.g., ARM vs. LEG). For example, while bEMG appears to be matched between the LEG and ARM&LEG tasks in all leg muscles, bEMG in these muscles during the ARM task is significantly different (p < .05) than both the LEG and ARM&LEG tasks (refer to the leg muscles in Table 3 and the left panel of Figures 9 and 10 where significant differences between the LEG and ARM&LEG tasks are indicated by the % and significant differences between the ARM and LEG tasks are indicated by the @). Interestingly, significant differences were also found between the ARM and ARM&LEG tasks in arm muscles (refer to the arm muscles in Table 3 and the # symbol in Figures 9 and 10).

**Task-dependent Reflex Modulation**

When examining leg muscles, middle latency reflex amplitudes (much like bEMG) between the LEG and ARM&LEG tasks are similarly modulated throughout the movement cycle. This is depicted in the left panel of Figures 9 and 10 where for the leg muscles the LEG (light grey lines) and ARM&LEG (black lines) follow the same pattern of modulation. Additionally, there were significant differences found in middle latency reflex amplitudes at specific phases in the movement cycle in which bEMG was matched across all three tasks. That is, middle latency reflex amplitudes were significantly
different between the LEG and ARM&LEG tasks at 9 o’clock for iPD and between the
ARM and LEG tasks in iBF at 4 o’clock (see the asterisks in Table 3 and the right panel
in Figure 9).

Table 3. Task-dependent differences in bEMG and middle latency reflex amplitudes during
focused contraction cycling.

<table>
<thead>
<tr>
<th>Muscle</th>
<th>bEMG ARM v.</th>
<th>bEMG LEG v.</th>
<th>bEMG ARM v. LEG</th>
<th>Middle Latency ARM v.</th>
<th>Middle Latency LEG v.</th>
<th>Middle Latency ARM v. LEG</th>
</tr>
</thead>
<tbody>
<tr>
<td>iVM</td>
<td>10,12,2-4,6,8,9</td>
<td></td>
<td>10,12,2-4,6,8,9</td>
<td>8</td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>iBF</td>
<td>10,12,2-4,6,8,9</td>
<td></td>
<td>10,12,2,3,6,8,9</td>
<td>4, 6</td>
<td>3,4*</td>
<td>3,4*</td>
</tr>
<tr>
<td>iMG</td>
<td>10,12,2-4,6,8,9</td>
<td></td>
<td>10,12,2-4,6,8,9</td>
<td>2-4,6</td>
<td>2,3</td>
<td>2,3</td>
</tr>
<tr>
<td>iPD</td>
<td>12,2-4,6,8,9</td>
<td>10,2,3,4</td>
<td>10,12,2-4,6,8,9</td>
<td>2</td>
<td>9*</td>
<td>9*</td>
</tr>
<tr>
<td>iFCR</td>
<td>10,12,2-4,6,8,9</td>
<td>10,12,2-4,6,8,9</td>
<td>10,12,2-4,6,8,9</td>
<td>6</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>cPD</td>
<td>10,12,2,8,9</td>
<td>10,12,2-4,6,8,9</td>
<td>10,12,2-4,6,8,9</td>
<td>6</td>
<td>10,6,8</td>
<td>10,6,8</td>
</tr>
<tr>
<td>cFCR</td>
<td>3,4,6,8</td>
<td>10,12,2-4,6,8,9</td>
<td>10,12,2-4,6,8,9</td>
<td>3</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>cMG</td>
<td>10,12,2-4,6,8,9</td>
<td></td>
<td>10,12,2-4,6,8,9</td>
<td>8</td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>cTA</td>
<td>10,12,2,3,6,8,9</td>
<td></td>
<td>10,12,2-4,6,8,9</td>
<td>10</td>
<td></td>
<td>10</td>
</tr>
</tbody>
</table>

