COOPERATION AND INTERFERENCE: AN INVESTIGATION OF NEURAL CROSSTALK

A Dissertation

by

DEANNA MICHELLE KENNEDY

Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSPHY

Chair of Committee,	Charles H. Shea
Committee Members,	John J. Buchanan
	Carl Gabbard
	James W. Grau
Head of Department,	Richard B. Kreider

August 2015

Major Subject: Kinesiology

ABSTRACT

Three experiments were designed to understand the influence of neural crosstalk on bimanual coordination by investigating how and when the forces produced in one limb affect the forces produced in the contralateral limb when different muscle groups are used (Experiment I), different limbs are used to perform the faster frequency (Experiment II), and different force levels are required to achieve the goal coordination pattern (Experiment III). Participants were required to produce a pattern of isometric force with one limb that was coordinated with a pattern of isometric forces produced by the contralateral limb. Experiment I required participants to coordinate a 1:2 pattern of force with homologous or non-homologous muscles, Experiment II required participants to coordinate 1:1, 1:2, and 2:1 patterns of force, and Experiment III required participants to coordinate a 1:2 pattern of force with a force requirement of 5N for one limb while the contralateral limb produced 5, 15, or 25N of force. Lissajous feedback was provided to guide performance. In all three experiments, distortions in the force produced by the left limb that could be associated with the force produced by the right limb were observed. However, similar distortions in the force produced by the right limb occurred only when the left limb was performing a faster frequency (Experiment II) or produced more force (Experiment III). Observed distortions in both the right and left limbs indicate that neural crosstalk affects both limbs; however, it manifests differently for each limb depending upon the frequency or force requirements of the task.

DEDICATION

I would like to dedicate this dissertation to my advisor, Dr. Charles Shea.

ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Charles Shea, for his help and guidance throughout this process. I would also like to thank the members of my committee (Dr. John Buchanan, Dr. Carl Gabbard, and Dr. James Grau) for their advice; my fellow graduate students (Jason Boyle, Judith Jimenez, Joohyun Rhee, and Chaoyi Wang) with data collection and/or programming; my participants for volunteering, and the College of Education and Human Development (CEHD) and the Huffines Institute for funding my research.

TABLE OF CONTENTS

Page

CHAPTER

Page

LIST OF FIGURES

FIGURE Page

CHAPTER I

INTRODUCTION

Coordinating actions between the limbs is necessary for many activities of daily living. For example, tying shoes, buttoning a shirt, slicing bread, and driving a car are activities that require some type of coordination between the limbs. Sometimes the activity may require the limbs to produce mirror actions (symmetric bimanual coordination), such as when you row a boat or clap your hands. Sometimes the task may require different relationships between the limbs (asymmetric bimanual coordination). For example, the activity may require one limb to act as a stabilizer while the other limb performs a specific movement such as slicing bread or opening a bottle. Other activities may require fundamentally different actions between the limbs, such as tying shoes or buttoning a shirt. Although these examples are typically easy for individuals to perform, other coordination patterns between the limbs can be difficult. Activities such as playing the guitar or piano underscore the difficulty that can be associated with asymmetric bimanual coordination.

Bimanual coordination patterns are often described by their relative phase or frequency relationship. Relative phase is a variable that reflects the spatiotemporal relationship between the limbs (e.g., Kelso 1986). For example, a relative phase value of 0^0 indicates that the limbs are at same point at the same time. Frequency relationships refer to the rate at which each limb is required to perform. A 3:2 multi-frequency coordination pattern, for example, indicates that one limb has to produce three actions with one limb for every two actions produced by the contralateral limb whereas a 1:1

bimanual pattern indicates that both limbs produce an action simultaneously. Coordination patterns with a relative phase goal other than zero or frequency relationship other than 1:1 have proved difficult to perform and/or learn without extensive practice (e.g., Byblow and Goodman 1994; Peper et al. 1995a,b,c; Zanone and Kelso 1992).

More recent findings, however, have demonstrated that a variety of asymmetric patterns (e.g., 90^0 relative phase relationships between the limbs; 5:3 multi-frequency coordination pattern) can be performed quite well within a few minutes of practice when provided online integrated feedback (e.g., Lissajous plots with a goal movement template) and attentional distractions are minimized (e.g., vision of the limbs, metronomes) (e.g., Kovacs et al. 2010a,b; Kovacs and Shea 2011).

This line of research has recently been extended to include the coordination of a multi-frequency pattern of force. More specifically, participants were required to coordinate a 1:2 pattern of isometric force when provided Lissajous feedback (Kennedy et al. in press). Similar to the previous investigations with reciprocal and circling motions participants were able to perform the multi-frequency force task within a few minutes of practice when provided Lissajous information. Interestingly, however, the results indicated consistent distortions in the forces produced by the left limb when the right limb initiated or released a force pulse. The observed distortions were consistent with the notion of neural crosstalk.

Neural crosstalk is a mirror image command sent to the homologous muscles of the contralateral limb (Cattaert et al. 1999; Cardoso de Oliveira 2002; Swinnen 2002). As such, neural crosstalk conveys the same information to both limbs via cortical and subcortical neural pathways. Symmetrical bimanual actions are stabilized when congruent contralateral and ipsilateral signals are integrated whereas asymmetric bimanual actions can suffer from ongoing interference due to conflicting information or partial intermingling of the signals controlling each limb (Cardoso de Oliveira 2002; Kagerer et al. 2003; Maki 2008; Marteniuk et al. 1984). However, a clear understanding of how and when neural crosstalk facilitates or inhibits coordinated actions between the limbs has yet to be proposed.

It has been hypothesized that the effects of neural crosstalk is dependent on force levels, with higher forces resulting in stronger crosstalk effects and lower forces weaker ones (Heuer et al. 2001). Therefore, to determine the influence of crosstalk on bimanual coordination it is necessary to explore how and when the forces produced in one limb affect the forces produced in the contralateral limb.

Experimental Hypothesis

A series of experiments were designed to better understand the influence of neural crosstalk on bimanual coordination by investigating how and when the forces produced in one limb affect the forces produced in the contralateral limb when different muscle groups are used (Experiment I), different limbs are used to perform the faster frequency (Experiment II), and different force levels are required to achieve the goal coordination pattern (Experiment III).

More specifically, Experiment I was designed to determine whether the activation of homologous or non-homologous muscles resulted in interference consistent with neural crosstalk. Given that neural crosstalk is defined as a mirror image command sent to the homologous muscles of the contralateral limb (Cattaert et al. 1999), it was hypothesized that neural crosstalk should be more easily detected and characterized when the task required the activation of homologous muscles compared to when the task required the activation of non-homologous muscles

Experiment II was designed to determine whether the influence of force produced by one limb on the contralateral limb is the result of the limb assigned the faster frequency on the limb performing the slower frequency or a bias associated with limb dominance. If the limb assigned the faster frequency was responsible for the distortions observed in the contralateral limb, it was hypothesized that distortions would only be observed in the force trace of the limb producing the slower pattern of force. If a bias associated with limb dominance was responsible for the distortions observed in the contralateral limb, it was hypothesized that in right-limb dominant participants the right limb would influence the left limb, regardless of limb assignment.

Experiment III was designed to determine whether an increase in the force requirements for one limb would result in an increase in the interference observed in the contralateral limb and to determine if the observed interference was influenced by the limb performing the higher force. It was hypothesized that an increase in the force requirements for one limb would result in an increase in interference in the contralateral limb. However, if interference is only detected in the left limb it would support the notion that neural crosstalk is asymmetric in nature, whereas if interference is also observed in the right limb when the left limb is producing more force it would suggest a more symmetrical influence.

The ability to identify and characterize neural crosstalk at the behavior level is an important step in understanding constraints acting on the perceptual-motor system. Further, understanding how and when the forces produced in one limb affect the forces produced in the contralateral limb has functional significance as the production and coordination of force is an essential aspect of many everyday bimanual coordination tasks.

CHAPTER II

LITERATURE REVIEW

Understanding how patterns of coordination emerge, stabilize, and transition has been the focus of a large body of research (see Kelso 1995; Oullier et al. 2006; Swinnen 2002; Swinnen and Wenderoth 2004 for reviews). This research has consistently demonstrated that tasks which require asymmetric coordination patterns are less stable and more difficult to perform than mirror symmetric coordination patterns (e.g., Carson et al. 1996; Carson et al. 2000; Cohen 1971; Kelso 1995; Riek et al. 1992; Scholz and Kelso 1989; Semjen et al. 1995; Summers et al. 2008; Temporade et al. 1999). The stability properties associated with bimanual coordination have been formally characterized, modeled, and extensively investigated using concepts taken from nonlinear dynamics (Haken et al. 1985; formally referred to as the Haken-Kelso-Bunz (HKB) model).

The HKB model provides a mathematical account of the attractor landscape in the form of a potential function ($V(\phi)$). The 1:1 in-phase and anti-phase coordination patterns are represented as stable fixed-point attractors, with the in-phase coordination pattern representing the more stable attractor state. In-phase (0^o) and anti-phase (180^o) refer to 1:1 frequency relationships between the actions of the two effectors. Other relative phase and frequency patterns, however, act as repellers. A repellar in the attractor landscape pushes a variable away from it and towards the attractor (e.g., in-phase coordination pattern).

The stability of the in-phase pattern has frequently been demonstrated in bimanual coordination tasks that required the simultaneous activation of homologous muscles (e.g., Carson et al. 2000; Cohen 1971; Riek et al. 1992). For example, in tasks such as left and right index finger flexion-extension (e.g., Riek et al. 1992; Scholz and Kelso 1989), forearm pronation-supination (e.g., Carson et al. 1996; Temporade et al. 1999), elbow flexion-extension (e.g., Kovacs et al. 2009a,b), and circle drawing (e.g., Semjen et al. 1995; Summers et al. 2008), the 1:1 in-phase coordination pattern required the simultaneous activation of homologous muscles. This pattern was more stable than the anti-phase coordination pattern that required the activation of non-homologous muscle groups. Note, however, stable in-phase movements have also been associated with the activation of non-homologous muscles when visual feedback was manipulated to create perceptual symmetry (e.g., Meschsner et al. 2001; Meschsner and Knoblich 2004), during multi-joint movements (e.g., Buchanan and Kelso 1993; Kelso et al. 1991), iso-directional movements with non-homologous limb combinations (e.g., Serrien et al. 2001; Serrien and Swinnen 1997) and interpersonal coordination (e.g., Oullier et al. 2008; Schmidt et al. 1990). Regardless of the muscle groups used or the movement of the limbs, the in-phase coordination pattern represents a powerful attractor state while the anti-phase pattern is subject to spontaneous phase transitions (loss of stability) to the in-phase pattern when the control parameter (i.e., frequency) is increased (e.g., Kelso 1981,1984, 1995; Kelso et al. 1986).

Similar stability characteristics have been associated with multi-frequency bimanual coordination (e.g., Kelso and deGuzman 1988; Peper and Beek 1998; Peper et al.

1995a,c). Multi-frequency bimanual tasks require the simultaneous production of two conflicting motor sequences (Summers et al. 1993b). For example, coordinating a 1:2 bimanual reciprocal movement task requires the right limb to produce two flexion/extension cycles while concurrently producing one cycle with the left limb. Because the 1:1 coordination pattern is a highly stable, attractor state (e.g., Kelso 1984), individuals tend to transition to the 1:1 or lower order frequency ratios while performing more difficult higher order ratios (e.g., e.g., 1:2, 2:3, 3:5)(e.g., Fraisse 1946; Peper et al. 1995a,b,c; Treffner and Turvey 1993).

Inherent and Incidental Constraints

Previous research has pointed to a coalition of constraints (e.g., Carson and Kelso 2004; Swinnen 2002; Swinnen and Wenderoth, 2004 for reviews) to account for the stability of symmetric in-phase (1:1) coordination pattern and to help identify the mechanism(s) responsible for the difficulty associated with producing asymmetrical bimanual coordination patterns. Constraints on the central nervous system (CNS) can be categorized into inherent and incidental categories. Inherent constraints are believed to arise from the structure of the neuromuscular system. For example, it has been proposed that the loss of stability from asymmetric coordination patterns to the in-phase pattern is due, at least in part, to interactions between the feed-forward motor commands as the result of shared neural pathways (Helmuth and Ivry 1996; Ivry and Richardson 2002; Ridderikhoff et al. 2005). Incidental constraints, on the other hand, are believed to arise from specific perceptual and attentional features associated with the task or task environment (Kelso et al. 2001).

Much debate surrounds the issue of whether the constraints associated with bimanual coordination are inherent or incidental in nature (e.g., Amazeen et al. 2004a,b; Mechsner et al. 2001). The traditional view is that the stability associated with symmetrical bimanual movements is due to inherent constraints or more specifically, the co-activation of homologous muscles (e.g., Cohen 1971; Kelso 1984; Li et al. 2004; Riek et al. 1992). However, research has also provided evidence that the symmetry bias can be toward perceptual symmetry regardless of the muscles involved (e.g., Kelso 1994; Kugler and Turvey 1987; Mechsner et al. 2001; Mechsner and Knoblich 2004). For example, Mechsner and colleagues (2001) manipulated hand positions (prone or supine) to create four bimanual conditions (prone-prone, supine-supine, prone-supine, supine-prone). This manipulation resulted in that activation of either homologous or non-homologous muscles to produce visually symmetric coordination patterns (in-phase) and visually parallel (anti-phase) coordination patterns, allowing for the inherent and incidental constraints to be disassociated. The results indicated that visually in-phase coordination was more stable than visually anti-phase coordination, regardless of whether homologous or non-homologous muscles were used to perform the task. As such, it was concluded that constraints associated with the stability of in-phase and anti-phase coordination patterns were due to only perceptual constraints.

These results are further supported by a series of experiments by Kovacs and colleagues demonstrating multi-frequency bimanual coordination patterns that were once thought to be difficult to perform without extensive practice could be quickly and effectively performed when integrated feedback was provided (e.g., Lissajous plots with a movement template) and attentional demands associated with the task were reduced (e.g., Kovacs et al. 2010a,b). Similar results were also demonstrated with relative phase feedback (Boyles et al. 2012) and visual/auditory models (Kennedy et al. 2013a).

However, Mechsner's view that perceptual constraints govern bimanual coordination has been questioned (e.g., Li et al.2004; Kennedy et al. 2015; Salter et al. 2004). For example, Li and colleagues (2004) argued that the experimental design (i.e., inversion of the hand) used by Mechsner and colleagues (2001) altered the activation patterns of the muscles, possibly changing the muscle length. It was also argued that the inversion of the hand could impact the torque generating capacities of the muscles, the way in which muscle torque is translated into joint motion, and alter the crossed modulation of excitability in corticospinal motor pathways (Carson et al. 2000; Li et al.2004).

To support their argument, Li and colleagues used the same type of manipulations as Mechsner and colleagues (2001), but they examined wrist abduction/adduction rather than finger abduction/adduction. Due to the additional degrees of freedom necessary to coordinate wrist movements compared to finger movements it was believed the role of inherent constraints in the coordination dynamics could be addressed. Indeed, as the control parameter (i.e., frequency) increased the results indicated an increase in the mechanical degrees of freedom via flexion-extension of the wrist. Furthermore, the results indicated that conditions in which the simultaneous activation of homologous muscles occurred were more accurate and stable than conditions that required the activation of non-homologous muscles. Therefore, it was concluded that the relative timing of homologous muscle activation was a major constraint for coordination stability.

Given the conflicting results and interpretations of experiments investigating constraints associated with bimanual coordination, the question remains about the role that inherent and incidental constraints play in bimanual coordination. It is important to note, however, that previous research comparing homologous and non-homologous muscles during coordination of the limbs have most often used in-phase and anti-phase tasks (e.g., Cohen 1971; Li et al. 2004; Mechsner and Knoblich 2004; Temprado et al. 2003; Riek et al. 1992; Salesse et al. 2005). Most likely because in-phase and anti-phase are stable and easy to perform without practice (Yamanishi et al. 1980) while other coordination patterns have proved difficult to perform without extensive practice (Byblow and Goodman 1994; Swinnen et al. 1997; Zanone and Kelso 1992).

However, given the recent success of feedback manipulations in allowing complex coordination patterns to be performed relatively quickly (e.g., Kovacs et al. 2010a,b; Kovacs and Shea 2011), it may be possible to explore these constraints in more challenging tasks (e.g., Puttemans et al. 2005; Summers et al. 2002; Swinnen et al. 1997). For example, continuous 1:2 bimanual tasks appear to pose difficult challenges for the central nervous system (CNS) (e.g., Beets et al. 2015; Puttemans et al. 2005; Summers et al. 2002; Swinnen et al. 1997). However, these difficulties appear to be minimized when integrated feedback (e.g., Lissajous displays) is provided (e.g., Boyles et al., 2012; Hessler et al. 2010; Kovacs et al. 2010a,b).

Lissajous Feedback

The Lissajous displays used by Kovacs and colleagues, for example, provided a goal template along with on-line integrated visual information regarding the position of the two limbs as a single point in one plane. It is believed that Lissajous feedback facilitate the successful performance of complex bimanual coordination patterns because the integrated information reduces the incidental constraints associated with the task (e.g., Kennedy et al., in press; Kovacs et al. 2009a; Kovacs et al. 2010a,b; Kovacs and Shea 2011). However, the manipulation of perceptual and attentional factors cannot fully explain the stability characteristics observed with relative phase or frequency relationships during bimanual tasks. More specifically, it cannot fully explain why individuals using these displays tend to produce more stable relative phase patterns for an in-phase task while other relative phase relationships are less stable (e.g., Kovacs et al.2009a, 2010b; Kovacs and Shea 2011) or why 1:1 patterns are more stable than other frequency ratios (e.g., Kovacs et al. 2010b; Sisti et al. 2011).

It is possible that the Lissajous displays provide an opportunity for the perceptual-motor system to reduce the incidental constraints associated with the task. However, it appears that the Lissajous displays do not eliminate all the constraints that tend to pull the system toward more stable coordination patterns. Rather, the displays likely decrease the influence of the incidental constraints on the coordination dynamics and provide feedback necessary to counter act the effects of the inherent constraints so that the goal pattern can be attained with relatively low error and variability (Kovacs et al., 2010b). Note that one would not expect Lissajous displays to influence more inherent constraints such as the influence of neural crosstalk. Thus, it may be possible to control many of the incidental constraints associated with bimanual tasks, providing an opportunity to more clearly observe the influence of inherent constraints on the coordination dynamics (Kennedy et al., in press).

Neural Crosstalk

One inherent constraint that may, in part, account for the stability differences, phase transitions, and difficulty in producing certain bimanual patterns is neural crosstalk (see Swinnen 2002; Swinnen and Wenderoth 2004 for reviews). Neural crosstalk is defined as a mirror image command sent to the homologous muscles of the contralateral limb (Cattaert et al. 1999; Swinnen 2002). It is a concept that is frequently used to account for interference in bimanual coordination tasks (e.g., Aramaki et al. 2010; Buchanan and Ryu 2012; Cattaert et al., 1999; Kasuga and Nozaki 2011; Maki et al. 2008; Spijkers and Heuer 1995; Steglich et al. 1999; Swinnen 2002; Swinnen and Winderoth 2004) and has been implicated in kinematic (e.g., Cattaert et al. 1999; Kasuga and Nozaki 2011; Park et al. 2013; Spijkers and Heuer 1995) and neuroimaging (e.g., Aramaki et al. 2006; Aramaki et al. 2010; Houweling et al. 2010; Maki et al. 2008) investigations.

According to the crosstalk model some fraction of the force command for one limb is diverted to the other limb (Cattaert et al. 1999). This occurs when both hemispheres send commands to the contralateral limb via the crossed corticospinal pathways while concurrently sending the same command to the ipsilateral limb via the uncrossed corticospinal pathways (Cardoso de Oliveira 2002; Cattaert et al. 1999). The corticospinal pathways provide direct and indirect routes from the motor cortex to the spinal cord. While the majority (≈90%) of the fibers associated with the corticospinal pathways cross at the medulla and terminate in the lateral portion of the ventral horn of the spinal cord around 10% of the fibers remain uncrossed running through the brainstem and entering the medial regions of the spinal cord, terminating ipsilaterally or contralaterally (Nathan et al. 1990; see Mai and Paxinos 2011, for a review). Thus, each limb is primarily controlled by the contralateral hemisphere; however, there is also an ipsilateral influence that is integrated with the contralateral command.

The ipsilateral influence is believed to alter the activation of the involved muscles (e.g., Cattaert 1999; Cardoso de Oliveira 2002; Swinnen 2002) likely adding to or subtracting from the contralateral muscle activation depending on whether the command is excitatory or inhibitory (e.g., Barral et al. 2006; 2010; Walter and Swinnen 1990). In symmetric 1:1 in-phase bimanual coordination task this ipsilateral influence is not likely to cause interference between the limbs because the commands to both limbs are congruent (Maki et al. 2008). In fact, it is believed that 1:1 in-phase task is stabilized when complementary contralateral and ipsilateral signals are integrated (e.g., Cardoso de Oliveira 2002; Kagerer et al. 2003; Maki et al. 2008; Marteniuk et al. 1984). However, during multi-frequency tasks, for example, the commands to each limb are often in conflict (Summers et al. 1993b). Thus, performance of these patterns can suffer from ongoing interference believed to result from the conflicting information or partial intermingling of signals controlling the two limbs (e.g., Cardoso de Oliveira 2002; Kagerer et al. 2003; Maki et al. 2008; Marteniuk et al. 1984).

In addition to ipsilateral corticospinal pathways, research has also pointed to inter-hemispheric interactions through the Corpus Callosum (CC) as a possible source of the interference typically observed in continuous asymmetric bimanual coordination performance (Cardoso de Oliveira 2002; Seidler 2010; Swinnen 2002). The CC is the primary structure for information exchange between the hemispheres. The exchange of information between the central hemispheres is necessary to successfully coordinate actions between the limbs. The primary evidence to support the role of the CC in bimanual interference is based on research with callosotomy patients. Research has demonstrated that split brain patients and those with agenesis of the CC do not exhibit the same interference effects associated with asymmetric bimanual performance displayed by the general population (Diedrichsen et al. 2003; Franz et al. 1996; Kennerely et al. 2002). For example, Kennerely and colleagues (2002) demonstrated that there were no differences between symmetric and asymmetric circle drawing tasks in split brain patients whereas the control group demonstrated the typical slower performance, increased variability, and phase transitions to the symmetric mode while performing the asymmetric circle drawing task.