Note. Significant differences from planned comparisons (p < .05) among tasks at specific phases within the
movement cycle are included. All phases (i.e., o’clock) refer to the position of the legs. The asterisks (*)
indicate significant differences in middle latency reflex amplitudes that were found at phases where bEMG
was matched.
Figure 9. Phase- and task-dependent modulation of bEMG and middle latency reflexes in all muscles ipsilateral to the site of stimulation. Amplitudes for middle latency reflexes and bEMG have been normalized to the peak value of the background (unstimulated) EMG obtained in the movement cycle for the LEG task for leg muscles and arm muscles are normalized to the peak bEMG from the ARM task in each subject and are expressed as percentages. Additionally, kinematics for the elbow and knee are represented in degrees range of motion. Significant differences between tasks are represented as follows: # ARM is different than ARM&LEG; % LEG is different than ARM&LEG; and @ ARM is different than LEG.
Figure 10. Phase- and task-dependent modulation of bEMG and middle latency reflexes in all muscles contralateral to the site of stimulation. Amplitudes for middle latency reflexes and bEMG have been normalized to the peak value of the background (unstimulated) EMG obtained in the movement cycle for the LEG task for leg muscles and arm muscles are normalized to the peak bEMG from the ARM task in each subject and are expressed as percentages. Additionally, kinematics for the elbow and knee are represented in degrees range of motion. Significant differences between tasks are represented as follows: # ARM is different than ARM&LEG; % LEG is different than ARM&LEG; and @ ARM is different than LEG.
Relationship between bEMG and Middle Latency Reflexes

When comparing the left and right panels of Figures 9 and 10 (group data for bEMG and middle latency reflex responses) it does not appear that modulation of bEMG and reflex amplitudes are highly related within a muscle for most tasks. Of the thirty correlations examined, in only four cases were the reflex and bEMG amplitudes significantly coupled (see the asterisks in Table 4 for significant correlations). These significant correlations were found during the ARM task in iBF, iMG, and cTA (compare the dark grey triangle symbols in both panels of Figures 9 and 10 for these muscles and notice their almost identical patterns); and during the LEG task in iPd (compare the grey circles in both panels of Figures 9 and 10 for this muscle). During the ARM&LEG task no muscles demonstrated a significant correlation between bEMG and middle latency reflex amplitudes. This result is most likely because all of the muscles examined were involved in the rhythmic task and therefore reflex modulation was independent of ongoing muscle activity during this task.

Table 4. Correlations between bEMG and middle latency reflex amplitudes in all muscles.

<table>
<thead>
<tr>
<th>Muscle</th>
<th>ARM n</th>
<th>Pearson r value</th>
<th>LEG n</th>
<th>Pearson r value</th>
<th>ARM&amp;LEG n</th>
<th>Pearson r value</th>
</tr>
</thead>
<tbody>
<tr>
<td>iPd</td>
<td>13</td>
<td>-0.23</td>
<td>14</td>
<td>-0.63*</td>
<td>13</td>
<td>0.00</td>
</tr>
<tr>
<td>ifcr</td>
<td>13</td>
<td>-0.10</td>
<td>13</td>
<td>-0.01</td>
<td>12</td>
<td>-0.19</td>
</tr>
<tr>
<td>ivm</td>
<td>13</td>
<td>-0.29</td>
<td>11</td>
<td>-0.33</td>
<td>11</td>
<td>-0.17</td>
</tr>
<tr>
<td>iBF</td>
<td>13</td>
<td>0.58*</td>
<td>11</td>
<td>0.08</td>
<td>13</td>
<td>0.17</td>
</tr>
<tr>
<td>iMG</td>
<td>11</td>
<td>0.81*</td>
<td>11</td>
<td>-0.53</td>
<td>11</td>
<td>-0.54</td>
</tr>
<tr>
<td>iTA</td>
<td>14</td>
<td>-0.18</td>
<td>14</td>
<td>-0.37</td>
<td>14</td>
<td>-0.32</td>
</tr>
<tr>
<td>cPD</td>
<td>13</td>
<td>-0.15</td>
<td>14</td>
<td>0.17</td>
<td>14</td>
<td>-0.11</td>
</tr>
<tr>
<td>cFcr</td>
<td>13</td>
<td>-0.06</td>
<td>13</td>
<td>-0.23</td>
<td>14</td>
<td>-0.21</td>
</tr>
<tr>
<td>cMG</td>
<td>13</td>
<td>0.08</td>
<td>12</td>
<td>0.13</td>
<td>12</td>
<td>0.31</td>
</tr>
<tr>
<td>cTA</td>
<td>14</td>
<td>-0.55*</td>
<td>14</td>
<td>-0.26</td>
<td>13</td>
<td>-0.30</td>
</tr>
</tbody>
</table>

Note. The critical r values for this 2-tail comparison (p < .05) were 0.62 (n = 11), 0.591 (n = 12), 0.568 (n = 13), and 0.544 (n = 14). Significant correlations are indicated by the asterisk (*).