Inter-hemispheric communication consists of a complex interplay of inhibitory and excitatory interactions (Liuzzi et al. 2011). Specifically, the ability to coordinate actions between the limbs require the exchange of activating and inhibiting messages between the cerebral structures controlling each limb (Ferbert et al. 1992). While the motor commands for symmetric bimanual actions need only activation (excitatory) messages, asymmetric coordination patterns require inhibitory signals to suppress the inherent tendency to produce symmetric actions. Thus, asymmetric bimanual actions require the selective inhibition of the contralateral crosstalk that triggers the activation of homologous muscle in the contralateral limb as well as the activation of specific commands to perform the task requirements (Barral et al. 2006; 2010).

Regardless of the source, it is believed interference occurs when a set of muscles in one limb is required to produce disparate activation patterns resulting from differences in amplitudes, directions, frequencies, forces, or phase relationships from the muscles activated in the contralateral limb (e.g., Cardoso de Oliveira 2002). When disparate activation patterns are required for the left and right limbs, an individual must inhibit or compensate for the crosstalk that is dispatched to the contralateral limb (Barral et al. 2006; Barral et al. 2010). If the inhibition or compensation for the crosstalk fails, the interference may challenge the stability of the coordination dynamics likely resulting in unwanted perturbations to the coordinated action or may even prompt a phase transition to a more stable coordination pattern (Houweling et al. 2010).

Force Control

It has been hypothesized that the effect of neural crosstalk is partially dependent on force levels, with higher forces resulting in stronger crosstalk effects and lower forces in weaker ones (Heuer et al. 2001). Therefore, to determine the influence of crosstalk on bimanual coordination, it is necessary to explore how and when the forces produced in one limb affect the forces exhibited by the contralateral limb. Bimanual tasks which require the production and coordination of forces may provide further insight into the constraints acting on the system by allowing for the detection and characterization of neural crosstalk at the behavioral level.

Recently Kennedy and colleagues (in press) designed a series of experiments to determine the extent to which the forces produced by one limb influenced the forces produced by the contralateral limb. In the first experiment participants were required to perform two force production tasks at two different force levels: unimanual left and right limb constant force, and bimanual constant force with feedback removed from the left or right limb. In the second experiment participants were required to perform a constant force production task with either the dominant or non-dominant limb while the contralateral limb performed a dynamic sine wave tracking task, feedback was removed for the limb performing the constant task. The results for both experiments showed relatively strong positive time series cross correlations between the left and right limb forces indicating increases or decreases in the forces produced by one limb resulted in corresponding changes in the forces produced by the homologous muscles of the contralateral limb. This form of coupling was also observed in the unimanual conditions in which an increase above baseline was observed in the non-instructed limb which appeared to be coupled with the forces produced from the instructed limb. These results support the notion that neural crosstalk is partially responsible for the stabilities and instabilities associated with bimanual coordination. However, further research is needed to support this conclusion.

Kennedy and colleagues (in press) conducted a third experiment to determine whether individuals can effectively produce and coordinate 1:1 and 1:2 patterns of force when provided Lissajous information and to determine if the force time series for the 1:2 task indicated distortions in the patterns of forces that could be attributed to neural crosstalk. The results indicated very effective temporal performance of the bimanual coordination patterns. This result was similar to that observed with reciprocal and circling motions, but is especially informative given that the increased forces required to produce the desired 1:2 multi-frequency bimanual coordination pattern resulted in a consistent distortions in the forces produced by the left limb that could be attributed to the production of force in the right. The distortions observed in the 1:2 task occurred in the forces produced by the left limb when the right limb was initiating or releasing a force pulse. However, distortions in the forces produced by the right limb that could be attributable to the forces produced by the left limb were not observed.

Similar distortions are typically not observed in multi-frequency coordination tasks performed in near frictionless environments (e.g., Kovacs et al. 2009a; Kovacs et al. 2010a,b; Kovacs and Shea 2011). However, distortions have been observed in a 1:2 coordination pattern in which participants were required to coordinate hand-held pendulums (Sternad et al. 1999c). The ability to coordinate the hand-held pendulums required increased force production compared to tasks performed in near frictionless environments. It is possible that the force requirement of 15N allowed for the detection and quantification of neural crosstalk at the behavioral level in the previous experiments by Kennedy and colleagues (2015, in press).

The ability to observe consistent distortions in the force times series for the left limb that could be attributed to the initiation and release of force by the right limb (Kennedy et al. 2015, in press) as well as the distortions observed in the displacement trace when participants were required to coordinate hand-held pendulums (Stenard et al., 1999a) supports the notion that an increase in the force requirements may modulate the strength of neural crosstalk (Heuer et al. 2001).

Asymmetric Influence

When participants are required to produce two conflicting motor sequences simultaneously, interference between the limbs is often observed (e.g., Byblow and Goodman 1994; Peper et al. 1995a,b,c; Summers et al. 1993b). Typically, the observed interference is asymmetric in nature (e.g., Aramaki et al. 2006; Cattaert et al. 1999; de Pool et al. 2007; Kennedy et al. 2015, in press; Kagerer et al. 2003; Maki et al. 2008; Peters 1985; Semjen et al., 1995). It appears that the dominant limb has a greater impact on the contralateral limb than vice versa. For example, Peters (1985) required participants to tap 1:2 and 2:1 rhythms. The results of the study indicated slower tapping rates and increased variability when right limb dominant participants were required to tap with the left limb at twice the frequency of the right limb (i.e., 2:1) than when they were required to tap with the right limb at twice the frequency of the left limb (i.e., 1:2). Consistent with this result, a number of investigations have provided evidence that bimanual performance is more accurate and/or stable when the dominant limb is assigned the faster frequency (e.g., Byblow and Goodman, 1994; Byblow et al. 1998; Summers et al. 2002).

It has been suggested that hand dominance affects bimanual coordination via an asymmetry in the strength of neural crosstalk (Treffner and Turvey, 1995). Research has indicated that the dominant hemisphere exerts a stronger influence on the non-dominant limb than the non-dominant hemisphere does on the dominant limb (Aramaki et al. 2006; Cattaert et al. 1999; Kagerer et al. 2003; Maki et al. 2008). As such, cortical and subcortical crosstalk has been identified as a potential source for the asymmetries noted in bimanual performance (Aramaki et al. 2006; Cattaert et al. 1999; Swinnen 2002).

Indeed, Cattaert and colleagues (1999) successfully developed a neural crosstalk model for bimanual interference based on the left limb receiving a mirror image of the commands sent to the right limb. The model successfully reproduced characteristics associated with asymmetric bimanual circle drawing with increasing movement frequencies including a decline of the circular trajectories and a weakening of the phase coupling between the limbs (Cattaert et al. 1999). The results from the third experiment by Kennedy and colleagues (in press) were consistent with the model produced by Cattaert and colleagues. Distortions in the forces produced by the left limb that could be attributable to the production of force in the right limb were observed. However, distortions of the forces produced by the right limb that could be attributable to the forces produced by the left limb did not occur.

Research has pointed to issues related to hand dominance as the source of the asymmetry associated with bimanual interference (Treffner and Turvey 1995). Performance differences between the dominant and non-dominant limbs can be observed in both unimanual and bimanual tasks. For example, individuals are more consistent and accurate with the dominant limb than with the non-dominant limb during unimanual finger tapping tasks (e.g., Peters 1981). During bimanual tasks individuals are more accurate at producing both the spatial and temporal goals of a task with the dominant limb than with the non-dominant limb during bimanual tasks (e.g., Carson et al. 1997; Gooijers et al. 2013; Semjen et al. 1995; Swinnen et al. 1997). Furthermore, research has indicated that trajectory distortions and direction reversals most often occur in the non-dominant hand during bimanual tasks (Byblow et al. 1999; Semjen et al. 1995).

During multi-frequency bimanual tasks several studies have indicated greater stability during when the preferred limb (right limb in right hand dominant individuals) is assigned the faster frequency (Byblow and Goodman 1994; Byblow et al. 1998). However, it is important to note that other studies have indicated that the faster limb performs more accurately than the slow limb regardless of hand dominance (Peper et al., 1995c; Summers et al., 1993b).

CHAPTER III

EXPERIMENT I*

Introduction

The ability to perform bimanual, multi-frequency coordination tasks requires the simultaneous production of two conflicting but isochronous motor sequences (Summers et al. 1993b). For example, coordinating a 1:2 bimanual reciprocal movement task requires one limb to produce two flexion/extension cycles while concurrently producing one cycle with the muscles of the contralateral limb. Numerous studies have demonstrated that many bimanual tasks which require frequency relationships other than 1:1 (e.g., 2:3, 3:5) are difficult to perform without extensive practice (e.g., Byblow et al. 1998; Byblow and Goodman 1994; Puttemans et al. 2005; Summers et al. 1993 a,b; Swinnen et al. 1997). Recent findings, however, have demonstrated that a variety of multi-frequency coordination patterns as well as other asymmetric patterns (e.g., 90^{o} relative phase relationships between the limbs) can be performed remarkably well when visual feedback is manipulated to create perceptual symmetry (Mechsner et al. 2001) and these patterns can be 'tuned-in' following only a few minutes of practice when provided online integrated feedback (e.g., Lissajous plots with goal movement template) and other attentional distractions are reduced (e.g., vision of the limbs, metronomes) (Kovacs et al. 2010a,b; Kovacs and Shea 2011).

---

*Reprinted with kind permission from Springer Science and Business Media "Rhythmical Bimanual Force Production: Homologous and Non-Homologous Muscles" by Kennedy DM, Boyle JB, Rhee J, Shea CH, 2015. *Experimental Brain Research*, 233,181-195, Copyright [2015] by Deanna M. Kennedy

This line of research has been extended to include the coordination of 1:2 bimanual patterns of isometric force (Kennedy et al. in press). Interestingly, when the bimanual task involved the production of isometric forces produced by homologous muscles of the two arms, identifiable and consistent distortions in the forces produced by left limb were observed when the right limb was initiating a force pulse. This result is consistent with the notion of neural crosstalk. Neural crosstalk is a mirror image command sent to the homologous muscles of the contralateral limb (Cattaert et al. 1999; Swinnen 2002). According to the crosstalk model, two independent motor plans exist for each limb and some fraction of the force command for one limb is diverted to the other limb (Cattaert et al. 1999). Therefore, interference from neural crosstalk during multi-frequency coordination patterns occurs when a set of muscles in one limb is required to produce disparate activation patterns (e.g., resulting from the differences in phase relationship or frequencies) from the homologous muscles in the contralateral limb (Cardoso de Oliveira 2002).

When disparate frequencies are required for the left and right limbs, an individual must inhibit or compensate for the crosstalk that is dispatched to the contralateral limb (Barral et al. 2006; Barral et al. 2010). The failure to inhibit, suppress or otherwise compensate for the neural crosstalk may result in unwanted perturbations to the coordinated action (Houweling et al. 2010). Indeed, the perturbations in the left limb forces that were observed when participants were required to coordinate a 1:2 pattern of force coincided with the initiation of right limb forces (Kennedy et al. in press). Note, however, that this task required the activation of homologous muscles. Given that crosstalk is defined as a mirror image command sent to the homologous muscles of the contralateral limb (Cattaert et al. 1999; Swinnen 2002), it is important to compare the crosstalk effects associated with the activation of homologous versus non-homologous muscles during bimanual force tasks.

Comparisons between the activation of homologous and non-homologous muscles have been made in a number of experiments to determine whether motoric and/or perceptual constraints govern bimanual coordination (e.g., Cohen 1971; Hu et al. 2011; Li et al. 2004; Mechsner et al. 2001; Mechsner and Knoblich 2004; Riek et al. 1992). Traditionally, bimanual coordination patterns that require the simultaneous activation of homologous muscles have been denoted as in-phase, while patterns that result from the simultaneous activation of non-homologous muscles have been denoted as anti-phase (Kelso 1984). Numerous studies have indicated that in-phase performance is more stable than anti-phase (e.g., Carson 1995; Kelso 1984; Semjen et al. 1995; Schöner and Kelso 1988; Yamanishi et al. 1980); as such, the stability of in-phase patterns have been attributed to the inherent tendency to co-activate homologous muscles (e.g., Carson et al. 2000; Cohen, 1971; Kelso 1984; Li et al. 2004; Riek et al. 1992). However, Mechsner and colleagues (2001), for example, challenged this muscle dependent account of coordination stability and proposed that the stability of in-phase coordination is actually related to perceptual constraints (Kelso 1994; Kugler and Turvey 1987; Mechsner et al. 2001; Mechsner and Knoblich 2004). To demonstrate their perceptual account of coordination stability, Mechsner and colleagues (2001) manipulated hand positions (prone or supine) during a finger abduction-adduction task to create four bimanual conditions (prone-prone, supine-supine, prone-supine, supine-prone). Conditions in which the hand position were the same (prone-prone, supine-supine) in-phase coordination required the simultaneous activation of homologous muscles and anti-phase required the simultaneous activation of non-homologous muscles. However, when the hand positions were different (prone-supine, supine-prone) in-phase coordination required the simultaneous activation of non-homologous muscles while anti-phase coordination required the simultaneous activation of homologous muscles. This manipulation allowed the experimenters to disassociate motoric and perceptual constraints. The results indicated that regardless of the muscle grouping (in-phase/homologous, anti-phase/non-homologous vs. in-phase/non-homologous, anti-phase/homologous), in-phase coordination was more stable than anti-phase coordination. As such, the investigators concluded that constraints associated with stability of in-phase and anti-phase coordination patterns were purely perceptual in nature.

It is important to note, however, that the appropriateness of such limb manipulations to investigate motoric and perceptual constraints has been questioned (Li et al. 2004; Salter et al. 2004). For example, Li and colleagues (2004) argued that the inversion of the hand posture used by Mechsner and colleagues (2001) fundamentally altered the recruitment and activation patterns of the involved muscles, possibly resulting in a change in muscle length and/or the muscle moment arms. They also argued that such changes could impact the torque generating capacities of the involved muscles, the manner in which muscle torque is translated into joint motion, and alter the crossed modulation of excitability in homologous corticospinal motor pathways (Carson et al.

2000; Li et al.2004). In support of their argument, Li and colleagues used the same type of manipulations as Mechsner and colleagues (2001), but they examined wrist abduction/adduction rather than finger abduction/adduction. Due to the additional degrees of freedom needed to coordinate wrist movements compared to finger movements they believed they could better address the role of motoric constraints in the coordination dynamics. Indeed, as the frequency of the task increased the results indicated an increase in the mechanical degrees of freedom via flexion-extension of the wrist. Furthermore, the results indicated that conditions in which the simultaneous activation of homologous muscles occurred were the most accurate and stable. Therefore, it was concluded that the relative timing of homologous muscle activation was a principal constraint upon the stability associated with bimanual coordination.

Given the differential results and interpretations of such experiments, the question remains about the role motoric and perceptual constraints play in bimanual coordination. It is important to note, however, that previous research directly comparing the activation of homologous and non-homologous muscles during bimanual coordination tasks have been limited to in-phase and anti-phase coordination patterns (e.g., Cohen 1971; Li et al. 2004; Mechsner and Knoblich 2004; Temprado et al. 2003; Riek et al. 1992; Salesse et al. 2005). This is likely because in-phase and anti-phase are stable and easy to perform without practice (Yamanishi et al. 1980) while coordination patterns with a goal frequency relationship other than 1:1 have proved difficult to perform without extensive practice (Byblow and Goodman 1994; Swinnen et al. 1997; Zanone and Kelso 1992). The difficulty associated with these coordination patterns has been attributed to phase attraction that draws the coordination between the limbs towards the more stable in-phase coordination pattern (Schöner and Kelso 1988) and the instability associated with the activation of non-homologous muscles via crossed and uncrossed cortical pathways (Kennerley et al. 2002).

However, given the recent success of feedback manipulations in allowing complex coordination patterns to be tuned in quickly (Kovacs et al. 2010a,b; Kovacs and Shea 2011), it may be possible to explore these constraints in tasks that are more challenging for the CNS (e.g., Puttemans et al. 2005; Summers et al. 2002; Swinnen et al. 1997). More specifically, it may be possible to explore constraints related to the activation of homologous and non-homologous muscles during the coordination of a multi-frequency coordination pattern. Because multi-frequency coordination tasks require the simultaneous production of two conflicting motor sequences (Summers et al. 1993b) it may allow for a clearer picture of how and when neural crosstalk influences bimanual coordination. If crosstalk is, in fact, dispatched to the homologous muscles of the contralateral limb, we hypothesized that neural crosstalk should be more easily detected and characterized when the task required the activation of homologous muscles compared to when the task required the activation of non-homologous muscles to produce the goal pattern of coordination. Therefore, the present experiment was designed to determine whether individuals can coordinate a bimanual 1:2 force pattern by activating either homologous or non-homologous muscles when provided integrated feedback in the form of Lissajous displays and if so, compare crosstalk effects between conditions in which homologous or non-homologous muscles were activated to coordinate the goal pattern.

Additionally, the experimental task (isometric force production) does not require changes in muscle length or moment arm. Rather, participants were required to activate agonist and antagonist muscles (i.e. triceps, biceps) to produce a pattern of isometric force while maintaining the same position for both limbs. That is, in the homologous muscle condition the triceps in both arms were activated to produce the goal force pattern whereas in the non-homologous muscle condition the triceps of the right arm and the biceps of the contralateral limb were activated to produce the goal pattern. As the manipulation of limb position to investigate bimanual constraints has been questioned (Li et al. 2004; Salter et al. 2004) this is an important distinction. Note that Chapter 3 of this dissertation has been published in *Experimental Brain Research*.

Methods

Participants

Self-declared right-handed undergraduate students (N=12, mean age=20.9, 6 males and 6 females) with little or no musical experience volunteered to participate in the experiment after reading and signing a consent form approved by IRB of Texas A&M University for the ethical treatment of experimental participants. The participants had no prior experience with the experimental task and were not aware of the specific purpose of the study.

Apparatus

The apparatus consisted of two static force measurement systems, each of which included a force transducer and an amplifier that converted the force exerted against the transducer into a voltage representing the instantaneous value of the applied force. One force transducer was attached to an adjustable metal frame mounted on the left side of a standard padded treatment table and the other force transducer was mounted on the right side. The voltages representing the applied forces were converted to digital values (16 bit) using an AD converter (DAS-16 Series Board, Keithley MegaByte Corp, MA, USA) installed on the computer. The computer was programmed to sample at 200 Hz. A goal template and a cursor representing the applied forces were displayed in a 1.64 x 1.23 m image projected on the wall in front of the participant.

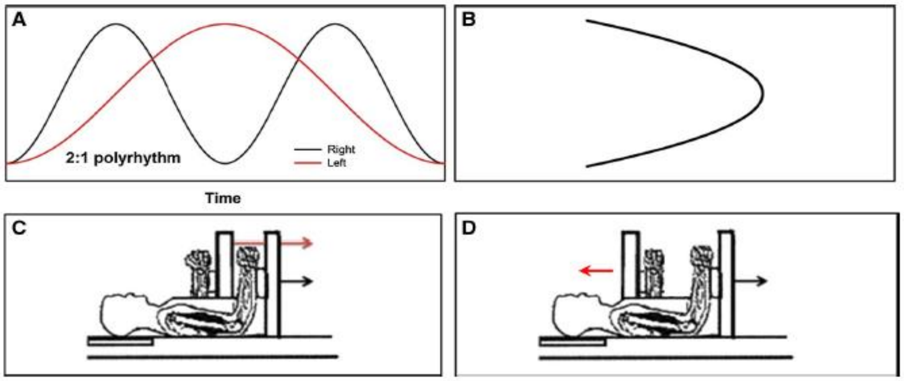


Fig. 1. Experimental arrangement for Experiment I. The goal coordination pattern (a), goal Lissajous template (b), and experimental setup for the homologous (c) and non-homologous (d) conditions are provided (Kennedy et al. 2015).

Procedure

Prior to entering the testing room participants were randomly assigned to one of two bimanual coordination groups (i.e., homologous or non-homologous). Upon entering the testing room, participants were asked to position themselves on the treatment table (supine). Their head was slightly elevated with a pillow so they could comfortably view the projected image on the wall located 2 m away. The force transducers were adjusted so that the participant’s arm just below the wrist contacted the transducer so that they could produce isometric force utilizing left and right triceps in the homologous condition or right triceps and left biceps in the non-homologous condition. The elbows were in contact with the table and the lower arms were at a 90° angle to the upper arm (see Fig. 1c, d). This position allows for isolation of force produced by the limbs without the effects of gravity and mechanical/elastic stretch properties of the muscles and tendons. Participants were asked to rhythmically produce a pattern of isometric forces on the left side transducer with the left arm that was coordinated with the pattern of isometric forces produced on the right sided force transducer with the right arm in a 1:2 coordination pattern (see Fig. 1a) using the display information to guide their performance. Note that the 1:2 bimanual force coordination pattern used in the present experiment required the right limb to produce two patterns of force (peak $\approx$15N) for each pattern produced by the left limb.

The display information consisted of a Lissajous plot that incorporated a goal template and a cursor indicating the forces produced with both limbs. The cursor moved from left to right as force was produced with the right arm and from bottom to top as force was produced by the left arm. The goal template illustrated the specific pattern of force requirements needed to produce the goal coordination pattern of 1:2 (see Fig. 1b). The maximum force required to produce the pattern illustrated by the template was 15N. Participants were required to perform 14 trials. Each trial was 20 s with a 10 s rest period between trials. After any trial in which the average frequency of the right limb was below 1.0 Hz, the experimenter encouraged the participants to increase the speed with which they produced the patterns of force without disrupting the goal pattern.

Measures & Data Analysis

All data reduction was performed using MATLAB. The analog signals from the limbs' force time series were low-pass filtered with a second order dual pass Butterworth with a cutoff frequency of 10 Hz. A 3-point difference algorithm was used to compute force velocity and acceleration signals. The force velocity and acceleration time series were filtered (Butterworth, 10 Hz) before performing the next differentiation. The analyses presented will focus on both unimanual force performance of the right and left limbs and bimanual force performance of the required force frequency ratio.