**Discussion**

In this study, the interaction between the control of rhythmic arm and leg movement was examined using cutaneous reflex modulation as a probe into the neural control of ARM, LEG, and ARM&LEG cycling. Examination of phase- and task-dependent reflex modulation focused on iTA, where bEMG was matched among movement tasks. This study is the first attempt to examine the specific interaction between the control of the arms and legs during a locomotor task involving all four limbs. The main findings suggest that activity within the pathways coupling the control centers for arm cycling and leg cycling is not suppressed during combined arm and leg cycling. While leg movement was found to dominate the expression of reflexes during the combined arm and leg task, arm movement was also found to have a significant contribution at certain phases within the cycle. Moreover, evidence suggests that all three tasks under examination are regulated by CPG activity; evidence for such mechanisms is discussed below.

**Methodological considerations**

There are three main methodological considerations that require discussion: EMG level; postsynaptic measures in iTA; and the relationship between cycling and walking.

First, in this study, participants completed three tasks which involved different levels of muscle activity (e.g., in arm muscles bEMG was significantly greater during the ARM task than during the LEG task where arms remained relaxed, see Figures 9 and 10 for bEMG among tasks). This made it difficult to examine task-dependent differences in reflex responses because reflex amplitude during movement can sometimes be affected by phasic muscle activity in that muscle. Therefore, to allow for proper comparisons between reflex amplitudes evoked during the different tasks, muscle activity in the TA muscle was controlled at a stable EMG level throughout the movement cycle within each task. When comparing the focused contracted cycling (FCC) condition to the normal cycling (NC) condition, it was concluded that the focused TA contraction did not significantly alter ongoing muscle activation or reflex modulation patterns in the other leg muscles (Figure 7). This is similar to the study by Brown et al. (1993) in which participants were asked to maintain a stable level of EMG in TA muscle and no disruptions in the overall pattern of muscle activity in other muscles were observed.
Second, presynaptic modulation of H-reflex amplitude has been inferred by earlier work (Frigon et al., 2004; Zehr et al., 2004) while using the soleus muscle to examine the remote effects of arm cycling. However, in the present study we chose to focus on cutaneous reflexes in tibialis anterior. The rectified and averaged surface EMG recordings obtained in this study include both presynaptic and postsynaptic effects and it is difficult to determine the individual effects from each. The reasons for choosing the TA muscle, instead of soleus, for this focused contraction, and as the primary muscle for examining cutaneous reflex modulation were: 1) in a similar study examining phase-dependent modulation of human flexor reflexes during leg cycling, the experimenters found that across all participants it was easier to maintain a stable level of TA activity than soleus activity (Brown & Kukulka, 1993); 2) robust and consistent responses to electrical stimulation have been observed in TA during walking and leg cycling (Yang & Stein, 1990; Zehr, Komiyama, & Stein, 1997; Van Wezel, Ottenhoff, & Duysens, 1997; Haridas & Zehr, 2003; Van de Crommert, Steijvers, Mulder, & Duysens, 2003); and 3) previous studies examining the effects of arm cycling have shown no significant modulation of cutaneous reflexes in the soleus muscle (Frigon et al., 2004; Zehr et al., 2004). Therefore, focusing on the TA muscle allowed for successful examination of reflex modulation patterns at comparable levels of muscle activation across tasks, and could be used to probe the effects of arm movement on the legs.