Unimanual measures. Inter-peak intervals and inter-peak variability were computed as the interval representing the time between two consecutive force peaks (Inter-peak interval = Forcepeak_{i+1} - Forcepeak_{i}). Inter-peak interval variability was defined as the standard deviation of the inter-peak intervals within a trial. These values were determined for both the left and right limb forces.

To quantify the deflections in the force-time series, force harmonicity (H) was determined. This value quantifies the harmonic nature of the forces produced by each limb for each half cycle. This measure is commonly used in research to quantify the harmonic nature of limb motion during repetitive aiming tasks (Buchanan et al. 2006; Guiard 1993). Recently, however, this measure has been used to quantify the perturbations in force time series (Kennedy et al. 2015; in press). An H index of 0 indicates that the force time series is inharmonic and that one or more adjustment or perturbation(s) has impacted the forces produced by the limb while an H index of 1 indicates a harmonic force production time series in which subtle adjustments and/or perturbations are not evident. Non-overlapping windows between pairs of force velocity zero crossings were defined in order to compute an index of force harmonicity (see Guiard 1993). Each window reflected the time interval from force onset to peak force velocity and the next interval reflected the time from force offset to peak force velocity release. Within each time window, all deflections in the force acceleration trace were identified. When an inflection occurred in the force acceleration trace within the window, H was computed as the ratio of minimum to maximum acceleration. When a single peak occurred in the force acceleration trace within this window, the value of H was set to 1. If the acceleration trace crossed from positive to negative (or vice versa) within this window, the value of H was set to 0. Finally, the individual force harmonicity values of each time window for a trial were averaged yielding a global estimate of force H.

To examine the control of force during the coordination task both the peak force and the mean force produced was calculated. The peak forces produced during the trial were calculated by averaging the peak force for each participant. The mean force produced was quantified by averaging the force produced during the trial. Note the goal coordination pattern required a peak force of 15 N and a mean force of 7.5 N.

Bimanual measures. Inter-peak intervals for the right and left limbs were used to determine point estimates of mean cycle duration and were used to compute a frequency ratio of right limb cycle duration to left limb cycle duration. This measure provides a temporal measure of goal attainment that is independent of limb coordination tendencies and actual limb force trajectories. An inter-peak interval ratio of 2.0 would indicate that the interval for the right limb was twice that of the left limb.

To examine the continuous spatial-temporal coordination of the limb forces, continuous phase angles for the two limbs were computed. The phase angle (θ_i) for each limb ($i = r,l$) was computed for each sample of the normalized force time series as follows (Kelso et al. 1986):

$$\theta_i = \tan^{-1}[(dX_i/dt)/X_i]$$

with X_i representing the normalized force of the right and left limbs and dX_i/dt the instantaneous normalized force velocities for the right and left limbs. Next, the individual phase angles θ_i were unwrapped by finding absolute jumps greater than 2π and adding appropriate multiples of 2π to each data point following the jump. After the unwrapping, regression analyses of the continuous relative phase angles for the right and left limbs were conducted to determine the slope of unwrapped left and right limb phase angles across the trial. The slope and R^2 of the right limb phase angles to left limb phase angles provides a continuous measure of bimanual goal attainment.

The mean inter-peak interval and phase angle slope ratios were analyzed in separate Condition (homologous, non-homologous) ANOVAs. Mean inter-peak interval, SD inter-peak interval, phase angle velocity, force harmonicity, peak force, and mean force were analyzed in separate Condition (homologous, non-homologous) x Limb (left, right) ANOVAs with repeated measure on limb. In the event of a significant interaction simple main effects analyses (Kirk, 1968) were performed to determine the locus of the interaction. An α =.05 was used for all tests.

Results

Fig. 2 provides sample force and force velocity times series (a) and resulting Lissajous displays (b) for two participant in the homologous condition while Fig. 3 provides sample force and force velocity times series (a) and resulting Lissajous displays (b) for two participants in the non-homologous conditions. The force and force velocity time series traces and normalized force velocity/normalized force plots resulting from the right (c,d) and left (e,f) limb forces are also provided in Fig. 2 and Fig. 3. In addition, grey bars are included to highlight the point of force initiation (force onset to peak force velocity) by the right limb while yellow bars highlight the release of force (force offset to peak force velocity release). The placement and width of the grey and yellow bars was determined by identifying peak velocity in each half cycle and then tracing backwards (force onset) and forwards (force offset) to 5% of peak velocity. Note, however, that determining force onset and offset was based upon kinematic measures and may not necessarily be a precise indicator of muscle activation and deactivation. Arrows are provided in the plot of the left limb force and velocity time series to indicate the proposed impact of right limb force onset and right limb force release on left limb forces.

Note the distinctly different pattern of interference observed between the homologous (Fig. 2e, f) and non-homologous (Fig. 3e, f) muscle conditions. In the homologous muscle condition both the grey and yellow bars capture the observed distortions in the left limb (Fig. 2e) while only the grey bars capture the observed distortions in the left limb in the non- homologous muscle condition (Fig. 3e). That is, in the homologous muscle condition it appears that as the right limb initiates force there is a corresponding increase in force in the left limb and when the right limb releases force there is a corresponding decrease in force produced by the left limb. However, in the non-homologous muscle condition it appears that only when the right limb initiates force as the left limb is releasing force is there a corresponding decrease in force in the left limb. The interference is not observed when the right limb is releasing force (yellow bars) in the non-homologous condition as it is observed in the homologous muscle condition (Fig. 2). Note, however, that in both the homologous and non-homologous muscle conditions that the observed interference in the force produced by the left limb continues until peak velocity is obtained by the right limb (c) resulting in observable distortions in both the force and velocity profiles of the left limb (e).

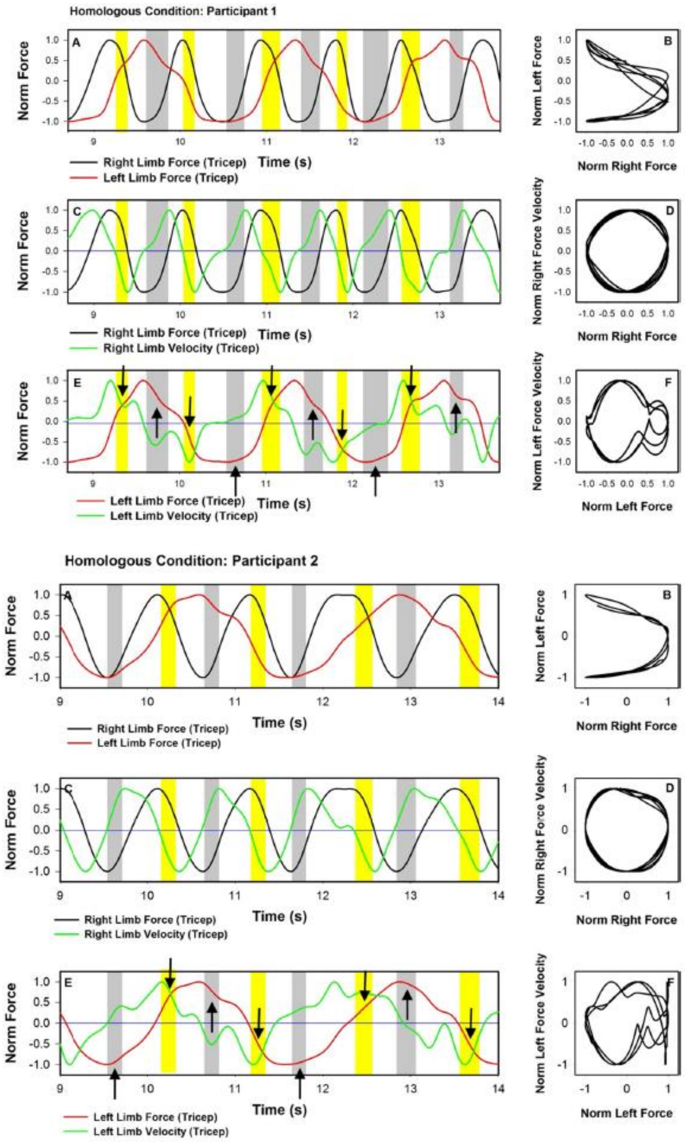


Fig. 2 Sample performance for homologous condition. The left and right limb force times series for a segment of the test trial and resulting Lissajous plot for two participants (*top* and *bottom* panels) are provided in a,b. In addition, the force and force velocity time series and velocity/force plots resulting from the right (c,d) and left (e,f) limb forces. The *gray bars* represent the time between force onset and peak force velocity for the right limb. The *yellow bars* represent the time between force release and peak force release velocity for the right limb. *Arrows* are provided in the plot of the left limb force and velocity time series to indicate the impact of right limb force onset on left limb forces (*upward pointing arrow*) and right limb force release on left limb forces (*downward pointing arrow*) (Kennedy et al. 2015).

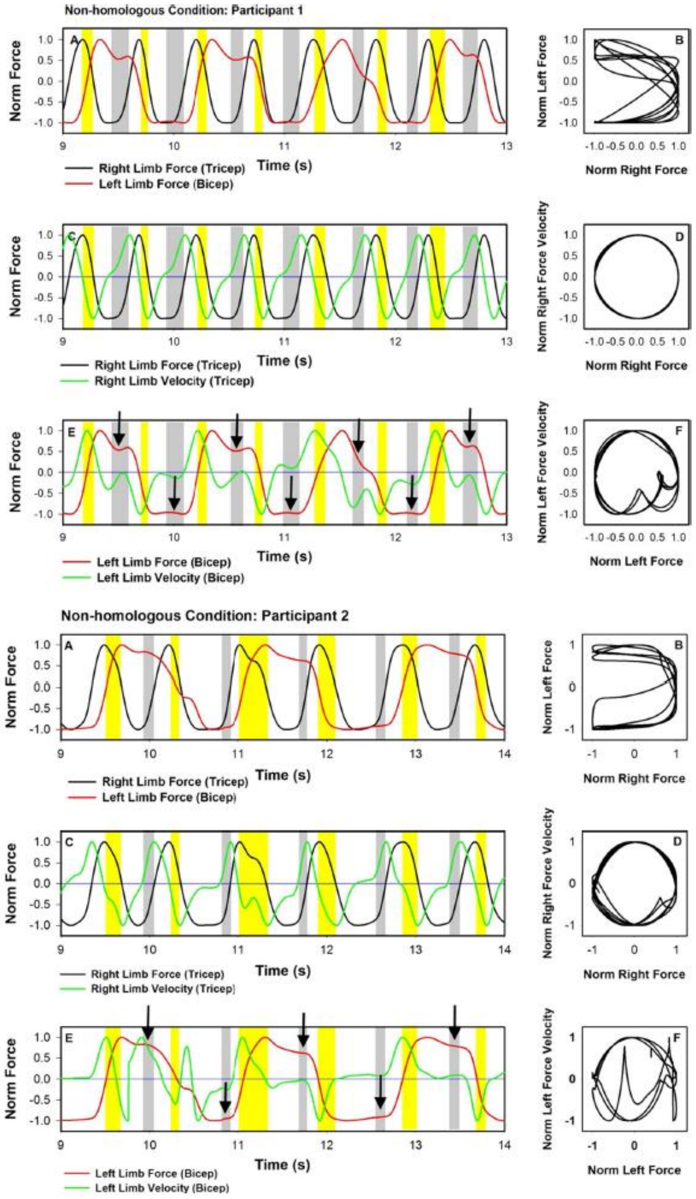


Fig. 3 Sample performance for non-homologous condition. The left and right limb force times series for a segment of the test trial and resulting Lissajous plot for two participants (*top* and *bottom* panels) are provided in a,b. In addition, the force and force velocity time series and velocity/force plots resulting from the right (c,d) and left (e,f) limb forces. The *gray bars* represent the time between force onset and peak force velocity for the right limb. The *yellow bars* represent the time between force release and peak force release velocity for the right limb. *Arrows* are provided in the plot of the left limb force and velocity time series to indicate the impact of right limb force onset on left limb forces (*upward pointing arrow*) and right limb force release on left limb forces (*downward pointing arrow*) (Kennedy et al. 2015).

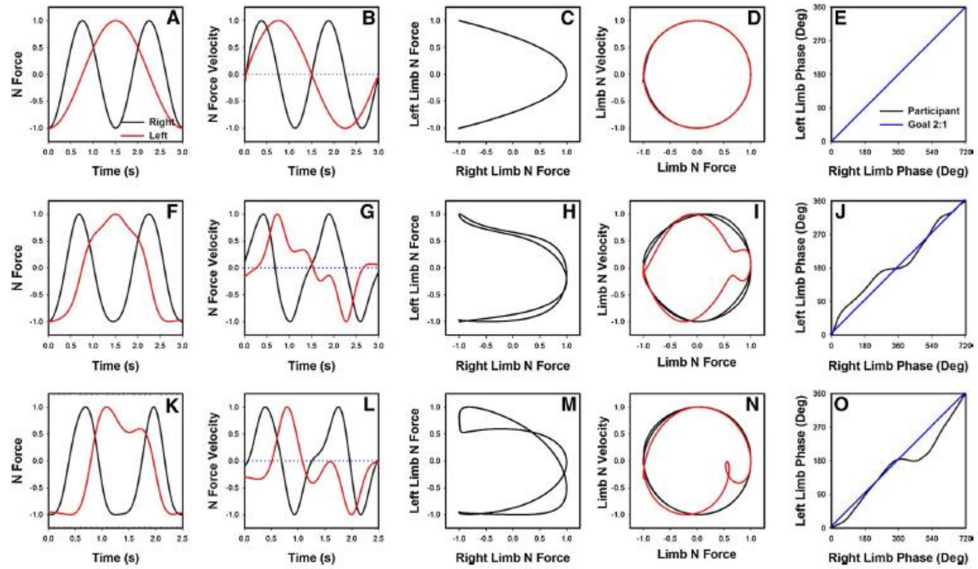


Fig. 4 One cycle of the 1:2 coordination pattern. The goal 1:2 (a-e) coordination pattern and examples of a participant's performance on one cycle of the 1:2 force coordination task in the homologous condition (f-j) and non-homologous condition (k-o) are provided. The figure includes left and right limb force (a,f,k), force velocity (b,g,l), Lissajous plots (c,h,m), force-force velocity plots (d,i,m), and relative angle phase plots (e,j,o). Note that the force-force velocity plots have the left (*red*) and right (*black*) limbs overlaid (Kennedy et al. 2015).

Fig. 4a-e depicts goal performance characteristics based on two cycles of force produced by the right limb for one cycle of force produced by the left limb (a-e). Sample performance for one participant in the homologous (f-j) and one participant in the non-homologous condition (k-o) are provided. For each condition the following plots are provided: the force and velocity times series for the left and right limbs (f,g and k,l), associated Lissajous plots (h and m), and overlaid force/force velocity plots for the left and right limbs (i and n), and left and right limb phase angle plots. These plots use the same examples depicted in Figs. 2 and 3. Note the distinctly different pattern of results for homologous and non-homologous muscle conditions. Mean unimanual measures for participants in the homologous and non-homologous conditions are provided in Fig. 5 and mean bimanual performance data are provided in Fig. 6.

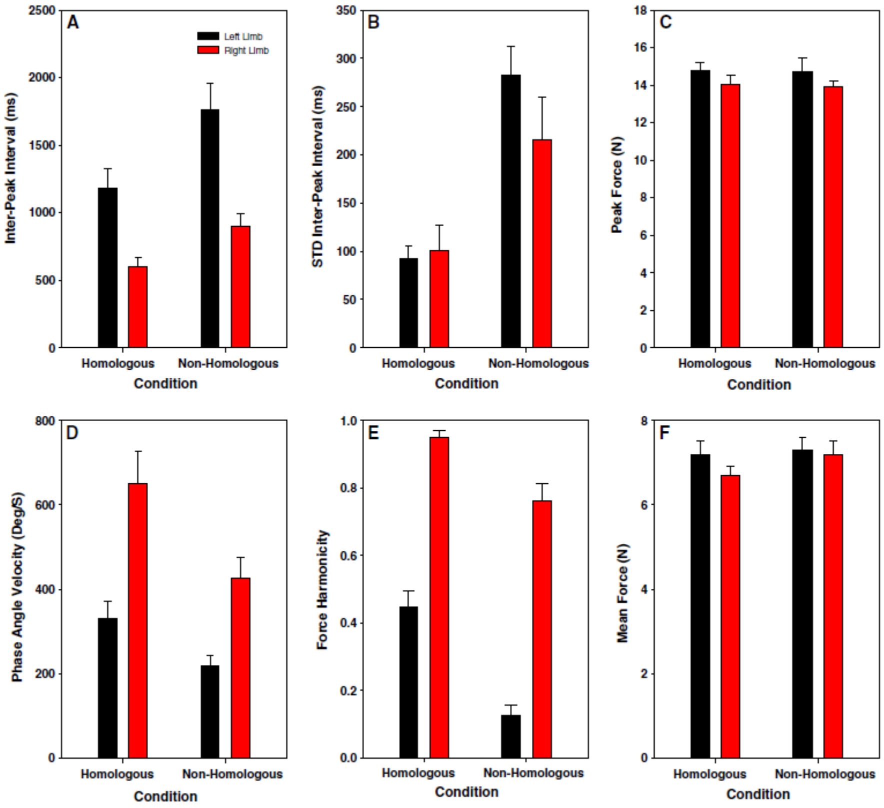


Fig. 5 Mean unimanual measures for Experiment I. The mean inter-peak interval (a), SD inter-peak interval (b), peak force (c), phase angle velocity (d), force harmonicity (e) and mean force (f), by task are provided. *Error bars* represent standard errors. Note that the right limb was faster and more harmonic than the left limb in both conditions (Kennedy et al. 2015).

Unimanual Analyses

Inter-peak interval. The analysis indicated main effects of Limb, F(1,10)=124.10, p<.01, and Condition, F(1,10)=5.92, p<.05. The Condition x Limb interaction, F(1,10)=4.88, p>.05 was not significant (Fig. 5A). The Limb effect, as would be expected for the task, indicated longer inter-peak-intervals for the left limb (M=1177 ms, SD=370 ms) than the right limb (M=599 ms, SD=176) in the homologous muscle condition and longer inter-peak intervals for the left limb (M=1766 ms, SD=465 ms) than the right limb (M=902 ms, SD=233) for the non-homologous muscle condition. The Condition effect indicated longer inter-peak-intervals for the non-homologous condition (M=1334 ms, SD=404 ms) than for the homologous muscle condition (M=888 ms, SD=294 ms).

SD Inter-peak interval. The analysis indicated a main effect of Condition, F(1,10) =19.21, p<.01. The main effect of Limb, F(1,10)=218, p>.05, and the Condition x Limb interaction, F(1,10)=1.24, p>.05, were not significant (Fig. 5b). The condition effect indicated the variability in the inter-peak-interval for Homologous muscle condition (M=22.48 ms, SD=12.5 ms) was lower than that for the Non-homologous muscle condition (M=51.59 ms, SD=7.23 ms).

Peak force. The analysis failed to detect main effects of Condition, F(1,10) = 0.07, p>.05, or Limb, F(1,10) =1.72, p>.05 (Fig. 5c). The Condition x Limb interaction also was not significant, F(1,10) <=10.0, p>.05. Note, participants were able to produce the maximum force required by the template (peak≈15N) with each (right and left) limb, in both conditions (homologous and non-homologous) (Fig. 5c).

Phase angle velocity. The main effects of Condition, F(1,10)=5.65, p<.05, and Limb F(1,10)=132.34, p<.01, were significant. The Condition x Limb interaction, F(1,10)=3.03, p<.05) was not significant (Fig. 5d). As expected for a 1:2 coordination task, the phase angle velocity for left limb was slower than for the right limb in both homologous and non-homologous conditions. However, the phase angle velocity for the respective left (M=330 deg/s, SD=100 deg/s) and right (M=649 deg/s, SD=191 deg/s) limbs in the homologous condition were higher than the phase angle velocities for the left (M=218 deg/s, SD=59 deg/s) and right (M=425, SD=125 deg/s) limbs in the non-homologous condition.

Force harmonicity. The analysis indicated main effects of Limb, F(1,10)=136.24, p<.01, and Condition, F(1,10)=6.42, p<.05. In addition, the Condition x Limb interaction, F(1,10)=8.34, p<.05, was significant (Fig. 5E). Simple main effect analysis indicated lower force harmonicity for the left (M=.44, SD=.12) compared to the right (M=0.95, SD=0.05) limb for the homologous condition. Lower force harmonicity was also observed in the left limb (M=0.13, SD=0.07) than the right limb (M=0.76, SD=0.012) for the non-homologous condition. This indicates more adjustments, hesitations, and/or perturbations to the left limb than to the right one.

Mean force. The analysis failed to detect main effects of Condition, F(1,10) = 0.01, p>.05, or Limb, F(1,10) =3.05, p>.05 (Fig. 5F). The Condition x Limb interaction also was not significant, F(1,10) =0.42, p>.05. Note, however, that participant's in both conditions and with both limbs were able to produce the required force (Fig. 5f).

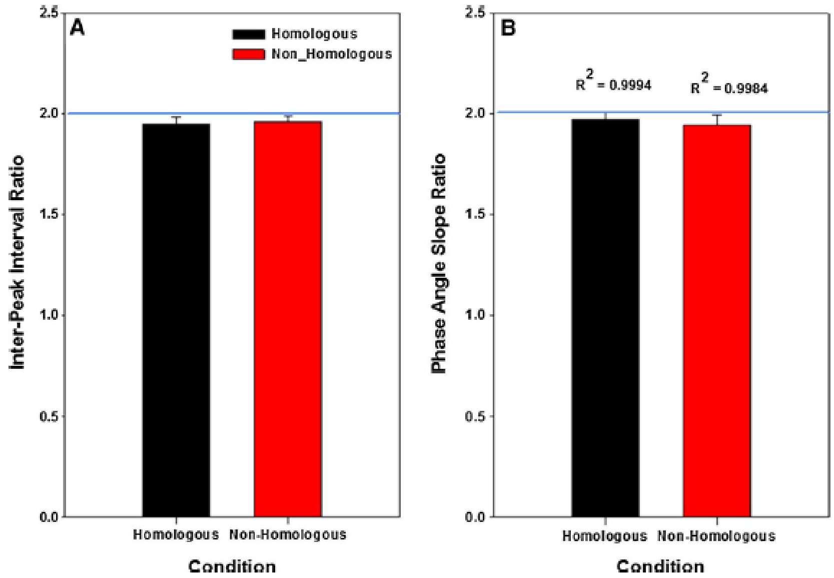


Fig. 6 Mean bimanual measures for Experiment I. The inter-peak interval ratio (a), and phase angle slope ratio (b), by task are provided. Note that the goal ratios (*blue*) are provided. *Error bars* represent standard errors. Both bimanual measures indicate the participants were able to perform the goal ratio within 14 trials (Kennedy et al. 2015).