Third, results from this study will be discussed in relation to walking and addressed from a functional perspective. It has been proposed that different forms of rhythmic human limb movement share a common central neural control ("common core hypothesis" (Zehr, 2005)), similar to that present in other animals. In a recent study, modulation of cutaneous reflexes was compared during walking and other forms of coupled arm and leg movement (i.e. arm/leg cycling and arm/leg seated stepping) to determine if all of the rhythmic motor tasks rely on similar neural circuits (Zehr et al., 2005). Similar analysis to this study was conducted in addition to principal components analysis which revealed that two common factors explained more than 70% of the variance for bEMG and middle latency reflexes across all three tasks. Zehr and colleagues (2005) suggested that similar neural substrates were responsible for controlling all of these rhythmic movements because the pattern of reflex modulation
during the coupled arm and leg movements (cycling and stepping) were found to be comparable to those seen during walking. Another study related the specific task mechanics of upright ergometer pedaling to that observed during walking (Ting, Raasch, Brown, Kautz, & Zajac, 1998). Ting and colleagues concluded that the alternating leg flexion and extension observed during pedaling is comparable to that seen during walking despite slight differences in kinematics. Specifically, flexion and extension are defined by their contributions to the acceleration of the foot (or foot contact point with the environment), either toward (i.e., flexion) or away from the pelvis (i.e., extension) (Ting, Kautz, Brown, & Zajac, 1999). These biomechanical functions outlined by Ting et al. (1998 & 1999) can be applied to this current cycling paradigm by relating the recovery phase of leg cycling to leg flexion, and the power phases to leg extension (refer to panels A and B in Figure 11). Furthermore, due to the previously mentioned definitions for the acceleration of the foot at each of these phases (Ting et al., 1999), and the study by Zehr and colleagues (2005) which demonstrated similar range of motion kinematics at the knee joint during recumbent cycling and treadmill walking (Zehr et al., 2005), the recovery phase of cycling (leg flexion) can be associated with the swing phase of walking while the power phase of cycling (leg extension) relates to the stance phase of walking (refer to panels B and D in Figure 11). Given these similarities between cycling and walking, the following interpretation of the findings will use walking as a reference task for the combined rhythmic task (i.e., ARM&LEG).
Figure 11. Comparison figure of the leg task mechanics. Using the previously defined terms of limb “flexion” and “extension” (Panel A) the recumbent cycling paradigm in this present study can be interpreted functionally (Panel B) and compared to similar phases within the gait cycle (Panel D). Additionally, the relative contributions from the ARM and LEG to reflex expression during the ARM&LEG task can be addressed according to the functional state of the legs (Panel C). The grey arrow on Panel C highlights the largest contribution from the ARM at heel strike which is a crucial point in the gait cycle.
Interaction between the Control Centers (CPGs) for Arm and Leg Movement

The ARM&LEG task was used as the task of reference to determine the interaction between the individual control of the arms and that of the legs, and the relative contribution of each during a combined arm and leg task. The neuronal coupling between the arms and legs has been previously examined in terms of neuromuscular activation during recumbent stepping at various levels of resistance (Huang & Ferris, 2004) and speeds (Kao & Ferris, 2005). The active arm and leg stepping condition in these studies served as the task of reference just as the ARM&LEG task was used in this study. Huang et al. (2004) reported that active upper limb movement increases neuromuscular activation in passively moving lower limbs and that the pattern of muscle activation observed is not significantly different than that seen during the active stepping condition. In contrast to the findings by Huang et al. (2004), no significant increases in muscle activity in the lower limbs were observed during the combined cycling task when compared to the leg cycling task (see task-dependent comparisons for bEMG in leg muscles in Table 3 and Figures 9 and 10). In this current study, this difference is most likely a result of the differing activity states of the lower limbs (i.e., passive vs. active movement). Additionally, examination of reflex amplitude modulation during the LEG and ARM&LEG tasks in iTA and other muscles where bEMG was matched across tasks, revealed no significant differences between the two tasks (refer to Figures 4 and 9).

Previous investigations into the influences of rhythmic arm movement on motor neuron excitability in the legs (reviewed in Zehr & Duysens, 2004) have suggested that presynaptic inhibition may be a likely mechanism responsible for the subtle interlimb reflex modulation observed. Consequently, it might be expected that any influence of the remote rhythmic arm activity on reflex modulation in the legs observed in this current study would also require more subtle and specific statistical techniques (e.g., planned comparisons and multiple regression analysis). That is, while the more general approach of an ANOVA determines how much of the variance is accounted for by the direct manipulation of the independent variables, multiple regression analysis focuses on the strength of relationships among variables and allows for the quantification of the total variance accounted for by multiple variables (Brace et al., 2003). Indeed, multiple regression analysis across the entire movement cycle as a whole revealed that the LEG
variable accounted for the largest amount of variance, while the ARM variable had a
minor, yet significant effect. Therefore, reflex modulation in a leg muscle during
combined rhythmic activity indicates that rhythm generation in the legs (i.e., the lumbar
region) remains dominant over rhythmic movement of the arms (i.e., the cervical region)
while still being sensitive to some inputs from the arms. This finding represents a
complimentary observation to a recent study (Juvin et al., 2005) that examined the nature
of propriospinal interactions between cervical and lumbar locomotor CPGs in an isolated
spinal cord preparation in neonatal rats. In addition to revealing independent
rhythmogenic capabilities in the cervical and lumbar locomotor regions, these authors
also reported dominance in locomotor drive from the lumbar generators over their
cervical counterparts. Furthermore, this finding was suggestive of an ascending
“caudorostral excitability gradient” mediating interlimb coordination because the
ascending influence of lumbar CPGs on the cervical counterparts increased as a function
of the number of thoracic segments exposed (Juvin et al., 2005).