Bimanual Analyses

Inter-peak interval ratio. Note that the goal inter-peak ratio for the 1:2 coordination task would be 2.00, with no variability. The inter-peak interval ratio for the homologous muscle condition (M=1.95, SD=.07) was very similar to the ratio for the non-homologous muscle condition (M=1.95, SD=.07) (Fig. 6a). Indeed, the analysis did not indicate a main effect of Condition, F(1,10) =0.36, p>.05. This indicates that based on point estimates that the participants were equally effective in producing the goal coordination pattern with both homologous and non-homologous muscles.

Phase angle slope ratio. As with the inter-peak interval ratio, the goal phase angle slope for the 1:2 coordination task would be 2.00, with no variability. The analysis did not indicate a main effect of Condition, F(1,10)=1.34, p>.05, with the phase angle slope for the Homologous muscles condition (M=1.97, SD=.02, R^2=0.99) similar to the phase angle slope for the Non-homologous muscle condition (M=1.94, SE=.05, R^2=.99) (Fig. 6B). This indicates that based on regression analyses of the continuous left and right limb phase angle data that the participants were equally effective in producing the goal coordination pattern with both homologous and non-homologous muscles.

Discussion

The present experiment was designed to determine participants' ability to coordinate a bimanual multi-frequency pattern of isometric force by activating either homologous (triceps-triceps) or non-homologous (triceps-biceps) muscles when provided integrated feedback in the form of Lissajous information. This form of integrated feedback has been shown to greatly reduce attentional and perceptual constraints on performance allowing motor constraints related to neural crosstalk to be more clearly observed. The purpose was to determine if the activation of homologous and non-homologous muscles resulted in perturbations in the pattern of force production consistent with neural crosstalk. The results indicated that participants were able to 'tune-in' the 1:2 goal pattern of rhythmical bimanual force with both homologous and non-homologous muscles when provided Lissajous feedback and a template of the goal pattern. Based upon the definition of neural crosstalk, it was hypothesized that interference should be more easily detected and characterized when the task required the activation of homologous muscles compared to when the task required the activation of non-homologous muscles. However, consistent and identifiable distortions in the left limb forces that could be associated with the production of force in the right limb in both conditions (Fig. 2-4) were observed. Interestingly, the pattern of distortion was different for the homologous and non-homologous tasks.

Lissajous Information

Research has consistently demonstrated that the 1:1 in-phase coordination pattern represents a powerful attractor state while other coordination patterns (e.g., anti-phase, 90^0 relative phase, 1:2, 3:5) are subject to spontaneous phase transitions to the more stable 1:1 in-phase pattern or lower order frequency ratios when the control parameter (e.g., frequency) is increased (Kelso 1984; Kelso 1995; Peper et al. 1995b,c; Treffner and Turvey 1993). These results have been explained using concepts taken from nonlinear dynamics and modeled using nonlinearly coupled limit cycle oscillators (Haken et al., 1985) formally referred to as the Haken, Kelso, and Bunz (HKB) model. The HKB model provides a mathematical description of the attractor landscape (i.e., coordination dynamics) in the form of a potential function ($V(\varphi)$), which represents the relative amount of energy required to maintain coordinated oscillation at a given relative phase (e.g., 0^0, 90^0, 180^0) (Bingham et al. 1999). A feature of this model is that both 1:1 (in-phase and anti-phase) coordination patterns are stable fixed point attractors, with the in-phase coordination pattern representing the more stable attractor state. Other phase and frequency patterns, however, act as repellers in the coordination landscape. Thus, when attempting to produce phase or frequency relationships other than 1:1 in-phase, any type of perturbation in one limb that pushes it toward the pattern of movement of the other limb could result in a phase transition to the more stable 1:1 in-phase coordination pattern.

In the current experiment, participants were able to 'tune-in' a 1:2 pattern of rhythmical bimanual force with both homologous and non-homologous muscles when provided Lissajous feedback. This result is similar to that observed with reciprocal and circling motion demonstrating that complex bimanual coordination patterns could be performed following relatively little practice when online integrated feedback (e.g. Lissajous displays) are provided and attentional distracters (i.e., metronome and vision of the limbs) are reduced (Boyles et al. 2012; Kovacs et al. 2009a; Kovacs et al. 2010a,b; Kovacs and Shea 2011). Extending this line of research to include multi-frequency patterns performed with non-homologous muscles provides further evidence for the robust utility of perceptual displays in facilitating complex bimanual coordination patterns (Boyles et al. 2012; Kennedy et al. 2013a; Kovacs et al. 2010a,b; Kovacs and Shea 201l; Mechsner et al. 2001).

The Lissajous displays used provided a goal template of the 1:2 coordination patterns along with on-line integrated visual information regarding the position of the two limbs as a single point in one plane. Participants were able to use this information to produce the goal pattern within a few minutes of practice with both homologous and non-homologous muscles. The Lissajous plots likely facilitated the successful performance of goal pattern because the integrated information greatly reduced the perceptual and attentional difficulties associated with the task (Kovacs et al. 2009a; Kovacs et al. 2010a,b; Kovacs and Shea 2011).

Despite the effectiveness of the Lissajous displays, it was possible to consistently detect perturbations in the forces exhibited by the left limb that could be attributed to the forces produced in the right limb. Note that Lissajous displays have been thought to reduce perceptual and attentional factors, but not constraints related to neural crosstalk. The existence of these perturbations points to motoric constraints still acting on the system. It is possible that the Lissajous information provided the system an opportunity to override the constraints that tend to pull the system toward more stable coordination patterns (e.g., 1:1), but do not totally eliminate the perturbations arising from motoric constraints (i.e., neural crosstalk). Presumably, if the Lissajous display was withdrawn, even these small perturbations to the left limb forces could result in unwanted shifts (i.e., phase transitions) in the coordination pattern.

Neural Crosstalk

In the homologous muscle conditions, as the right limb increased or decreased force production there were similar unintended increases or decreases in the force produced by the left limb. That is, as the right limb was initiating force production, the force in the left limb was also increased (at that point in the force time series) despite the fact that the left limb should have been decreasing force to maintain the desired coordination pattern. Similarly, as the right limb was initiating the release of force, the force in the left limb also decreased despite the need for the left limb to gradually increase force at this point. These results are consistent with neural crosstalk.

Neural crosstalk is a mirror image command dispatched to the homologous muscles of the contralateral limb (Cattaert et al. 1999; Swinnen 2002). Because neural crosstalk conveys the same information to the homologous muscles of both limbs (Aramaki et al. 2010; Cardoso de Oliveira 2002; Swinnen 2002), an assimilation effect may occur in which both limbs tend to produce similar activation patterns despite the task goal requiring disparate activation patterns. Assimilations effects have been noted with amplitude (e.g., Heuer et al. 2001; Sherwood 1994; Spijkers and Heuer 1995), directions (e.g., Franz et al. 1996; Swinnen et al. 2002; Swinnen et al. 2001), frequencies (e.g., Peper et al. 1995a,b,c; Treffner and Turvey 1993), and forces (e.g., Diedrichsen et al. 2003; Heuer et al. 2002; Steglich et al. 1999).

It is believed that symmetrical movements (i.e., 1:1 in-phase) are facilitated when the contralateral and ipsilateral signals are integrated while asymmetric movements (e.g., multi-frequency coordination patterns) suffer from perturbations due to conflicting information or partial intermingling of signals controlling the two arms (Cardoso de Oliveira 2002; Kagerer et al. 2003; Marteniuk et al. 1984). Therefore, interference from neural crosstalk occurs when a set of muscles in one limb is required to produce disparate activation patterns resulting from differences in amplitudes, directions, frequencies, forces, or phase relationships from the homologous muscles activated in the contralateral limb (Cardoso de Oliveira 2002). The failure to inhibit, suppress, or otherwise compensate for, the neural crosstalk may result in unwanted perturbations to the coordinated action or even prompt a phase transition to the more stable coordination pattern (Houweling et al. 2010). Indeed, in the homologous muscle conditions perturbations in the force produced by the left limb that were consistent with the notion of neural crosstalk were noted. That is, as the right limb was initiating the force pulse it is possible a consistent increase occurred in the left limb and when the right limb was initiating the release of force a consistent decrease in force occurred in the left limb. According to the crosstalk model this increase or decrease in the force noted in the left limb occurred when a mirror image command to increase or decrease force was also dispatched to the left limb.

Not only do the perturbations in the force produced by the left limb appear to be linked to the point of initiation and release of force in the right limb (Kennedy et al. 2013b), this influence continues to act on the left limb until the right limb achieves peak force velocity (Fig. 2). This result is consistent with previous research that examined the tri-phasic pattern of muscle activation in the triceps and biceps during an isometric contraction and found that the initial burst in the agonist muscle terminates at the point peak velocity is achieved (Gordon and Ghez 1984). If interference occurs in the left limb at the point of muscle activation in the right limb, it stands to reason that the interference continues until peak velocity is achieved.

Despite our initial hypothesis, interference in the condition which required the activation of non-homologous muscles occurred. Interference during the activation of non-homologous muscles was inconsistent with our initial predictions related to neural crosstalk. However, after further analysis, the point at which the interference occurred (Fig. 3) may provide further support for the argument that interference occurs when neural crosstalk conveys the same information to bilateral homologous muscles

(Aramaki et al.2010; Cardoso de Oliveira 2002; Swinnen 2002). In the non-homologous conditions, it appeared that interference only occurred when the right limb was initiating force production while the left limb was releasing force. More specifically, the non-homologous task required the right limb to activate the triceps to produce force while the left limb activated the biceps. When both the right triceps and left biceps (non-homologous muscles) were producing force distortions in the left limb were not observed. However, distortions were observed in the force trace when the right triceps was initiating force production while the left biceps was simultaneously releasing force. This result is consistent with a recent study examining the interactions between simultaneous contraction and relaxation of different limbs (Kato et al. 2014). The results of the study indicated the contraction in one limb induced unintended EMG activity in the antagonists of the relaxing muscle of the contralateral limb.

In the present experiment, there are two plausible explanations for the interference observed in the non-homologous muscle conditions that would be consistent with neural crosstalk. First, co-contraction in which the left triceps (antagonist) was activated to decelerate the force produced by the left biceps (agonist) may be occurring. That is, the antagonist muscle performs the opposite activation of the agonist to relax or slow down the contraction of the agonist muscle (Baechle and Earle 2000). Previous research investigating EMG patterns in the triceps and biceps during isometric contractions found that a small amount of co-activation occurred in the antagonist muscle during the initial burst of the agonist muscle (Gordon and Ghez 1984). If co-contraction of the antagonist muscle (left triceps) is occurring to slow down or break the force produced by the agonist (left biceps), there would be simultaneous activation in the triceps of both limbs resulting in homologous muscle activation during the non-homologous muscle condition. Therefore, it is possible the left biceps is releasing force by activating the antagonist muscle (left triceps) when a mirror image command to activate the right triceps is dispatched to the left triceps resulting in increased triceps activation. An increase in the activation to the triceps (antagonistic activity to the goal coordination pattern) could result in an increase in the breaking of the force produced by the left biceps or possibly even stop the release of force in the left biceps. However, antagonistic activity when the goal coordination pattern requires the left biceps to increase force would be to decrease triceps activation. A mirror image command to decrease force in the triceps would therefore facilitate the production of force in the left biceps and no interference would be observed. This may account for interference that was observed only when the biceps was releasing force (Fig 3 and 4k) during the non-homologous condition. This explanation is also consistent with the results of the recent study that found the contraction in one limb induced unintended EMG activity in the antagonists of the relaxing muscle of the contralateral limb (Kato et al. 2014). However, further research examining the pattern of agonist/antagonistic muscle activation during a multi-frequency pattern is needed to confirm this possibility.

Another possibility is motor overflow (crosstalk) from the right limb. Similar to motor overflow in unimanual force production (Todor and Lazarus 1986), when the left limb was not producing force the system failed to suppress the crosstalk from force production in the right limb. That is, interference only occurred in the left limb when the left limb was releasing force, essentially making the task a unimanual right limb task at the point the interference occurred. Motor overflow in the contralateral limb has been recognized in a number of unimanual studies (e.g., Armatas and Summers 2001; Cincotta et al. 2006; Ridderikhoff et al. 2005). Similar to the time scale observed in the homologous muscle condition, the interference observed in the non-homologous muscle condition occurred in the left limb from the point of force initiation in the right limb until peak velocity was achieved.

While consistent and identifiable distortions in the left limb forces that could be associated with the production of force in the contralateral limb were observed in both homologous and non-homologous conditions, a distinctive pattern of interference could be associated with the activation of homologous and non-homologous muscles. The overall results indicate that neural crosstalk manifests differently during the coordination of the limbs depending upon whether homologous or non-homologous muscles are activated.

Summary

The present experiment was designed to determine whether individuals can coordinate a bimanual 1:2 force pattern by activating either homologous (triceps-triceps) or non-homologous (triceps-biceps) muscles when provided integrated feedback in the form of Lissajous information and to determine if the activation of homologous and non-homologous muscles resulted in perturbation in the pattern of force production consistent with neural crosstalk. Participants were able to quickly ‘tune-in’ the pattern of rhythmical bimanual force with both homologous and non-homologous muscles.

Consistent and identifiable distortions in the left limb forces that could be associated with the production of force in the contralateral limb were detected in both the homologous and non-homologous conditions. However, distinctive patterns of interference were associated with the activation of homologous and non-homologous muscles. It appears that the interference occurred in the left limb at the point of homologous muscle activation and/or when the right limb was releasing force. The results also indicated that this interference continued from the point of force initiation and/or release to peak force velocity. The overall results indicated that neural crosstalk manifests differently during the coordination of the limbs depending upon whether homologous or non-homologous muscles were activated.

CHAPTER IV

EXPERIMENT II

Introduction

Numerous investigations have demonstrated that many bimanual tasks which require frequency relationship other than 1:1 in-phase (e.g., 2:3, 3:5) are difficult to perform without extensive practice (e.g., Byblow et al. 1998; Byblow and Goodman 1994; Puttemans et al. 2005; Summers et al. 1993 a,b; Swinnen et al. 1997). However, more recent research has indicated that a variety of multi-frequency coordination patterns can be performed remarkably well following only a few minutes of practice when provided online integrated feedback (e.g., Lissajous plots with goal movement template) and other attentional distractions are reduced (e.g., vision of the limbs, metronomes) (Kovacs et al. 2010a,b; Kovacs and Shea 2011). Recently, this line of research has been extended to include the coordination of multi-frequency bimanual patterns of force (Kennedy et al. 2015, in press). Interestingly, when the bimanual task involved the production of isometric forces identifiable and consistent perturbations were observed in the forces produced by the left limb that were coincident with the initiation and release of force in the right limb.

A possible source of these distortions is neural crosstalk. Neural crosstalk is believed to occur when a mirror image of the command(s) sent to one muscle group is also dispatched to the homologous muscles of the contralateral limb (e.g., Cattaert et al. 1999; Swinnen 2002). As such, neural crosstalk conveys the same information to both limbs via cortical and subcortical pathways. In symmetric 1:1 in-phase bimanual coordination task neural crosstalk is not likely to cause interference between the limbs because the commands to both limbs are congruent (Maki et al. 2008). In fact, it is believed that 1:1 in-phase task is stabilized when complementary contralateral and ipsilateral signals are integrated (e.g., Cardoso de Oliveira 2002; Kagerer et al. 2003; Maki et al. 2008; Marteniuk et al. 1984). However, during multi-frequency tasks the commands to each limb are often in conflict (Summers et al. 1993b). Thus, performance of multi-frequency coordination patterns can suffer from ongoing interference believed to result from the conflicting information or partial intermingling of signals controlling the two limbs (e.g., Cardoso de Oliveira 2002; Kagerer et al. 2003; Maki et al. 2008; Marteniuk et al. 1984). Indeed, Kennedy, Boyle, Wang, and Shea (in press) compared the bimanual production of 1:1 in-phase and 1:2 force patterns (Experiment 3). Consistent with the notion of neural crosstalk, the results from the 1:2 task indicated distortions in the left limb forces and force velocity time series for participants that were not present in the 1:1 task. The distortions observed in the 1:2 task occurred in the forces produced by the left limb when the right limb was initiating or releasing a force pulse. However, distortions in the forces produced by the right limb that could be attributable to the forces produced by the left limb were not observed.

This type of asymmetric neural crosstalk has been associated with hemisphere/hand dominance (e.g., Cattaert et al. 1999; de Poel et al. 2007; Serrien et al. 2003; Treffner and Turvey 1995). That is, in right limb dominant individuals, the dominant left hemisphere exerts a stronger influence on the non-dominant left limb than the non-dominant right hemisphere on the dominant right limb (e.g., Kagerer et al. 2003; Maki et al. 2008). Consistent with this notion several studies have indicated greater stability during multi-frequency bimanual tasks when the preferred (right limb in right limb dominant participants) limb is assigned the higher frequency (e.g., Byblow and Goodman 1994; Byblow et al. 1998; Peters 1980, 1985). Other studies, however, has provided evidence that the faster moving limb performs more accurately than the slower moving limb regardless of hand dominance (e.g., Peper et al. 1995c; Peter and Schwartz 1989; Summers et al. 1993b). As such, it has been suggested that the slower moving limb is coupled to the faster moving limb (Peper et al. 1995c). Therefore, it is possible that the influence of the right limb on the left limb forces observed in the previous experiments by Kennedy and colleagues (2015, in press) was the result of the faster frequency and hence the greater force velocity changes in the right limb rather than a bias strictly associated with limb dominance.

It is important to note, that attentional factors have also been implicated as a possible source for the conflicting results regarding the role of limb dominance and limb assignment in the performance asymmetries observed in bimanual coordination tasks (e.g., Amazeen et al. 1997; 2004a; Peters 1985, 1987; Peters and Schwartz 1989). That is, the effect of limb dominance in bimanual tasks may be related to the amount of attention that is directed to each limb (Peters 1985; 1987). In multi-frequency coordination tasks, participants are more likely to focus attention on the fast limb (Peters and Schwartz 1989). However, when participants were instructed to deliberately focus attention on the non-dominate limb the asymmetry typically associated with limb dominance was reduced (de Poel et al. 2006). Given this attentional bias noted in previous research, the use of Lissajous feedback may prove advantageous in determining whether limb assignment or a bias associated with limb dominance is responsible for the asymmetries often noted in multi-frequency coordination tasks (e.g., Peper et al. 1995c; Peters 1985; Peters and Schwartz 1989).

Lissajous feedback has been used in several experiments involving a variety of bimanual coordination tasks (e.g., Boyles et al. 2012; Kovacs et al. 2010a,b; Kovacs and Shea 2011; Swinnen et al. 1997). The general results of such studies have indicated that this type of feedback information allowed participants to produce a wide variety of multi-frequency (e.g., 1:2; 2:1, 3:2, 4:3, 5:3) coordination patterns following only a few minutes of practice. It is believed that Lissajous displays facilitate the successful performance of complex multi-frequency coordination patterns because the integrated information greatly reduces the attentional difficulties associated with the task (Kovacs et al. 2009a, 2010a,b; Kovacs and Shea 2011). That is, participants do not need to split their attentional focus between two limbs because the Lissajous feedback provides information regarding the position of the two limbs as a single point in one plane. As such, it may be possible to more clearly determine the influence of limb assignment without regard to attentional bias on the coordination dynamics when Lissajous displays are used.

Therefore, the present experiment was designed to determine if the influence of force produced by one limb on the forces produced by the contralateral limb could be a result of the limb assigned the faster frequency on the limb performing the slower frequency or a bias associated with limb dominance. Participants were required to rhythmically coordinate a pattern of isometric forces in a 1:1, 1:2, or 2:1 coordination pattern. Lissajous displays with goal templates were provided to guide performance. The 1:2 task required the right limb to perform the faster rhythm while the 2:1 task required the left limb to perform the faster rhythm. The 1:1 task was used as a control. If the limb producing the faster frequency was responsible for the distortions observed in the slower limb it was hypothesized that distortions would only be observed in the limb performing the slower pattern of force. If a bias associated with limb dominance was responsible for the distortions observed in the contralateral limb, it was hypothesized that in right-limb dominant participants the right limb would influence the left limb, regardless of whether the limb was responsible for the fast or slow frequency.

Methods

Participants

Ten young adults (mean age=21.7, 6 males and 4 females) with little or no musical experience volunteered to participate in the experiment. All participants were right limb dominant according to a standardized survey (Oldfield 1971). The Institutional Review Board at Texas A&M University approved the procedures, and participants provided written informed consent before participation in the study.