Additional examination at specific movement phases revealed that the relative
contributions from the arms and legs were phase dependent (refer to Figure 6 for the
individual contributions from the arms and legs to overall variance accounted for during
the combined task and panel C in Figure 11 which represents these contributions in
relation to the functional phase of leg movement). That is, the relative contribution from
the arms was the largest during the power phase of leg cycling (i.e., limb extension) while
the leg contribution was dominant during the recovery phase (i.e., limb flexion).
Interestingly, this outcome parallels similar observations in the cat in which descending
propriospinal paths were found to facilitate extension in hindlimbs (Lloyd & McIntyre,
1948; Miller et al., 1975). Additionally, Ting et al. suggested that, “the default strategy
during locomotor tasks, such as pedalling and walking, may be to modulate the gain of
afferent pathways such that they are strongly effective during limb extension, or the
power phase, and ineffective during flexion, or the recovery phase” (1998). These current
findings corroborate this suggestion by Ting and colleagues (1998) and earlier findings in
the cat (Lloyd & McIntyre, 1948) because the arm contribution was found to be
significant only during limb extension while the legs were the main contributor during
the remainder of the cycle (especially during limb flexion).
Further examination of the phase-dependent contribution from the ARM variable to reflex expression in TA during the ARM&LEG task revealed that its greatest contribution was at a leg position that is comparable to the transition from swing to stance phase (indicated by large arrow on panel C in Figure 11). This significant contribution from the arms to reflex expression in the legs at this crucial point in the gait cycle can be explained by a possible increased reliance on afferent feedback that may be necessary to help guide the limb and ensure proper foot placement. Also, it has been suggested that an increase in inhibition within the pathway to tibialis anterior is essential in balancing the increased excitation experienced during heel strike during this specific phase of the gait cycle (Zehr & Duysens, 2004).

Furthermore, the question arises as to whether this significant contribution from the legs is due to the fact that the legs are moving, or because the input is specific to the legs. Discussion of this issue will center around the postsynaptic measures of arm movement on reflexes in static legs since no previous studies have explored this in moving legs. That is, any detectible changes in motor neuronal excitability within the legs that can be attributed to movement of the arms will be addressed. First, no significant effects of arm cycling on cutaneous reflex amplitudes measured in the soleus muscle have been found following stimulation of the sural and common peroneal nerves (Frigon et al., 2004) and superficial radial nerve (Zehr et al., 2004). In addition, cutaneous stimulation at the wrist was found to increase the H-reflex amplitude during static conditions and countered the suppression of the soleus H-reflex amplitude occurring during arm cycling. This finding suggests that sensory feedback between the arms and legs is not suppressed during rhythmic arm movement (Zehr et al., 2004); although this has yet to be determined during rhythmic leg movement. These authors further speculate that remote influences (e.g., arm cycling or cutaneous stimulation at the wrist) have access to the motor neuron pools of leg muscles while local inputs (e.g., cutaneous stimulation in the legs) have limited access during arm movement (Zehr et al., 2004). Furthermore, it appears that the activity state of the limb receiving the input (i.e., movement or stimulation) is given priority over inputs evoked from stationary limbs (Carroll, Zehr, & Collins, 2005). Current findings support this idea that the addition of rhythmic arm movement onto legs that are moving and receiving electrical stimulation to
evoke reflexes was not found to be significantly different from leg movement alone. That is, somatosensory conditioning within the legs is given priority, although it remains difficult to determine whether this is due to the movement-induced afferent feedback from leg cycling or the local cutaneous nerve stimulation delivered to the leg. Findings from this study suggest that commands from the control centers regulating arm movement are given access to the legs at certain phases of movement (i.e., during limb extension or the power phase of cycling); although the contribution from arms appears to be minor in comparison to the contribution from rhythmic leg movement.