Apparatus

The apparatus used in Experiment II was identical to that used in Experiment I**.**

Procedure

The procedure for Experiment II was similar to Experiment 1 except participants were asked to rhythmically produce 1:1, 1:2, and 2:1 patterns of isometric forces with

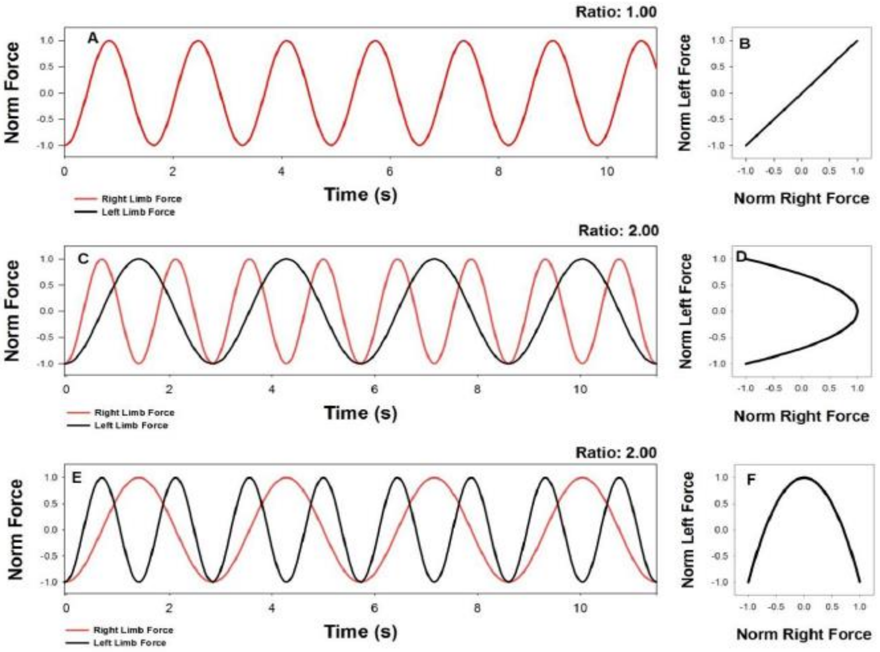


Fig. 7**.** Goal coordination patterns and templates for Experiment II. The goal coordination pattern and corresponding Lissajous template for the 1:1(a,b), 1:2 (c,d), and 2:1 (e,f) tasks. Note that the 1:2 task required the right limb to produce two patterns of force for every one pattern produced by the left limb while the 2:1 task required the left limb to produce two patterns of force for every one pattern produced by the right limb.

homologous muscles. Note that the 1:2 bimanual force coordination pattern required the right limb to produce two patterns of force for each pattern produced by the left limb while the 2:1 pattern required the left limb to produce two patterns of force for each pattern produced by the right limb. The 1:1 control coordination pattern required both limbs to produce the same pattern of force simultaneously. The goal template illustrated the specific pattern of force requirements needed to produce the goal coordination pattern of 1:1, 1:2, or 2:1 (see Fig. 7).

Measures & Data Analysis.

Data measures in Experiment II used the same calculations as in Experiment I. Note, however, for the bimanual measures a fast to slow ratio was computed rather than the traditional right limb to left limb ratio (2.0, 0.5) to allow for a more direct comparison of the frequency ratios for the 1:2 and 2:1 tasks. More specifically, an inter-peak interval ratio of 2.0 would indicate that the interval for the right limb is twice as fast as the left limb whereas an inter-peak interval ratio of 0.5 would indicate that the interval for the left limb is twice as fast as the right limb. However, by calculating a fast to slow ratio rather than the typical right to left ratio an inter-peak interval of 2.0 would indicate that one limb is twice as fast as the contralateral limb.

The mean inter-peak interval ratio, and phase angle slope were analyzed in separate Task (1:1, 1:2, 2:1) ANOVA with repeated measures on Task. Mean inter-peak interval, SD inter-peak interval, phase angle velocity, force harmonicity, peak force, and mean force were analyzed in separate Task (1:1, 1:2, 2:1) x Limb (left, right) ANOVAs with repeated measure on all factors. In the event of a significant interaction simple main effects analyses (Kirk, 1968) were performed to determine the locus of the interaction. An $\alpha = .05$ was used for all tests.

Results

Fig. 8-10 provides sample force and force velocity times series (a) and resulting Lissajous displays (b) for one participant in the 1:1 (Fig. 8), 1:2 (Fig. 9), and 2:1 (Fig. 10) tasks. The force and force velocity time series traces and normalized force velocity/normalized force plots resulting from the right (8c-d, 9d-f, 10d-f) and left (8e-f, 9g-i,10g-i) limb forces are also provided. In addition, grey bars are included in Fig. 9-10 to highlight the point of force initiation (force onset) to peak force and the onset of force release to peak force release velocity by the right limb (left panel) while yellow bars highlight force initiation (force onset) to peak force velocity and the release of force (force offset) to peak force release velocity by the left limb (right panel). The placement and width of the grey and yellow bars was determined by identifying peak force velocity and peak force velocity release in each half cycle and then tracing backwards to 5% of peak velocity (force onset or force release onset).

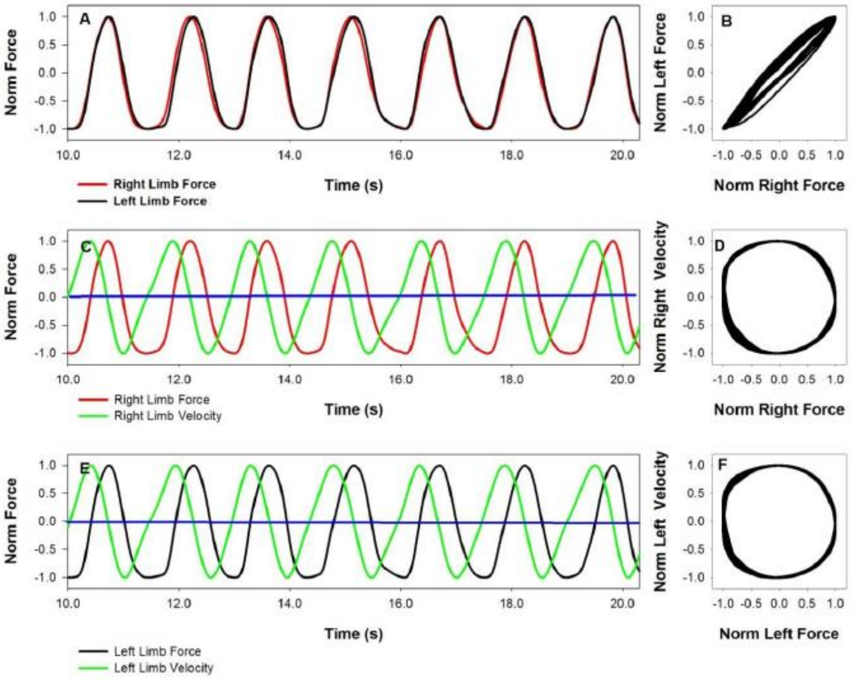


Fig. 8. Sample performance for 1:1 task. The left and right limb force times series for a segment of the test trial and resulting Lissajous plot for one participant are provided in a,b. In addition, the force and force velocity time series and velocity/force plots resulting from the right (f, g) and left (h,i) limb forces.

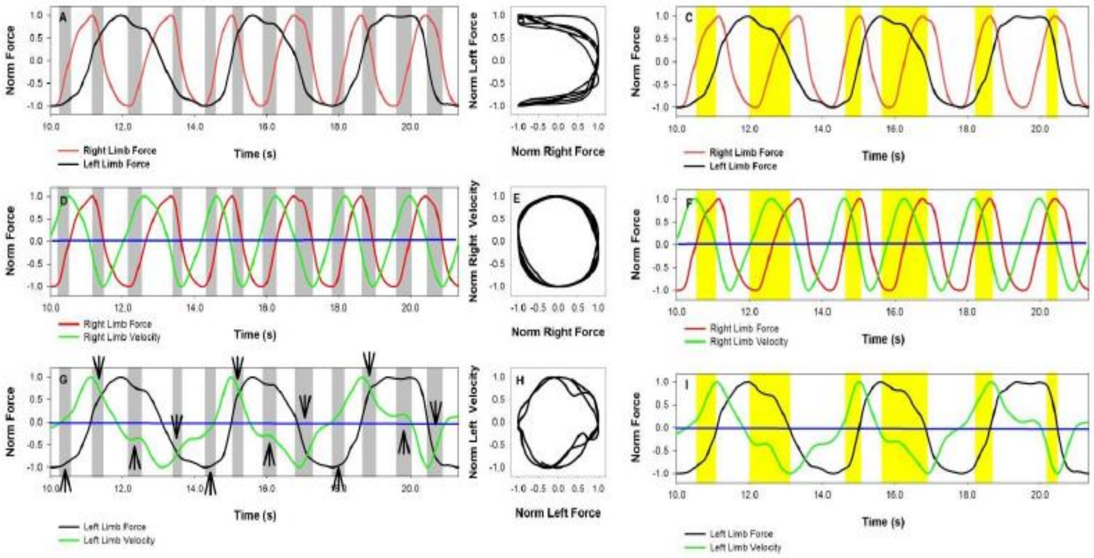


Fig. 9 Sample performance for 1:2 task. The left and right limb force times series for a segment of the test trial and resulting Lissajous plot for one participant are provided in a, b and c. In addition, the force and force velocity time series and velocity/force plots resulting from the right (d-f) and left (g-i) limb forces. The *gray bars (left panel)* represent the time between force onset or force release and peak force velocity for the right limb. The *yellow bars (right panel)* represent the time between force onset or force release and peak force velocity for the left limb. Note that the *gray bars* capture the distortions in the left limb trace (a, *black trace*) indicating the initiation and release of force in the right limb is influencing the force produced by the left limb. However, the *yellow bars* do not capture distortions in the right limb. This indicates that the initiation or release of force in the left limb is not influencing the force produced by the right limb. *Arrows* are provided to demonstrate the impact the initiation (*upward pointing arrow*) or release of force (*downward pointing arrow*) by one limb has on the force and force velocity of the contralateral limb.

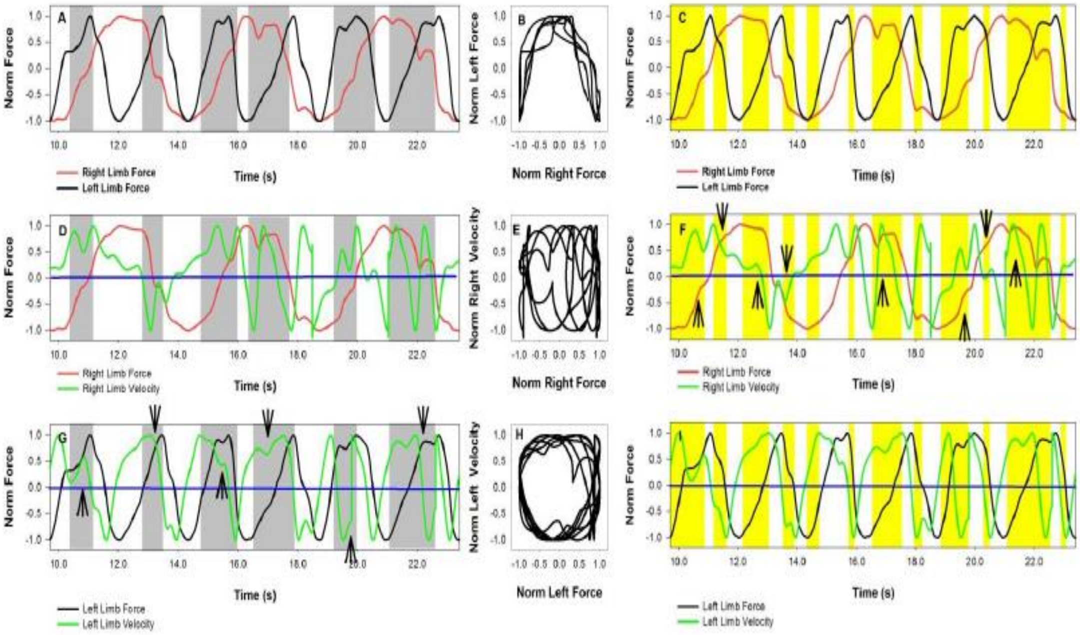


Fig. 10. Sample performance for 2:1 task. The left and right limb force times series for a segment of the test trial and resulting Lissajous plot for one participant are provided in a, b and c. In addition, the force and force velocity time series and velocity/force plots resulting from the right (d-f) and left (g-i) limb forces. The *gray bars (left panel)* represent the time between force onset or force release and peak force velocity for the right limb. The *yellow bars (right panel)* represent the time between force onset or force release and peak force velocity for the left limb. Note that both the *gray* and *yellow bars* capture the distortions observed in the force-time series. This indicates that the initiation or release of force in one limb influenced the force produced by the contralateral limb. *Arrows* are provided to demonstrate the impact the initiation (*upward pointing arrow*) or release of force (*downward pointing arrow*) by one limb has on the force and force velocity of the contralateral limb.

Note that distinctly different patterns of interference were observed between the 1:2 (Fig. 9) and 2:1 (Fig. 10) tasks, while interference was not observed in the 1:1inphase (Fig. 8) task. The interference in the 1:2 task occurred in the left limb when the right limb was initiating and releasing force while interference in the force produced by the right limb that could be associated with the initiation and/or release of force by the left limb was minimal. In the 2:1 task it appears that interference occurs in both the left and right limb (Fig. 10). Note, both the grey and yellow bars capture the time interval where distortions were observed in the 2:1 (Fig. 10a,c) task while only the grey bars capture the time interval where distortions were observed in the left limb in the 1:2 (Fig. 9a) task. Also note that the interference continues until peak velocity is achieved (width of gray and yellow bars). Mean unimanual measures for participants by task are provided in Fig. 11 and mean bimanual performance data are provided in Fig. 12.

Unimanual Analyses

Inter-peak interval. The analysis failed to detect main effects of Task, F(2,45) =1.17, p>.05, or Limb, F(1,45) <1.0, p>.05. However, the analysis indicated a significant Task x Limb interaction, F(2,45)=52.26, p<.0001. Simple main effects analysis indicated similar inter-peak intervals for the left (M=566.08 ms, SD=73.64 ms) and the right (M=577.91 ms, SD=74.21 ms) limbs for the 1:1 task, but longer inter-peak intervals for the left (M=879.86 ms, SD=144.31 ms) limb than the right (M=449.87 ms, SD=76.1 ms) limb for the 1:2 task while the inter-peak intervals for the right (M=476.4 ms, SD=56.85 ms) limb was longer than the left (M=948.92 ms, SD=122.68 ms) limb for the 2:1 task (Figure 11a).

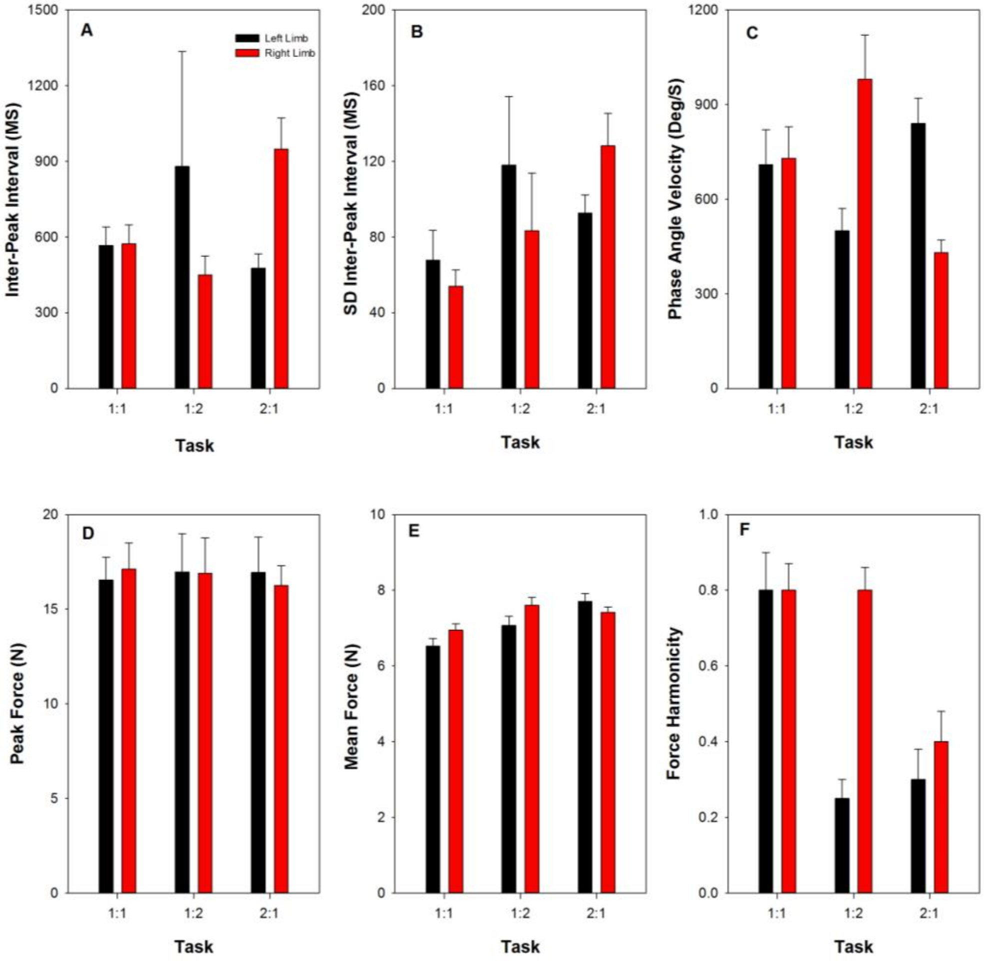


Fig. 11. Mean unimanual measures for Experiment II. Mean inter-peak intervals (a), SD inter-peak intervals (b), phase angle velocity (c), peak force (d), mean force (e), and force harmonicity (f), by task are provided. Error bars represent standard errors. Note the reduced harmonicity in the left limb in the 1:2 task and both the right and left limbs in the 2:1 task when compared to the 1:1 task.

SD Inter-peak interval. The analysis failed to detect main effects of Task, F(2,45)=1.5, p>.05, or Limb, F(1,45) <1.0, p>.05. However, the analysis indicated a significant Task x Limb interaction, F(2,45)=8.17, p<.01. Simple main effects analysis indicated larger SD inter-peak intervals for the left (M=67.74 ms, SD=50.11 ms) than the right (M=54.11 ms, SD=27.17 ms) limbs for the 1:1 task and larger SD inter-peak intervals for the left (M=117.94 ms, SD=114.95 ms) limb than the right (M=83.33 ms, SD=96.43 ms) limb for the 1:2 task. However, the SD inter-peak intervals for the left (M=92.62 ms, SD=30.76 ms) limb was smaller than the right (M=128.24 ms, SD=54.49 ms) limb for the 2:1 task (Figure 11b).

Phase angle velocity. The analysis failed to detect main effects of Task, F(2,45) < 1, p>.05, or Limb, F(1,45) =1.44, p>.05. However, the Task x Limb interaction, F(2,45) = 85.36, p<.01 was significant. Simple main effects analysis indicated similar phase angle velocities for the left (M=713^{o}/s, SD=348^{o}/s) and the right (M=728^{o}/s , SD=330^{o}/s) limbs for the 1:1 task, but the phase angle velocity for the left (M=499^{o}/s, SD=217^{o}/s) limb was slower than the right (M=976^{o}/s, SD=428^{o}/s) limb in the 1:2 task and the phase angle for the right (M=429^{o}/s, SD=141^{o}/s) limb was slower than the left (M=827^{o}/s, SD=245^{o}/s) limb in the 2:1 task (Fig. 11c).

Peak force. The analysis failed to detect main effects of Task, F(2,45) < 1.0 p>.05, or Limb, F(1,45) < 1.0, p>.05. The Task x Limb interaction also was not significant, F(2,45)=1.86, p>.05 (Fig. 11d).

Mean force. The analysis indicated a main effect of Task, F(2,45) =8.91, p<.01. Duncan's Multiple Range Test indicated that the mean force produced by participants in the 1:1 (M=6.74, SD=.59) task was significantly lower than the mean force produced by participants in the 1:2 (M=7.34, SD=.75) and the 2:1 (M=7.58, SD=.61) tasks, which did not differ. The main effect of Limb, F(1,45)= 2.06, p>.05 was not significant nor was the Task x Limb interaction, F(2,45)=2.62, p>.05 (Fig. 11e).

Force harmonicity. The analysis indicated main effects of Task, F(2,45)=14.24, p<.001, and Limb, F(1,45)=22.0, p<.01. In addition, the Task x Limb interaction, F(2,48)=10.03, p<.01, was significant. Simple main effect analysis indicated similar force harmonicity for the left (M=0.8, SD=.07) and the right (M=0.8, SD=0.1) limbs in the 1:1 task. In the 1:2 task force harmonicity was higher in the right limb (M=0.8, SD=0.05) than in the left (M=0.2, SD=0.05) limb. In the 2:1 task, no differences were detected between the right (M=0.4, SD=0.05) and left (M=0.3, SD=0.08) limbs although the harmonicity values were smaller than those observed in the 1:1 control task (Fig. 11f). Low harmonicity scores indicate more adjustments, hesitations, and/or perturbation are occurring.

Bimanual Analyses

Inter-peak interval ratio. Note that the goal inter-peak ratio for the 1:1 coordination task would be 1.00 while the goal inter-peak ratio for the 1:2 and 2:1 coordination tasks would be 2:00, with no variability. The analysis indicated a main effect of task, F(2,18)=415.28, p<.01, with the ratio for the 1:1 coordination task (M=0.99, SD=.03), as expected, lower than for the 1:2 and 2:1 coordination tasks which did not differ. Indeed, the inter-peak interval ratio for the 1:2 task (M=1.97, SD=.07) was very similar to the ratio for the 2:1 task (M=1.99, SD=.15). Although the results indicate a main effect of task, it is important note that participants effectively produced the inter-peak ratio required for the each goal coordination pattern (Fig. 12a).

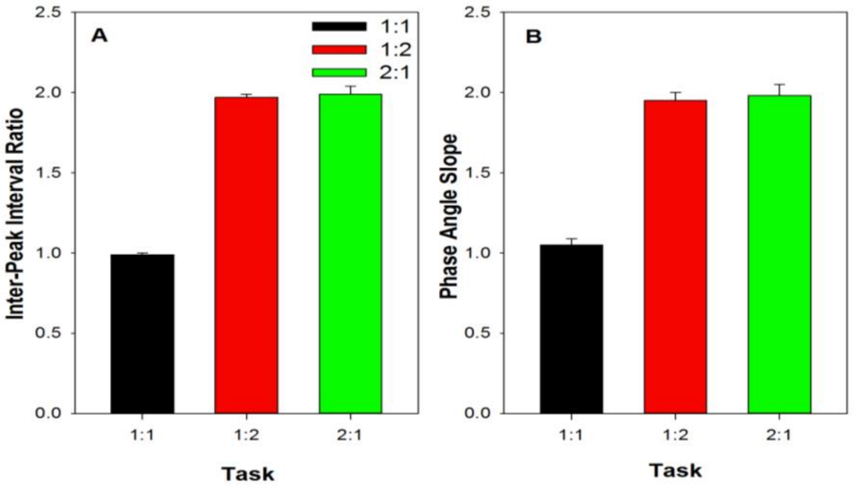


Fig.12 Mean bimanual measures for Experiment II. The inter-peak interval ratio (a), and phase angle slope (b), by task are provided. *Error bars* represent standard errors.