**Phase-dependent Reflex Modulation**

**Leg Cycling**

Previous studies have examined reflex modulation during active leg cycling (Brown & Kukulka, 1993; Zehr et al., 2001; Mileva, Green, & Turner, 2004). This study however, is most comparable to Brown’s study (1993) where human flexor reflexes (HFR) in tibialis anterior and soleus, evoked by stimulation of the distal tibial nerve were examined during normal upright leg cycling and cycling while maintaining a focused contraction of TA or soleus.

As shown in Figures 6 and 7, significant phase-dependent modulation of middle latency reflex amplitudes, evoked by electrical stimulation of the superficial peroneal nerve, was observed during both the FCC and NC conditions. These findings are similar to earlier work which demonstrated phase-modulation of cutaneous reflexes during both contracted (Brown & Kukulka, 1993; Zehr et al., 2001) and normal (Mileva et al., 2004) upright leg cycling. While this observation of phase-dependent reflex amplitude modulation applies to all leg muscles, ipsilateral to the site of stimulation, the focus of this discussion will be on phase-modulation of middle latency reflex amplitudes in iTA during the focused contraction cycling (FCC).

During FCC, the most prominent phase-modulation of middle latency reflexes in iTA was observed during the power phase (refer to Figure 4). Specifically, a significant decrease in inhibitory amplitude, or release of inhibition was observed when the leg was at 11,12, and 1 o’clock. This decrease in inhibition observed during the power phase of recumbent cycling is similar to the reported increase in HFR amplitude at the terminal power and initial recovery phases during contracted TA upright cycling (Brown &
Kukulka, 1993). Brown and colleagues (1993) suggested that reflex amplitude modulation at these points may enhance the probability of forward acceleration of the limb under a perturbed situation, much like a flexion withdrawal response. That is, the HFR is most potent in flexor muscles (e.g., tibialis anterior) at the transition from the power to recovery phase, where unloading assists in forward progression of the pedal (Brown & Kukulka, 1993). Results from this current study can be interpreted similarly to Brown et al. (1993) because the observed release of inhibition in iTA during the power phase of cycling aids in increased ankle dorsiflexion in an attempt to overcome an obstacle and proceed with forward progression. Furthermore, this response is dampened during the remainder of the movement cycle since the obstacle is less difficult to overcome while maintaining cycling during these phases.

**Arm Cycling**

Examination of the effects of arm cycling on cutaneous reflex amplitudes measured in the legs revealed that rhythmic movement of the arms (that was remote to both the site of stimulation and where the reflexes were being measured) had no significant effect on middle latency reflex amplitude modulation in iTA (refer to Figures 2 and 3). However, previous work (Frigon et al., 2004; Zehr et al., 2004) would suggest that the effect of arm movement on reflex modulation in the legs is presynaptic in nature and therefore would be difficult to detect using a technique that by definition contains both pre- and postsynaptic effects (i.e., cutaneous reflex modulation) as was the case in this present study. Therefore, further investigations are necessary to elucidate the possible remote effects of arm cycling on reflexes in the legs.

**Arm&Leg Cycling**

Examination of reflex amplitude modulation in iTA during the ARM&LEG task revealed similar phase-dependent reflex modulation patterns to those observed during the LEG task (refer to Figure 4). While the combined rhythmic task (ARM&LEG) used in this study can be considered somewhat novel in nature, the neural coupling observed is similar to that during walking (Zehr et al., 2005). Since phase dependency of reflexes evoked in the legs has been studied extensively during walking (Yang & Stein, 1990; Tax, Van Wezel, & Dietz, 1995; Zehr et al., 1997; Van Wezel et al., 1997; Haridas &
Zehr, 2003; Zehr & Haridas, 2003) the following section will use walking as a reference task for discussing the findings during the ARM&LEG task.