*Phase angle slope***.** As with the inter-peak interval ratio, the goal phase angle slope for the 1:1 coordination task would be 1.00 while the goal phase angle slope for the 1:2 and 2:1 coordination tasks would be 2:00, with no variability. The analysis indicated a main effect of Task, F(2,18)=81.84, p<.01, with the phase angle slope for the 1:1 (M=1.05, SD=.12, R^2=0.99) coordination task, as expected, lower than for both the 1:2 and 2:1 coordination tasks while the phase angle slope for the 1:2 task (M=1.95, SD=.16, R^2=0.98) was similar to the phase angle slope for the 2:1 task (M=1.98, SD=.21, R^2=.90) (Fig. 12b). This indicates that based on regression analyses of the continuous left and right limb phase angle data that the participants were able to effectively produce all three of the goal coordination patterns.

Discussion

The present experiment was designed to determine if the influence of the forces produced by one limb on the contralateral limb could be the result of the limb assigned the faster frequency on the limb performing the slower frequency and/or a bias associated with limb dominance. Participants (N=10) were required to rhythmically coordinate bimanual patterns of isometric forces in a 1:1, 1:2, or 2:1 coordination pattern. The 1:2 task required the right limb to perform the faster frequency while the 2:1 task required the left limb to perform the faster frequency. The 1:1 task was used as a control. If the limb assigned the faster rhythm was responsible for the distortions observed in the slower limb, it was hypothesized that distortions would only be observed in the force trace of the limb producing the slower pattern of force. If a bias associated with limb dominance was responsible for the distortions observed in the contralateral limb, it was hypothesized that in right-limb dominant participants the right limb would influence the left limb, regardless of whether the right limb was performing the faster or slower frequency. In the 1:2 task distortions in the force produced by the left limb were observed that could be attributed to the production of force by the right limb, however, no such distortions were observed in the right limb. In 2:1 task identifiable distortions were observed in the force produced by both the left and right limb that could be associated with the production of force in the contralateral limb. This suggests that both the increased rate of force production in the faster limb and limb dominance played roles in the influence the production of force in one limb has on the production of force in contralateral limb.

Lissajous Feedback

During the coordination of multi-frequency patterns, previous research has often demonstrated that the movement of the dominant limb is more accurate and stable when assigned the faster frequency (e.g., Peters and Schwartz 1989) whereas if the non-dominant limb is assigned the faster frequency it has a detrimental effect on participants ability to coordinate the required frequency ratio (e.g., Byblow and Goodman 1994; Byblow et al. 1998, Summers et al. 2002). More recent research, however, has indicated that many of the difficulties associated with coordinating multi-frequency patterns appear to be circumvented, or at least minimized, when online integrated feedback (e.g., Lissajous displays) is provided (e.g., Boyles et al. 2012; Hessler et al. 2010; Kovacs et al. 2010b). The use of Lissajous displays to coordinate multi-frequency patterns of force, however, have been limited to investigations in which the right, dominant limb has been assigned the faster frequency (Kennedy et al. 2015; in press). As such, it remained to be determined whether participants could use Lissajous information to quickly produce the required coordination pattern when the left, non-dominant limb was required to perform the faster pattern of force. Based upon two global measures of goal attainment (i.e., inter-peak interval ratio and phase angle slope ratio) the results of the current investigation indicated that participants were able to perform the required frequency ratios equally well when the left limb was required to perform the faster frequency as when the right limb was required to perform the faster frequency (Fig. 6). This result provides further evidence for the robust utility of perceptual displays in facilitating multi-frequency bimanual coordination patterns (Boyles et al. 2012; Kennedy et al. 2015, in press; Kovacs et al. 2010a,b; Kovacs and Shea 201l; Mechsner et al. 2001).

Despite the effectiveness of the Lissajous displays in facilitating the goal coordination patterns, in the multi-frequency tasks different patterns of interference were observed in the forces produced by the limb assigned the faster frequency. When the right limb was assigned the faster frequency (1:2 task), only distortions in the forces produced by the left (slower) limb that could be associated with the initiation or release of force by the right (faster) limb were observed (Fig. 9). However, when the left limb was assigned the faster frequency (2:1 task) distortions in the force produced by both the left (faster) and right (slower) limb that could be associated with the initiation or release of force by the contralateral (faster and slower) limb were observed (Fig. 10). Note, that no such distortions were observed in the in-phase 1:1 task (Fig. 8). This finding is consistent with the decreased harmonicity values for both the left and right limbs when the left limb was assigned the faster frequency, and the decreased harmonicity values for the left limb when the right limb was assigned the faster frequency compared to the relatively high harmonicity values (≈ 0.8) for both limbs when producing the same frequency. Note that reductions in harmonicity are consistent with the increased perturbations observed in the force time series. Observed distortions in the left limb, when assigned the faster rhythm is consistent with the notion that the source of interference is not strictly related to the influence of the faster frequency on the slower frequency limb and provides evidence that the dominant limb has an influence on the non-dominant limb even when the dominant limb is performing the slower pattern of force.

Limb Dominance and Neural Crosstalk

When participants are required to produce two conflicting motor sequences simultaneously, interference between the limbs is often observed (e.g., Byblow and Goodman 1994; Peper et al. 1995c; Summers et al. 1993). Typically, the observed interference is asymmetric in nature (e.g., Aramaki et al. 2006; Cattaert et al. 1999; de Pool et al. 2007; Kennedy et al. 2015, in press; Kragerer et al. 2003; Maki et al. 2008; Peters 1985; Semjen et al., 1995). That is, the dominant limb appears to have a greater impact on the contralateral limb than vice versa. For example, Peters (1985) required participants to tap 1:2 and 2:1 rhythms. The results of the study indicated slower tapping rates and increased variability when right limb dominant participants were required to tap with the left limb at twice the frequency of the right limb (i.e., 2:1) than when they were required to tap with the right limb at twice the frequency of the left limb (i.e., 1:2). Consistent with this result, a number of investigations have provided evidence that bimanual performance is more accurate and/or stable when the dominant limb is assigned the faster frequency (e.g., Byblow and Goodman, 1994; Byblow et al. 1998; Summers et al. 2002). It has been suggested that hand dominance affects bimanual coordination via an asymmetry in the strength of neural crosstalk (Treffner and Turvey, 1995). That is, the dominant hemisphere exerts a stronger influence on the non-dominant limb than the non-dominant hemisphere does on the dominant limb (Aramaki et al. 2006; Cattaert et al. 1999; Kragerer et al. 2003; Maki et al. 2008). As such, cortical and subcortical crosstalk has been identified as a potential source for the asymmetries noted in bimanual performance (Aramaki et al. 2006; Cattaert et al. 1999; Swinnen 2002). Indeed, Cattaert and colleagues (1999) successfully simulated a neural crosstalk model for bimanual interference predicated on the notion that the left limb received an attenuated mirror image of the commands sent to the right limb. Their simulation successfully reproduced characteristics associated with asymmetric bimanual circle drawing with increasing movement frequencies including a deterioration of the circular trajectories and a weakening of the phase coupling between the hands (Cattaert et al. 1999).

The results of the current study also support the notion of neural crosstalk. That is, the right, dominant limb influenced the left limb in both the 1:2 (Fig. 9) and 2:1 (Fig. 10) tasks. The distortions observed in the left limb, when assigned the faster frequency indicates that the right, dominant limb is influencing the left, non-dominant limb regardless of whether the right limb is assigned the faster frequency. However, this type of right to left limb influence, which may be attributable to asymmetric neural crosstalk was not evident in an experiment in which participants were required to produce a constant force with one limb while the contralateral limb was required to produce a pattern of force using a template placed in the display (Kennedy et al., in press, Experiment 2). The results indicated that increases and decreased in the force generated by one limb resulted in corresponding changes in the forces produced by the homologous muscles of the contralateral limb. This relationship, however, was not influenced by the limb (left or right) producing the force. This indicates a more symmetric influence of one limb on the other.

It may be important to also note that similar distortions are typically not observed in multi-frequency coordination tasks performed in near frictionless environments (Kovacs et al., 2009a; Kovacs et al., 2010a,b; Kovacs & Shea, 2011). However, isolated distortions have been observed in a 1:2 coordination pattern in which participants were required to coordinate hand-held pendulums (Sternad et al., 1999c). Interestingly, the ability to coordinate the hand-held pendulums required increased force production compared to tasks performed in near frictionless environments. It has been hypothesized that the effect of neural crosstalk is partially dependent on force levels, with higher forces resulting in stronger crosstalk effects and lower forces in weaker ones (Heuer et al. 2001). As such, patterns of interference may differ in tasks with relatively low force requirements. In the current investigation, the pattern of force produced by each limb required a peak force of 15 N. It is possible that such a force requirement allowed for the detection and quantification of neural crosstalk at the behavioral level. Indeed, recent research has indicated consistent distortions in the force produced by the left limb that could be associated with the production of force by the right limb (Kennedy et al 2015, in press). However, the results of the current investigation indicate that there are differences in the pattern of distortions depending on whether the dominant or non-dominant limb produced the faster pattern of force. This result is consistent with the notion that hand dominance affects bimanual coordination via an asymmetry in the strength of neural crosstalk (Treffner and Turvey 1995).

It has been suggested that the effects of hand dominance may be the result of the dominant hemisphere being more efficient at inhibiting neural crosstalk from the non-dominant hemisphere than vice versa (e.g., de Poel et al. 2007; Serrien et al. 2003; Stinear and Byblow 2004). As such, the dominant limb is more efficient at inhibiting, compensating, and/or overriding the crosstalk from the non-dominant limb than the non-dominant limb is to the dominant limb (de Poel et al. 2007). Indeed, in the current experiment it appears when the dominant right limb was required to perform the faster frequency the dominant hemisphere/ limb was able to almost completely resist the crosstalk from the non-dominant hemisphere/limb. However, when the non-dominant left limb was required to produce the faster frequency the left limb was not able to fully inhibit, compensate, and/or override the crosstalk from the dominant hemisphere/limb. This may explain why multi-frequency coordination patterns are often more stable when the dominant limb is assigned the faster frequency (e.g., Byblow and Goodman 1994; Byblow et al. 1998; Peters 1980).

Limb Assignment and Attentional Factors

Although a number of investigations have indicated greater stability during multi-frequency bimanual tasks when the preferred (right limb in right limb dominant participants) limb is assigned the higher frequency (e.g., Byblow and Goodman 1994; Byblow et al. 1998; Peters 1980), other studies have provided evidence that the faster limb performs more accurately than the slow limb regardless of hand dominance (e.g., Peper et al. 1995c; Peter and Schwartz 1989; Summers et al. 1993b). The results of the current investigation provide evidence that the fast limb influenced the slow limb. That is, in the 1:2 task distortions in the force produced by the left (slower) limb were observed that could be attributed to force produced by the right (faster) limb while in 2:1 task distortions in the force produced by the right (slower) limb were observed that could be attributed to force produced by the left (faster) limb. It is important to note, however, that the in 2:1 task distortions were observed in the left (faster) limb that could be attributed to force produced in the right (slower) limb as well. If the distortions observed in the current investigation were strictly related to the limb assignment, distortions would not be expected in the faster limb.

Previous research has attributed the influence of the fast limb on the slow limb to attentional factors related to the fast limb receiving the focal attention (e.g., Amazeen et al. 1997; Byblow et al. 1998; Peters 1987). A number of investigations have examined the influence of attention on bimanual coordination (e.g., Amazeen et al. 1997; De Poel et al., 2006; Peters and Schwartz 1989). In general, results of such studies have indicated that bimanual coordination is more accurate and stable when attention is focused on the dominant limb (e.g., Amazeen et al. 1997; de Poel et al. 2006; Peters and Schwartz 1989). Interestingly, however, focusing attention on the non-dominant limb decreased the asymmetry in interlimb coordination strength (de Poel et al. 2006). Thus, deliberating focusing attention on either limb influences coordination similar to hand dominance (Amazeen et al. 1997; de Poel et al. 2006). Such findings support the notion that the asymmetry between the limbs may reflect an attentional bias (Peters 1987; Peters & Schwartz 1989).

The results of the current investigation, however, are interesting in that attention is not a major confounding variable. That is, the current investigation used Lissajous Feedback. The Lissajous displays used provided a goal template of the required coordination patterns along with on-line integrated visual information regarding the position of the two limbs as a single point in one plane. The advantage of using this type of feedback is that participants do not need to split their attention between limbs nor do they have to give one limb attentional priority over the other. As such, it is possible to address whether the asymmetry often noted in bimanual coordination tasks reflect an attentional bias (Peters 1987; Peters and Schwartz 1989).

The results of the current investigation indicated that the right limb influenced the left limb regardless of whether it was performing the faster or slower frequency whereas the left limb only influenced the right limb when the left limb was performing the faster frequency. Not only can this influence be observed in the force and force velocity plots (Fig. 9-10), it is also reflected in the harmonicity values (Fig 11f). Given that a functional asymmetry was observed when Lissajous feedback was provided, our results indicate that a bias associated with limb dominance exists even when attentional constraints have been reduced. Note that Lissajous displays have been thought to reduce attentional factors but not constraints related to neural crosstalk (e.g., Kovavs et al. 2009).

Summary

The present experiment was designed to determine if the influence of the forces produced by one limb on the contralateral limb could be the result of the limb assigned the faster frequency on the limb performing the slower frequency or a bias associated with limb dominance. The results of the bimanual data indicated that when participants were provided Lissajous information they were able to perform the required frequency ratios equally well when the left limb was required to perform the faster frequency as when the right limb was required to perform the faster frequency. Despite the effectiveness of the Lissajous information, during the multi-frequency coordination tasks consistent perturbations were observed in one limb that could be associated with the force produced in the contralateral limb. However, a distinctive pattern of interference could be associated with the right limb when assigned the faster frequency compared to when the left limb was assigned the faster frequency. In the 1:2 task distortions were only observed in the force produced by the left limb that could be attributed to the production of force by the right limb. In 2:1 task identifiable distortions were observed in the force produced by both the left and right limb that could be associated with the production of force in the contralateral limb. Observed distortions in the left limb, when assigned the faster rhythm indicated that the source of interference is not strictly related to limb assignment but also increased interference resulting from producing the faster production of force pulses.

CHAPTER V

EXPERIMENT III

Introduction

When participants are required to produce two conflicting motor sequences simultaneously, interference between the limbs is often observed (e.g., Byblow and Goodman 1994; Peper et al. 1995c; Summers et al. 1993a,b). For example, when participants are required to produce bimanual actions with different amplitudes (e.g., Heuer et al. 2001; Sherwood 1994; Spijkers and Heuer 1995), directions (e.g., Franz et al. 1996; Swinnen et al. 2002; Swinnen et al. 2001), frequencies (e.g., Peper et al., 1995a,b,c; Treffner and Turvey 1993), or forces (e.g., Diedrichsen et al. 2003; Heuer et al. 2002; Steglich et al. 1999) an assimilation effect occurs whereby both limbs tend to produce similar actions despite the task goal to produce disparate activation patterns for the two limbs.

It is believed that this interference results, at least in part, to interactions between the feed-forward motor commands (neural crosstalk) as the result of shared neural pathways (e.g., see Cardoso de Oliveira 2002; Swinnen 2002; Swinnen and Wenderoth 2004 for reviews). According to the crosstalk model, two independent motor plans exist for each limb and some fraction of the force command for one limb is diverted to the other limb (Cattaert et al. 1999). This occurs when both hemispheres send commands to the contralateral limb via the crossed corticospinal pathways while concurrently sending the same command to the ipsilateral limb via the uncrossed corticospinal pathways (Cardoso de Oliveira 2002; Cattaert et al. 1999). Thus, each limb is primarily controlled by the contralateral hemisphere; however, there is also an ipsilateral influence that is integrated with the contralateral command.

This ipsilateral influence is believed to alter the activation of the involved muscles (e.g., Cattaert 1999; Cardoso de Oliveira 2002; Swinnen 2002) likely adding to or subtracting from the contralateral muscle activation depending on whether the command is excitatory or inhibitory (e.g., Barral et al. 2006; 2010; Walter and Swinnen 1990). In symmetric 1:1 in-phase bimanual coordination task this ipsilateral influence is not likely to cause interference between the limbs because the commands to both limbs are congruent (Maki et al. 2008). In fact, it is believed that 1:1 in-phase task is stabilized when complementary contralateral and ipsilateral signals are integrated (e.g., Cardoso de Oliveira 2002; Kagerer et al. 2003; Maki et al. 2008; Marteniuk et al. 1984). However, multi-frequency bimanual coordination tasks require the simultaneous production of two conflicting motor sequences (Summers et al. 1993b). For example, coordinating a 1:2 bimanual reciprocal movement task requires the right limb to produce two movement cycles while concurrently producing one cycle with the left limb. Because the commands to each limb are often in conflict (Summers et al. 1993b) performance of multi-frequency tasks can suffer from ongoing interference believed to result from the conflicting information or partial intermingling of signals controlling the two limbs (e.g., Cardoso de Oliveira 2002; Kagerer et al. 2003; Maki et al. 2008; Marteniuk et al. 1984).

Indeed, Kennedy, Boyle, Wang, and Shea (in press) recently compared the bimanual production of 1:1 and 1:2 force patterns. Consistent with the notion of neural crosstalk, the results from the 1:2 task indicated interference in the left limb force and force velocity time series for participants that were not present in the 1:1 task. The distortions observed in the 1:2 task occurred in the forces produced by the left limb when the right limb was initiating or releasing a force pulse. However, distortions in the forces produced by the right limb that could be attributable to the forces produced by the left limb were not observed.

This result is consistent with a number of investigations demonstrating an asymmetric pattern of interference during bimanual tasks (e.g., Aramaki et al. 2006; Cattaert et al. 1999; de Pool et al. 2007; Kennedy et al. 2015, in press; Kagerer et al. 2003; Maki et al. 2008; Peters 1985; Semjen et al. 1995). That is, one limb is more affected by the interference than the other limb. It has been suggested that the dominant hemisphere exerts a stronger influence on the non-dominant limb than the non-dominant hemisphere does on the dominant limb (Aramaki et al. 2006; Cattaert et al. 1999; Kagerer et al. 2003; Maki et al. 2008). Indeed, Cattaert and colleagues (1999) successfully simulated a neural crosstalk model for bimanual interference predicated on the notion that the left limb received an attenuated mirror image of the commands sent to the right limb. Their simulation successfully reproduced characteristics associated with asymmetric bimanual circle drawing with increasing movement frequencies including a deterioration of the circular trajectories and a weakening of the phase coupling between the limbs (Cattaert et al. 1999).

The results from the experiment by Kennedy et al. (in press) were consistent with the model produced by Cattaert and colleagues. That is, distortion of the left limb forces that could be attributable to the production of right limb forces was observed. However, distortions of the forces produced by the right limb that could be attributable to the forces produced by the left limb did not occur. It is important to note, however, this type of right to left limb influence, which may be attributable to asymmetric neural crosstalk was not evident in an experiment in which participants were required to produce a constant force with one limb while the contralateral limb was required to produce a pattern of force using a template placed in the display (Kennedy et al. in press, Experiment 2). The results indicated that increases and decreased in the force generated by one limb resulted in corresponding changes in the forces produced by the homologous muscles of the contralateral limb. This relationship was not influenced by the limb producing the force. This indicates a more symmetric influence of one limb on the other.

It may be important to also note that similar distortions are typically not observed in multi-frequency coordination tasks performed in near frictionless environments (e.g., Kovacs et al. 2009; Kovacs et al. 2010a,b; Kovacs and Shea 2011). However, isolated distortions have been observed in a 1:2 coordination pattern in which participants were required to coordinate hand-held pendulums (Sternad et al. 1999c). Note the ability to coordinate the hand-held pendulums required increased force production compared to tasks performed in near frictionless environments. It has been hypothesized that the effect of neural crosstalk is partially dependent on force levels, with higher forces resulting in stronger crosstalk effects and lower forces in weaker ones (Heuer et al. 2001). Therefore, it is possible that the force requirement of 15N allowed for the detection and quantification of neural crosstalk at the behavioral level in the previous experiments by Kennedy and colleagues (2015, in press).

The ability to observe relatively consistent distortions in the force times series for the left limb that could be attributed to the forces produced by the right limb (Kennedy et al. 2015, in press) as well as the distortions observed in the displacement trace during the coordination of hand-held pendulums (Stenard et al., 1999a) supports the notion that an increase in the force requirements may modulate the strength of neural crosstalk (Heuer et al. 2001) If the effect of neural crosstalk is partially dependent on force levels, with higher forces resulting in stronger crosstalk effects than an increase in the force requirements for one limb should result in more interference in the contralateral limb.

Recently, Hu and Newell (2012) examined the influence of asymmetric force production on asymmetric interference during a bimanual coordination task. Participants were required to produce a constant force of 5% maximum voluntary contraction (MVC) with one finger while the other finger produced 5%, 20%, and 50% MVC. The results indicated that the finger producing the low force showed stronger interference than the finger performing the higher force. In addition, the results indicated stronger interference when the non-dominant left limb produced the higher force. It is important to note, however, that the bimanual task performed by Hu and colleagues (2012) required the production of constant forces. As such, it is not clear whether the same pattern of interference would be observed with asymmetric force requirements in tasks that also require conflicting timing goals, such as a 1:2 multi-frequency force task.

If the increase in the force requirements for one limb results in more interference in the contralateral limb during a multi-frequency task it may provide additional insight into symmetric and/or asymmetric nature of neural crosstalk. As previously mentioned distortions were not detected in the right limb that could be attributed to the force produced by the left limb in the previous experiments by Kennedy and colleagues (Kennedy et al. 2015, in press). This result was consistent with the notion that neural crosstalk is asymmetric in nature. However, it is possible that the force level was not strong enough to detect the interference in the right limb. If interference is only detected in the left limb even when the left limb is required to produce more force to perform the goal coordination pattern it would support the notion that neural crosstalk is asymmetric in nature, whereas if during the left limb load condition interference is observed in the right limb as well it would suggest a more symmetrical influence.