During walking it has been reported that stimulation of different cutaneous nerves in the foot (i.e., sural, peroneal, and posterior tibial nerves) yields phase modulated middle latency reflex responses with both nerve-specific and nerve-aspecific features (reviewed in Zehr & Duysens, 2004). As reviewed, an example of nerve-aspecific responses was observed in TA where a suppressive middle latency reflex was observed at the end of the swing phase, independent of the nerve stimulated (Zehr & Duysens, 2004). Additionally, stimulation at the wrist during walking yielded a similar suppressive middle latency reflex during the end of swing to that which was observed following stimulation of the foot (Haridas & Zehr, 2003). This consistent suppressive reflex response in TA at the end of swing phase is thought to be representative of a widespread convergence of suppressive pathways to TA (reviewed in Zehr & Duysens, 2004).

In relation to the present cycling tasks, there appeared to be an overall suppressive reflex response measured in TA during all cycling tasks and it was found to persist through the majority of the movement cycle, with exception of the significant decrease in inhibition observed during the middle of the power phase of leg cycling (refer to Figure 4). Using the previously mentioned biomechanical definitions of limb flexion and extension (Ting et al., 1998 & 1999) this suppressive reflex in TA was found to persist throughout the entire recovery phase (i.e., limb flexion) and both transitions points between flexion and extension. This is similar to the suppressive responses observed in TA at the end of swing phase during walking (reviewed in Zehr & Duysens, 2004). Therefore, the phase-modulation of reflex amplitudes in iTA observed during the ARM&LEG task appears to be associated with phase-modulation reported during walking. This finding supports earlier evidence of similar neural circuits controlling three different rhythmic arm and leg locomotor tasks (arm/leg cycling, arm/leg seated stepping, and walking) (Zehr et al., 2005).

**Task-dependent Reflex Modulation**

When comparing reflex modulation (i.e., patterns and response amplitudes) across the tasks and cycling conditions, there were no extreme differences observed. That is,
overall there were only subtle differences in reflex amplitudes and few reversals of reflex sign when comparing across cycling tasks (refer to Figure 4) and conditions (refer to Figure 8). However, the following task-dependent differences were observed in iTA: 1) a release of inhibition during tasks involving rhythmic leg movement (LEG and ARM&LEG) when compared to tasks in which the legs were static (ARM and STATIC); and 2) significant differences in reflex amplitude and sign between focused TA contraction cycling (FCC) and normal cycling (NC).

First, a task-dependent difference in middle latency reflex amplitude in iTA was observed at 12 o’clock (refer to Figure 4) where reflex amplitudes expressed during static and cycling trials differed within the LEG and ARM&LEG tasks. This difference was expressed as a significant decrease in inhibitory reflex amplitude during rhythmic movement of the legs (LEG and ARM&LEG tasks) when compared to static legs (AVG static). Similarly, reflex amplitudes expressed during rhythmic arm movement alone (ARM) were found to be significantly more inhibitory than those expressed during leg movement at 11, 12, and 1 o’clock (refer to Figure 4). This release of inhibition observed during the power phase of leg cycling may be explained as a corrective response used to overcome the perturbation and continue the movement (Brown & Kukulka, 1993). Furthermore, these significant differences in reflex amplitudes between static and moving legs appear to be independent of ongoing muscle activity because a stable level of EMG was maintained in iTA across all tasks. These findings are similar to previous studies that demonstrated facilitation of middle latency reflexes in the legs during walking when compared to standing (Duyssens, Tax, Trippel, & Dietz, 1993; Komiyama, Zehr, & Stein, 2000) and during leg cycling when compared to static leg positioning (Brown & Kukulka, 1993; Zehr et al., 2001).

Second, middle latency reflexes in all leg muscles ipsilateral to the site of stimulation were compared between the two cycling conditions (FCC and NC) (refer to Figure 8). Reflex amplitudes were found to be modulated similarly during both cycling conditions in all leg muscles except iTA. That is, with the exception of iTA, excitatory or inhibitory responses of similar amplitudes were observed at comparable phases within the movement cycle. This finding was addressed in the “Methodological Considerations” section as part of the rationale for focusing on the FCC condition to compare the patterns
of reflex modulation across the three cycling tasks. However, in iTA the middle latency reflex responses were significantly different in the LEG and ARM&LEG task depending on the cycling condition being performed. More specifically, middle latency reflex responses in iTA differed within the LEG task between the NC and FCC conditions at 1, 4, and 7 o’clock; while during the ARM&LEG task, NC was different from FCC at 3, 4, and 7 o’clock. Of particular interest is the significant reflex sign reversal (inhibitory during FCC to excitatory during NC) observed in iTA at 1 o’clock when comparing the middle latency reflexes evoked during each cycling condition within the LEG task (refer to the solid grey arrow in Figure 8). These task-dependent differences in reflex amplitudes in iTA between the NC and FCC conditions may be a result of differing levels of bEMG at specific phases of cycling during the NC condition. Specifically, the excitatory response observed at 1 o’clock during the LEG task may be attributed to the fact that inhibitory responses can only be observed against a background level of EMG activity (Frigon et al., 2004), and during the NC condition there was a minimal amount of bEMG at this specific phase. In a similar study by Brown and colleagues (1993), similar patterns of HFR modulation were observed during the static, contracted cycling, and free-form cycling tasks, and slight differences in HFR onset latencies in TA were observed when comparing the contracted and free-form cycling tasks (Brown & Kukulka, 1993).

**Possible Mechanisms**

As stated in the “Introduction” the rationale for using cutaneous reflexes to probe the neural control of rhythmic movement is that they are highly sensitive probes because they are both phase- and task-dependent (Zehr & Duysens, 2004). Therefore, reflex modulation patterns during movement can provide insight into the mechanisms controlling the movement itself. Specifically, reflex modulation that is independent of the level of ongoing EMG would suggest that premotor neuronal mechanisms (e.g. CPGs) are most likely responsible for this modulation (reviewed in Zehr & Duysens, 2004).

Of the three cycling tasks examined, the LEG and ARM&LEG tasks demonstrated significant phase-dependent reflex modulation and the pattern of reflex modulation in muscles that were active during these cycling tasks were found to be independent of ongoing muscle activity in those muscles (refer to Pearson r values in Table 4). When determining the mechanisms responsible for this reflex modulation
during these cycling tasks, it is also important to examine the effect of different postures and limb positions on cutaneous reflex modulation since differing cutaneous, muscular, and joint afferents are potentially activated at different limb positions. Static middle latency reflexes were only reported for iTA, and no significant phase-dependent reflex modulation was found among these static positions across all tasks. This finding is similar to other studies which have shown that the peripheral sensory inputs mentioned above are not likely responsible for cutaneous reflex modulation in muscles throughout the body during walking (Duysens et al., 1993; Zehr & Haridas, 2003), arm cycling (Zehr & Kido, 2001), and leg cycling (Brown & Kukulka, 1993; Brooke, McIlroy, Staines, Angerilli, & Peritore, 1999).

Significant differences in cutaneous reflex amplitudes between static and cycling tasks, and between cycling conditions (FCC and NC) demonstrate that cutaneous reflexes are task-dependent. This task-dependent behavior further supports the existing rationale for premotor neuronal mechanisms (e.g., CPGs) being responsible for this modulation, since the afferent feedback related to limb loading and muscle stretch is presumably the same between tasks (Zehr et al., 2001).

These characteristic modulation patterns (i.e., phase- and task-dependent) provide inferential evidence for CPG contributions to arm and leg movement, suggesting similar neural mechanisms are responsible for these cycling tasks.

Conclusions

In this study, cutaneous reflexes were used as a tool to probe the interaction between the control centers responsible for arm and leg movements. The paradigm allowed for the partitioning out of the relative contributions from arm and leg movement to the reflexes expressed during a combined task. The main finding is that during a combined arm and leg task, the arms have a small, but significant, effect on reflexes expressed in the legs, but what matters most is the activity state of the legs. In addition, the relative contributions from the arms and legs were found to be phase-dependent. Specifically, the contribution from the arms to reflex expression in the legs appears to be gated according to the functional state of the legs. That is, during the power phase of leg cycling there may be an increased reliance on feedback from the arms, as evidenced by a significant contribution observed from the arms onto the legs. Furthermore, the
observation that the expression of reflexes in iTA during the ARM&LEG task throughout the recovery phase of movement is dominated by the legs can possibly be explained by the fact that input from the arms (via the CPGs for the arms) may come via common interneuron(s) and have limited access to the motor neurons responsible for the observed CPG output during leg cycling. This would explain why no significant differences in reflex amplitudes were observed when comparing the LEG and ARM&LEG tasks. Furthermore, it could be the case that during leg cycling the gate by which information may be relayed from the arms to the legs is closed or limited in terms of access at certain phases within the movement cycle.
References


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