Therefore, the present experiment was designed to determine whether an increase in the force requirements for one limb would result in an increase in the interference observed in the contralateral limb and to determine if the strength of the interference was influenced by the limb performing the higher force during a multi-frequency coordination task. Participants were required to rhythmically coordinate a pattern of isometric forces in a 1:2 coordination pattern. The right or left limb was required to produce a force pattern of 5 N while the contralateral limb was required to produce a 5N, 15N, or 25N force pattern. It was hypothesized that an increase in the force requirements for one limb would result in an increase in interference in the contralateral limb.

Methods

Participants

Twenty young adults (mean age=22.5, 10 males and 10 females) with little or no musical experience volunteered to participate in the experiment. All participants were right limb dominant according to a standardized survey (Oldfield 1971). The Institutional Review Board at Texas A&M University approved the procedures, and participants provided written informed consent before participation in the study.

Apparatus

The apparatus used in Experiment III was identical to that used in Experiments I & II**.**

Procedure

Prior to entering the testing environment participants were randomly assigned to one of two possible test conditions (right limb load, left limb load). The same procedures used in Experiments I & II were used in Experiment 1 except the goal template also illustrated the specific pattern of force requirements needed to produce the goal coordination pattern. For Condition 1 (right limb load), the maximum force required to produce each pattern illustrated by the template was fixed at 5N for the left limb while the right limb required 5, 15, or 25 N of force whereas the force requirements were fixed at 5N for the right limb while the left limb required 5, 15, 25 N of force for Condition 2 (left limb load) (see Fig. 13).

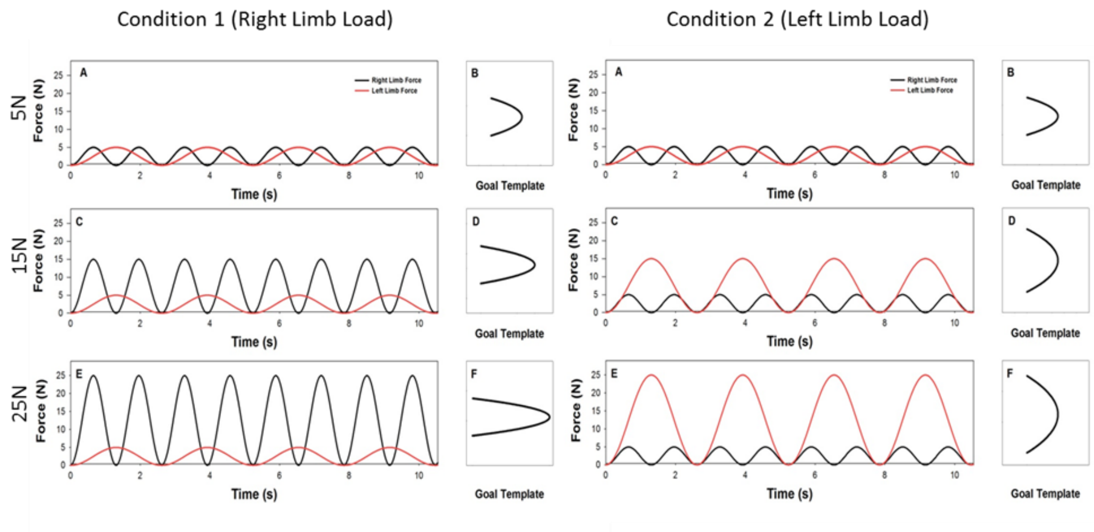


Fig. 13 Goal force requirements for Experiment III. The goal coordination pattern and the force requirements for each limb, as well as the corresponding goal template during condition 1 (right limb load, left panel) and condition 2 (left limb load, right panel) are provided. At the 5N force level (a,b) the task required both limbs to produce 5N of force. At the 15N force level (c,d) the task required one limb to produce 5N of force while the contralateral limb produced 15N of force and at 25N force level (e,f) the task required one limb to produce 5N of force while the contralateral limb produced 25N of force. Note that the right limb load condition required an increase in the force requirements for the right limb while the left limb load condition required an increase in the force requirements for the left limb.

Measures & Data Analysis

Data measures in Experiment III use the same calculations as in Experiment I & II. The mean inter-peak interval ratio and phase angle slope ratio were analyzed in separate Condition (1-right limb load, 2-left limb load) x Force (1-5N, 2-15N, 25N) ANOVA's with repeated measure on Force. Mean inter-peak interval, SD inter-peak interval, phase angle slope, peak force, and force harmonicity were analyzed in separate Condition (1-

right limb load, 2-left limb load) x Force (1-5N, 2-15 N, 3-25 N) x Limb (left, right) ANOVAs with repeated measure on Force and Limb. In the event of a significant interaction simple main effect analyses (Kirk 1968) were performed to determine the locus of the interaction. An α =.05 was used for all tests.

Results

Fig. 14 provides sample left and right limb force times series for a segment of the test trial for one participant in the right load condition and one participant in the left limb condtion at each of the three force levels. Note that the force time series for each of the force levels have been normalized.

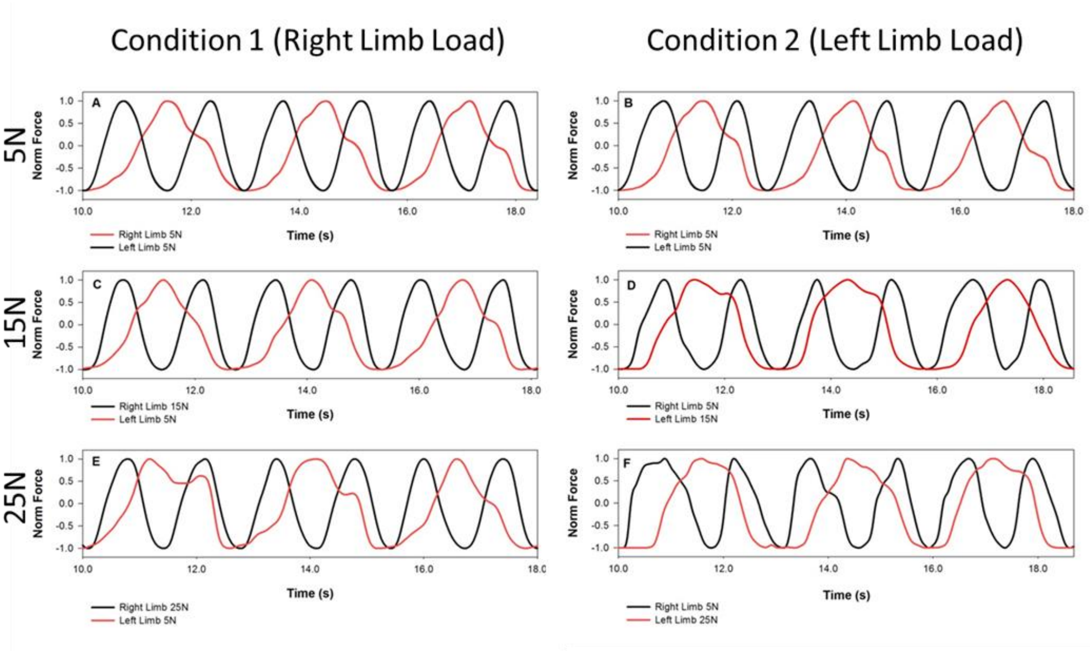


Fig. 14. Sample performance for right and left limb load conditions. The left and right limb force times series for a segment of the test trial for one participant in condition 1 (right limb load, a,b,c) and one participant in the condition 2 (left limb load, b,d,f) at each of the three force levels are provided. Note that the force time series for each of the force levels have been normalized.

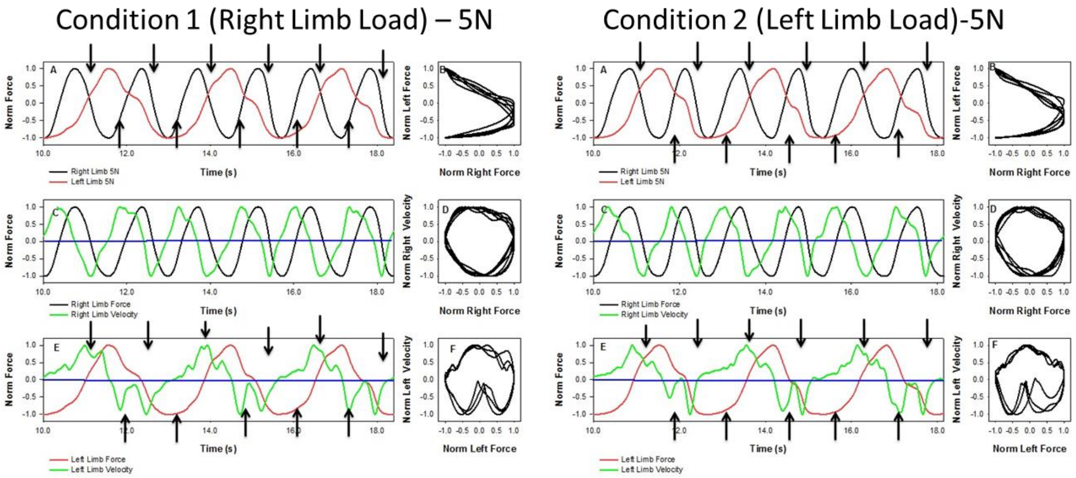
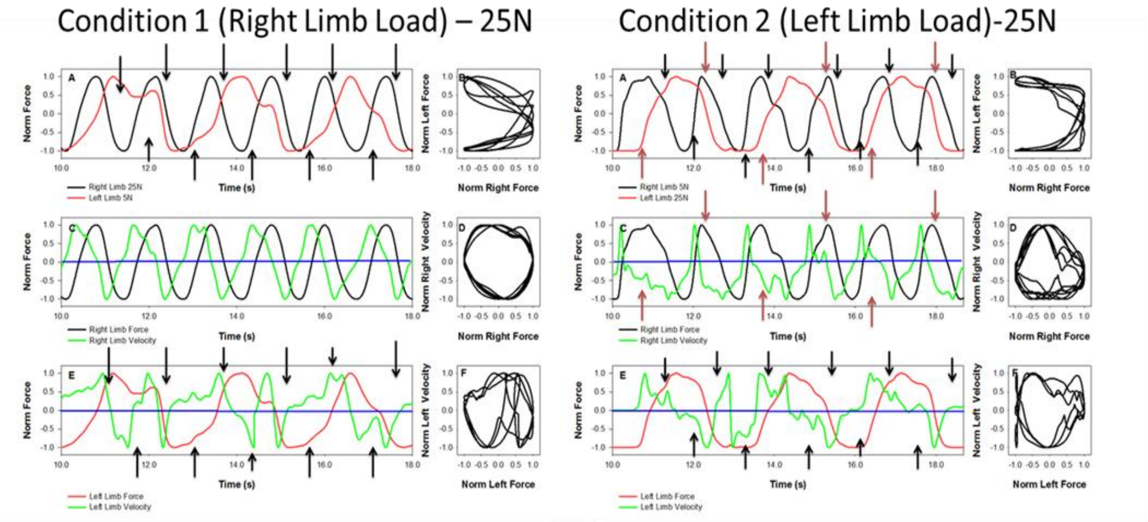


Fig. 15. Sample performance at 5N. The left and right limb force times series for a segment of the test trial and resulting Lissajous plot for one participant in the right limb load condition and one participant in left limb load condition are provided in a,b (left and right panel, respectively). In addition, the force and force velocity time series and velocity/force plots resulting from the right (f, g) and left (h, i) limb forces are provided. Black arrows are provided to demonstrate the impact the initiation (upward pointing arrow) or release of force (downward pointing arrow) by the right limb has on the force and force velocity of the left limb. Note that both conditions require the left and right limbs to produce 5N of force.

Fig. 15-16 provide sample force and force velocity times series (a) and resulting Lissajous displays (b) for one participant in the right load condition (left panel) and one participant in the left limb load condition (right panel) at the 5N force level (Fig. 15) and the 25N force level (Fig. 16). The force and force velocity time series traces and normalized force velocity/normalized force plots resulting from the right (c-d) and left (g-i) limb forces are also provided. In addition, arrows are provided to demonstrate the impact the initiation (upward pointing arrow) or release of force (downward pointing arrow) by one limb has on the force and force velocity of the contralateral limb.


Condition 1 (Right Limb Load) – 25N

Condition 2 (Left Limb Load)-25N

Fig. 16. Sample performance at 25N. The left and right limb force times series for a segment of the test trial and resulting Lissajous plot for one participant in the right limb load conditon and one participant in condition 2 (left limb load condition) are provided in a,b (left and right panel, respectively). In addition, the force and force velocity time series and velocity/force plots resulting from the right (f, g) and left (h, i) limb forces are provided. Black arrows are provided to demonstrate the impact the initiation (upward pointing arrow) or release of force (downward pointing arrow) by the right limb has on the force and force velocity of the left limb. Red arrows are provided to demonstrate the impact the initiation (upward pointing arrow) or release of force (downward pointing arrow) by the left limb has on the force and force velocity of the left limb. Note that distortions in the right limb are only observable in the left limb load (left panel) condition.

Previous research has indicated that the influence of one limb occurs at the point of force initiation or release and continues until peak force velocity or peak force velocity release is achieved (Kennedy et al. 2015). Therefore, the placement of the arrows was determined by identifying the point of peak force velocity and peak force velocity release in one limb and then placing the arrow at the same point in the right and left limb force time series and the contralateral force velocity time series. Note that the black arrows indicate the influence the initiation and release of force by the right limb has on the left limb while the red arrows indicate the influence the initiation and release of force by the left limb has on the right limb. Also note, that the influence of the left limb on the right limb only occurs in the left limb load condition at the 25N force level.

Mean unimanual measures for participants by condition and force are provided in Fig. 17 and mean bimanual performance data are provided in Fig. 18.

Unimanual Analyses

Inter-peak interval. The analysis indicated main effects of Force, F(2,98) =6.57, p<.01,and Limb, F(1,98) =202.29, p<.0001. The Force x Limb, F (2, 98) = 5.62, p<.01, interaction was also significant. As per the goal of the task, simple main effects analysis indicated longer inter-peak intervals for the left than the right limb, this relationship did not change with the force requirements. However, longer inter-peak intervals for both the right (M=499.2 ms, SD=203.6 ms) and left (M=986.9 ms, SD=423.3 ms) limbs were observed during the 5N force level compared to the right (M=388.2, SD=149.2) and left (M=770.0 ms, SD=290.0 ms) limbs at 15N and the right (M=384.2, SD=99.0) and left (M=762.4, SD=194.2) limbs at 25N force levels. The inter-peak interval at 15N and 25N of force did not differ (Fig. 17a). All other main effects and interactions were not significant.

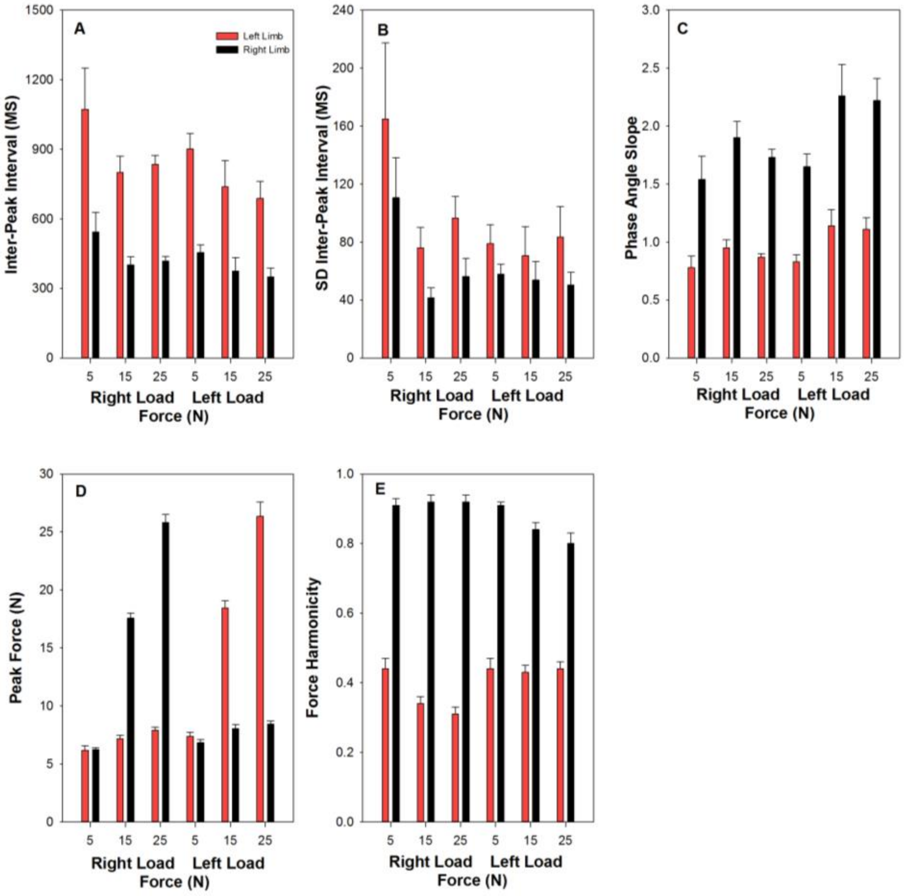


Fig. 17. Mean unimanual measures for Experiment III. The mean inter-peak intervals (a), SD inter-peak intervals (b), phase angle velocity (c), peak force (d), and force harmonicity (e), by condition and force are provided. Error bars represent standard errors. Note the reduced harmonicity in the left limb in the right limb load condition and the reduced harmonicity in the right limb in the left limb load condition.

SD Inter-peak interval. The analysis indicated a main effect of Limb, F(1,98) =22.63, p<.001. Significantly smaller SD inter-peak intervals for the right (M=61.8, SD=46.28) limb than the left (M=95.0, SD=81.4) limb were observed (Fig. 17b). All other main effects and interactions were not significant.

Phase angle slope. The analysis indicated main effects of Force, F(2,98) =9.98, p<.001, and Limb, F(1,98) =314.58, p<.0001. The Force x Limb, F (2, 98) = 10.32, p<.001, interaction was also significant. Simple main effect analysis indicated the slope for the left (M=.80, SD=.26) limb was lower than the right (M=1.6, SD=.51) limb at 5N of force. The slope for the left (M=1.04, SD=.34) limb was lower than the right (M=2.08, SD=.7) limb at 15 N of force and the left (M=.99, SD=.26) limb was lower than the right (M=1.98, SD=.51) at 25 N of force. However, the slope for left and right limbs at 15N and 25N of force did not differ (Fig. 17c). All other main effects and interactions were not significant.

Peak force. As expected due to the experimental design the analysis indicated a main effect of Force, F(2,98) =491.96, p<.0001., a significant Condition x Limb, F(1,98)=766.87, p<.0001, interaction, and a significant Condition x Force x Limb, F(2,98)=338.58, p<.0001, interaction. Indeed, as per the goal of the task simple main effects analysis indicated that during the 5N task participants produced similar peak forces with the right (M=6.3N, SD=.53N) and left (M=6.2N, SD=1.2N) limbs during condition 1(right limb load) and similar right (M=6.8N, SD=.85N) and left (M=7.4N, SD=1.15N) limb peak forces during condition 2 (left limb load). Note the task goal was to produce 5N of force with both the left and right limb in both conditions. At 15N and

25N force levels, the analysis indicated that participants produced a higher peak force with the right (M=17.6N, SD=1.38N; M=25.8N, SD=2.24N) compared to the left (M=7.18N, SD=.87N; M=7.9N, SD=.77N) limbs in the right limb load condition and a higher peak force with the left (M=18.5N, SD=1.2N; M=26.36N, SD=3.95N) compared to the right (M=8.0N, SD=1.2N; M=8.45N, SD=.84N) in the left limb load condition (Fig. 17d). Note the task goal was to produce 15N or 25N with the right limb while the left limb was required to produce 5N in the right limb load condition whereas in the left limb load condition the left limb produced the higher force requirements. The results confirmed that participants were able to perform the force requirements associated with the task. All other main effects and interactions were not significant.

Force harmonicity. The analysis indicated main effects of Force, F(2,98) =8.27, p<.001, and Limb, F(1,98) =854.92, p<.0001. The analysis also indicated significant Condition x Limb, F(2,98)=854.92, p<.001, and Condition x Force x Limb, F(2,98)=11.84, p<.0001,interactions. Simple main effects analysis indicated that when force was increased in one limb there was a corresponding decrease in harmonicity values for the contralateral limb (Fig 17e). More specifically, in the right limb load condition the harmonicity values for the left limb decreased with the increase in force requirements from 5N (M=0.44, SD=.09) to 15N (M=0.34, SD=.07) to 25N (M=0.31, SD=.10) while the harmonicity values for the right limb remained relatively constant with the increase in force (M=0.91, SD=.07, M=0.91, SD=.07, M=0.92, SD=.07) whereas in left limb load condition the harmonicity values for the left limb remained relatively constant with the increase in force (M=0.44, SD=.10, M=0.43, SD=.06, M=0.44, SD=.08) while the harmonicity values for the right limb decreased with the increase in force from 5N (M=0.91, SD=.03) to 15N (M=0.84, SD=.06) to 25N (M=0.78, SD=.08). A decrease in harmonicity values indicate more adjustments, hesitations, and/or perturbation are occurring. All other main effects and interactions were not significant.

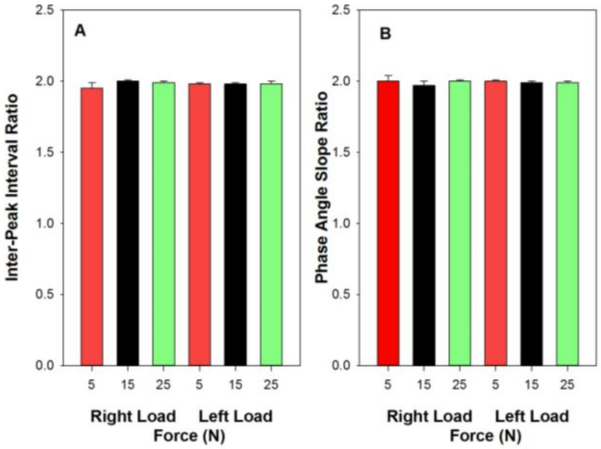


Fig. 18. Mean bimanual measures for Experiment III. The inter-peak interval ratio (a),and phase angle slope ratio (b), by condition and force level are provided. Error bars represent standard errors.

Bimanual Analyses

Inter-peak interval ratio. The mean inter-peak interval ratio in each condition at all three force levels ranged from 1.96-2.0 (Fig. 18a). Note that the goal inter-peak ratio for the 1:2 coordination tasks would be 2:00, with no variability. This indicates that participants were able to effectively produce the inter-peak ratio required for each condition at all three force levels. Accordingly, all main effects and interactions were not significant.

*Phase angle slope***.** The phase angle slope ratio in each condition at all three force levels ranged from 1.97-2.0 (Fig. 18b). As with the inter-peak interval ratio, the goal inter-peak ratio for the 1:2 coordination tasks would be 2:00, with no variability. This indicates that based on regression analyses of the continuous left and right limb phase angle data that the participants were able to effectively produce the goal coordination pattern. Accordingly, all main effects and interactions were not significant.

Discussion

An experiment was designed to determine whether an increase in the force requirements for one limb would result in an increase in the interference observed in the contralateral limb and to determine if the strength of the interference was influenced by the limb performing the higher force. Participants were required to rhythmically coordinate a pattern of isometric forces in a 1:2 coordination pattern. The right or left limb was required to produce a force pattern of 5 N while the contralateral limb was required to produce a 5N, 15N, or 25N force pattern. It was hypothesized that an increase in the force requirements for one limb would result in an increase in interference in the contralateral limb.

Replicating the results of previous experiments by Kennedy and colleagues (2015, in press), the results of the present experiment indicated consistent and identifiable distortion in the left limb forces that could be attributable to the production of right limb forces. Distortions in the left limb forces occurred regardless of force level or loading condition (right or left limb). Interestingly, however consistent and identifiable distortions in the right limb forces that were attributable to the production of left limb forces only occurred when the left limb was required to produce more force than the right limb. This result is consistent with the notion that neural crosstalk is symmetrical in nature but manifest differently depending upon the force requirements of the task.

Lissajous Feedback

Numerous investigations have demonstrated that many bimanual tasks that require frequency relationships other than symmetric 1:1 (e.g., 1:2, 2:3, 3:5) coordination patterns are difficult to perform without extensive practice (e.g., Byblow et al. 1998; Byblow and Goodman 1994; Puttemans et al. 2005; Summers et al. 1993 a,b; Swinnen et al. 1997) or without feedback manipulations to reduce the perceptual and/or attentional constraints (e.g., Kovacs et al. 2010a,b: Mechsner et al. 2001; Swinnen et al. 1997) associated with the task.

One type of feedback manipulation that has proved quite effective in facilitating multi-frequency coordination patterns is Lissajous displays (e.g., Boyles et al. 2012; Kennedy et al. 2015; Kovacs et al. 2010a,b; Wang et al. 2013). The displays used in these experiments provided a template of the goal coordination pattern along with on-line integrated visual information regarding the position of the two limbs as a single point in one plane. Within a few minutes of practice participants were able to use this information to produce a wide variety of multi-frequency coordination patterns (e.g., Boyles et al. 2012; Kennedy et al. 2015; Kovacs et al. 2010a,b; Wang et al. 2013) that were once thought to be difficult without extensive practice. Based upon two global measures of goal attainment (i.e., inter-peak interval ratio and phase angle slope ratio) the results of the current investigation also indicated that participants were able to perform the required frequency ratio within a few minutes of practice (Fig. 18).

Despite the effectiveness of the Lissajous displays in facilitating the 1:2 multi-frequency force task, distortions in the forces produced by the right limb that could be associated with the forces produced by the left limb were observed in both the right left limb load conditions (Fig. 14-16). Distortions were also observed in the right limb that could be associated with the force produced by left limb in the left limb load condition, especially at the highest force level (Fig. 16, red arrows). These distortions are consistent with the decreased harmonicity values in the left limb in the right limb load condition and the decreased harmonicity values in the right limb in the left limb load condition (Fig. 17f). Note that Lissajous displays have been thought to reduce constraints related to perceptual and attentional factors but not constraints related to motoric factors such as neural crosstalk.

Neural Crosstalk and Force Control

When participants are required to produce two conflicting motor sequences simultaneously, interference between the limbs is often observed (e.g., Byblow and Goodman 1994; Peper et al. 1995a,b,c; Summers et al. 1993a,b). It is believed that this interference results, at least in part, to interactions between the feed-forward motor commands (neural crosstalk) as the result of shared neural pathways (e.g., see Cardoso de Oliveira 2002; Swinnen 2002; Swinnen and Wenderoth 2004 for reviews). Neural crosstalk is defined as a mirror image command sent to the homologous muscles of the contralateral limb (Cattaert et al. 1999; Swinnen 2002). It has been hypothesized that the effect of neural crosstalk is partially dependent on force levels, with higher forces resulting in stronger crosstalk effects and lower forces in weaker ones (Heuer et al. 2001).

Indeed, previous investigations have identified and quantified distortions consistent with notion of neural crosstalk in multi-frequency bimanual force tasks (Kennedy et al. 2015, in press), however no such distortions were observed in similar multi-frequency tasks performed in relatively frictionless environments (e.g., Boyles et al. 2013; Kovacs et al. 2010a,b). Therefore, it is possible that the force requirement of 15N allowed for the detection and quantification of neural crosstalk at the behavioral level in the previous experiments. The current investigation required participants to coordinate a 1:2 bimanual force pattern with a 5N force requirement. Distortions consistent with neural crosstalk and similar to the distortions observed in the previous experiments at 15N were observed at 5N as well (Fig. 15). It may be important to note, however, that distortions in the right limb that could be associated with the force produced by the left limb were not observed at 5N or in the previous experiments at 15 N. However, distortions in the right limb were quite evident when the left limb was required to produce 25N of force (Fig. 16).

It has been suggested that the dominant hemisphere is more efficient at inhibiting neural crosstalk from the non-dominant hemisphere than vice versa (e.g. de Poel et al. 2007; Serrien et al. 2003; Stinear and Byblow 2004). As such, the dominant limb is more efficient at inhibiting, compensating, and/or overriding the crosstalk from the non-dominant limb than the non-dominant limb is to the dominant limb (de Poel et al. 2007).

With an increase in the strength of the neural signals it is possible that at higher force levels the dominant limb is less efficient at inhibiting crosstalk from the non-dominant limb. It is important to note, however, that small distortions were also observed in the right limb when the left limb was producing 15N while the left limb was required to produce 5N. As previously mentioned distortions were not observed in the right limb in the previous experiments in which participants were producing 15N with both limbs. Therefore, it is possible that the distortions observed in the right limb when the left limb was producing 15N, was related to the asymmetric force requirements rather than the force level of 25N.

Previous research has shown that simultaneous movements with different amplitudes give rise to interference effects, such that the larger amplitude is reduced while the smaller amplitude is increased (e.g., Franz 1997; Sherwood 1994, Spijkers and Heuer 1995). The interference observed in these types of tasks has displayed an asymmetric effect depending upon which limb performs the larger amplitude (Marteniuk et al. 1984; Buchanan and Ryu 2006). For example, Marteniuk et al. (1984) required participants to perform rapid bimanual aiming movements with either the same or disparate amplitudes. The results indicate that amplitude assimilation occurred only when the right hand was performing the longer amplitude but not when the left hand performed the longer amplitude. When the left hand was assigned the larger amplitude, both hands overshot the target amplitude. As such, it may be interesting to investigate whether distortions are observed in the right limb when both limbs are producing 25N of force during the multi-frequency force task.

Symmetric and Asymmetric Neural Crosstalk

Kennedy, Boyle, Wang, and Shea (in press) recently examined the bimanual production of a 1:2 force patterns. The results from the 1:2 task indicated interference in the left limb force and force velocity time series for participants that were not present in the right limb. The distortions observed in the left limb occurred when the right limb was initiating or releasing a force pulse. However, distortions in the forces produced by the right limb that could be attributable to the forces produced by the left limb were not observed. This result was consistent with a number of investigations that have demonstrated that interference between the limbs is asymmetrical (e.g., Aramaki et al. 2006; Cattaert et al. 1999; de Pool et al. 2007; Kennedy et al. 2015, in press; Kagerer et al. 2003; Maki et al. 2008; Peters 1985; Semjen et al. 1995). That is, one limb is more affected by the interference than the other limb. For example, previous research has provided evidence that bimanual performance is more accurate and/or stable when the dominant limb is assigned the faster frequency (e.g., Byblow and Goodman, 1994; Byblow et al. 1998; Summers et al. 2002). One such study, required participants to tap 1:2 and 2:1 rhythms (Peters 1995). The results indicated slower tapping rates and increased variability when right limb dominant participants were required to tap with the left limb at twice the frequency of the right limb (i.e., 2:1) than when they were required to tap with the right limb at twice the frequency of the left limb (i.e., 1:2). Similarly, research has indicated that trajectory distortions and direction reversals primarily occur in the non-dominant limb during bimanual performance (Byblow et al. 1999; Semjen et al. 1995). It is important to note, however, this type of right to left limb influence, which may be attributable to asymmetric neural crosstalk was not evident in an experiment in which participants were required to produce a constant force with one limb while the contralateral limb was required to produce a pattern of force using a template placed in the display (Kennedy et al., in press, Experiment 2). The results indicated that increases and decreased in the force generated by one limb resulted in corresponding changes in the forces produced by the homologous muscles of the contralateral limb. This relationship was not influenced by the limb producing the force. This indicates a more symmetric influence of one limb on the other.

Given that the dominant hemisphere is more efficient at inhibiting neural crosstalk from the non-dominant hemisphere than vice versa (e.g. de Poel et al. 2007; Serrien et al. 2003; Stinear and Byblow 2004), it is possible that the neural signals from the non-dominant hemisphere needs to be stronger than that required from the dominant hemisphere to elicit interference in the corresponding limb. The results of the current investigation support such a possibility. That is, when the force requirements were increased for the left limb, distortions were observed in the right limb (Fig. 17, red arrows). In addition, this finding is consistent with the decreased harmonicity values for the right limb observed when the left limb was required to produce more force than the right limb (Fig. 17e). Given that distortions were detected in the right, dominant limb when the left limb was required to produce more force and the decreased harmonicity values in the right limb with the increase in force requirements for the left limb supports the notion that neural crosstalk affects both limbs (symmetric influence); however, it manifests differently (asymmetric influence) depending upon the force requirements of the task.

Summary

The present experiment was designed to determine whether an increase in the force requirements for one limb would result in an increase in the interference observed in the contralateral limb and to determine if the strength of the interference was influenced by the limb performing the higher force. The results of the bimanual data indicated that when participants were provided Lissajous displays that were able to perform the required frequency ratio in both the right and left limb load conditions. Despite the effectiveness of the Lissajous displays, consistent perturbations were observed in the force produced by one limb that coincided with the initiation or release of force in the contralateral limb. Regardless of whether both limbs were required to produce the same force load or whether the left or right limb had to produce more force than the contralateral limb to perform the goal coordination pattern, consistent distortions in the force produced by the left limb that could be associated with the force produced by the right limb were observed. Interestingly, however, distortions in the right limb were only observed when the left limb was required to produce more force than the right limb to perform the goal coordination pattern. This result is consistent with the notion that neural crosstalk affects both limbs (symmetric influence); however, it manifests differently (asymmetric influence) depending upon the force requirements of the task.

CHAPTER VI

GENERAL DISCUSSION AND CONCLUSION

A series of experiments were conducted to better understand the influence of neural crosstalk on bimanual coordination by investigating how and when the forces produced by one limb affect the forces produced in the contralateral limb. Given that neural crosstalk is defined as a mirror image command sent to the homologous muscles of the contralateral limb (Cattaert et al. 1999), the purpose of Experiment I was to determine whether the activation of homologous or non-homologous muscles resulted in interference consistent with neural crosstalk. It was hypothesized that neural crosstalk should be more easily detected and characterized when the task required the activation of homologous muscles compared to when the task required the activation of non-homologous muscles. However, the results indicated consistent and identifiable distortions in the left limb forces that could be associated with the production of force in the right limb in both conditions. Interestingly, however, the pattern of distortions was different for the homologous and non-homologous tasks. For the homologous task the interference occurred in the left limb when the right limb was initiating and releasing force. For the non-homologous task the interference in the left limb force occurred only when the right limb was releasing force.

Interference during the activation of non-homologous muscles was inconsistent with our initial predictions related to neural crosstalk. However, after further analysis, the point at which the interference occurred may provide further support for the argument that interference occurs when neural crosstalk conveys the same information to bilateral homologous muscles. That is, observable interference only occurred during the non-homologous condition when the right limb was initiating a force pulse while the left limb was releasing force. It is possible, that co-contraction occurred in which the left triceps (antagonist) was activated to decelerate the force produced by the left biceps (agonist). If co-contraction of the antagonist muscle (left triceps) occurred to slow down or break the force produced by the agonist (left biceps), there would be simultaneous activation in the triceps of both limbs resulting in homologous muscle activation during the non-homologous muscle condition resulting in interference consistent with the notion of neural crosstalk.

Nonetheless, an identifiable influence of right limb forces on the left limb force time series were observed in both conditions that appeared to continue from the point of force initiation and/or release to peak force velocity. However, no such influence from the left limb on the right limb force time series was observed. This type of asymmetric neural crosstalk has been associated with hemisphere/hand dominance (e.g., Cattaert et al. 1999; de Poel et al. 2007; Serrien et al. 2003; Treffner and Turvey 1995). That is, in right limb dominant individuals, the dominant left hemisphere exerts a stronger influence on the non-dominant left limb than the non-dominant right hemisphere on the dominant right limb (e.g., Kagerer et al. 2003; Maki et al. 2008).

Consistent with this notion several studies have indicated greater stability during multi-frequency bimanual tasks when the preferred (right limb in right limb dominant participants) limb is assigned the higher frequency (e.g., Byblow and Goodman 1994; Byblow et al. 1998; Peters 1980, 1985). Other studies, however, has provided evidence that the faster moving limb performs more accurately than the slower moving limb regardless of hand dominance (e.g., Peper et al. 1995; Peter and Schwartz 1989; Summers et al. 1993b). As such, it has been suggested that the slower moving limb is coupled to the faster moving limb (Peper et al. 1995). Therefore, it is possible that the influence of the right limb on the left limb forces observed in Experiment 1 was the result of the faster frequency and hence the greater force velocity changes in the right limb rather than a bias strictly associated with limb dominance.

Therefore, the purpose of Experiment II was to determine whether the influence of force produced by one limb on the contralateral limb is the result of the limb assigned the faster frequency on the limb performing the slower frequency or a bias associated with limb dominance. If the limb assigned the faster frequency was responsible for the distortions observed in the contralateral limb, it was hypothesized that distortions would only be observed in the force trace of the limb producing the slower pattern of force. If a bias associated with limb dominance was responsible for the distortions observed in the contralateral limb, it was hypothesized that in right-limb dominant participants the right limb would influence the left limb, regardless of limb assignment.

To do this, participants were required to rhythmically coordinate a pattern of isometric forces in a 1:1, 1:2, or 2:1 coordination pattern. The 1:2 task required the right limb to perform the faster rhythm while the 2:1 task required the left limb to perform the faster rhythm. The 1:1 task was used as a control. Replicating the results of Experiment I, only distortions in the left limb were observed in the 1:2 coordination task that could be attributed to the production of force by the right limb. However, identifiable distortions were observed in the force produced by both the left and right limb in the 2:1 coordination task. Observed distortions in the left limb, when assigned the faster rhythm indicated that the source of interference is not limited to limb assignment but also a function of limb dominance.

It may be important to note that similar distortions are typically not observed in multi-frequency coordination tasks performed in near frictionless environments (e.g., Kovacs et al. 2009; Kovacs et al. 2010a,b; Kovacs and Shea 2011). However, isolated distortions have been observed in a 1:2 coordination pattern in which participants were required to coordinate hand-held pendulums (Sternad et al. 1999). Note the ability to coordinate the hand-held pendulums required increased force production compared to tasks performed in near frictionless environments. It has been hypothesized that the effect of neural crosstalk is partially dependent on force levels, with higher forces resulting in stronger crosstalk effects and lower forces in weaker ones (Heuer et al. 2001). Therefore, it is possible that the force requirement of 15N allowed for the detection and quantification of neural crosstalk at the behavioral level in Experiment I and II.

As such, Experiment III was designed to determine whether an increase in the force requirements for one limb would result in an increase in the interference observed in the contralateral limb and to determine if the observed interference was influenced by the limb performing the higher force. It was hypothesized that an increase in the force requirements for one limb would result in an increase in interference in the contralateral limb. However, if interference is only detected in the left limb it would support the notion that neural crosstalk is asymmetric in nature, whereas if interference is also observed in the right limb when the left limb is producing more force it would suggest a more symmetrical influence. The results indicated that the right limb influenced the left limb regardless of force level or loading condition (right or left limb). However, the left limb only appeared to influence the right limb when the left limb was required to produce more force. This result is consistent with the notion that neural crosstalk affects both limbs (symmetric influence); however, it manifests differently (asymmetric influence) depending upon the force requirements of the task.

Theoretical Considerations

A large number of experiments over the last 40 years have proposed a coalition of constraints, including cortical and subcortical crosstalk that appear to influence stability, phase transitions, and the level of difficulty associated with certain bimanual coordination patterns. However, these difficulties appear to be circumvented, or at least minimized, when integrated feedback (e.g., Lissajous displays) is provided (e.g., Boyles et al., 2012; Hessler et al. 2010; Kovacs et al. 2010a,b). However, the manipulation of perceptual and attentional factors cannot fully explain the stability characteristics observed with relative phase or frequency relationships during bimanual movements. More specifically, it cannot fully explain why individuals using these types of displays tend to produce more stable relative phase patterns for an in-phase task while other relative phase are somewhat less stable (e.g., Kovacs et al.2009a, 2010b; Kovacs and Shea 2011) or why 1:1 patterns are more stable than other frequency ratios (e.g., Kovacs et al. 2010b; Sisti et al. 2011).

It appears that the Lissajous displays may provide an opportunity for the perceptual-motor system to minimize the incidental constraints associated with the task. Likely, however, that Lissajous displays do not eliminate all the constraints that tend to pull the system toward more stable coordination patterns. Rather, the displays appear to decrease the influence of the perceptual and attentional constraints on the coordination dynamics and provide feedback necessary to counter act the effects of the inherent constraints so that the goal pattern can be attained with relatively low error and variability (Kovacs et al., 2010b). Note that one would not expect these types of displays to influence more inherent constraints such as the influence of neural crosstalk. Thus, it may be possible to control many of the perceptual and attentional constraints associated with bimanual tasks, providing an opportunity to more clearly observe the influence of inherent constraints on the coordination dynamics.

Indeed, participants in all three experiments participants were able to quickly and effectively perform the multi-frequency force tasks when Lissajous information was provided. Despite the effectiveness of these displays, however, consistent distortions in the force produced by one limb that could be attributed to the production of force in the contralateral limb were observed in all three experiments. The ability to observe relatively consistent distortions in the force time series for one limb that could be attributed to the forces produced by the contralateral limb when participants were required to coordinate a force pattern supports the notion that an increase in the force requirements may allow for the detection and characterization of crosstalk at the behavior level. The ability to detect and characterize crosstalk at the behavioral level is an important step in understanding constraints acting on the perceptual-motor system.

The emerging picture from our multi-frequency force tasks indicates that neural crosstalk is likely symmetrical. That is, the left and right limbs both receive an attenuated mirror image of the commands sent to the contralateral limb. This notion is based upon the results from Experiment II and III in which distortions were observed in the force produced by the right limb that could be associated with the force produced by the left limb. This is contrary to the neural crosstalk simulation produced by Catteart and colleagues (1999). Their simulation was predicated on the notion that only the left limb received an attenuated mirror image of the commands sent to the right limb.

However, the difference may be that the dominant limb is more efficient at inhibiting neural crosstalk from the non-dominant hemisphere than vice versa (e.g., de Poel et al. 2007; Serrient et al. 2003; Stinear and Byblow 2004). As such, the dominant limb is more efficient at inhibiting, compensating, and/or overriding the crosstalk from the non-dominant limb than the non-dominant limb is to the dominant limb (de Poel et al. 2007). Indeed, in all three experiments it appears when the dominant right limb was required to perform the faster frequency the dominant hemisphere/ limb was able to almost completely resist the crosstalk from the non-dominant hemisphere/limb (see Experiment III for an exception). That is, distortions were not observed in the left limb, in right limb dominant participants, when the right limb was assigned the higher frequency (Experiment I and II, and III (at the low force levels)).

However, it is important to note that interference was observed in the right limb that could be attributed to the force produced by the left limb in a 1:2 coordination task during Experiment III when the left limb had to produce more force than the right limb. Therefore, at greater force levels, when the neural signals from the non-dominant hemisphere are stronger (Heuer 2001) the dominant hemisphere may be less efficient at inhibiting and/or compensating for the crosstalk from the non-dominant hemisphere. This results provides further evidence that the effect of neural crosstalk is partially dependent on force levels, with higher forces resulting in stronger crosstalk effects and lower forces in weaker ones (Heuer et al. 2001).

The ability to detect and characterize crosstalk in the behavior data is an important step in understanding constraints acting on the perceptual-motor system. Further, understanding how and when the forces produced in one limb affect the forces produced in the contralateral limb has functional significance as the production and coordination of force is an essential aspect of many everyday bimanual coordination tasks. For example, bimanual training protocols have recently gained attention as a therapeutic modality for stroke rehabilitation (Lodha, Coombes, & Cauraugh, 2012; Rose & Winstein, 2004; Stewart, Cauraugh, & Summers, 2006). Bimanual training protocols for stroke rehabilitation are based upon principles of neural crosstalk (cross education/ cross facilitation) (Carson ,2005; Dragert & Zehr ,2011; 2013). Specifically, training protocols utilizing bimanual coordination are believed to be advantageous when homologous muscles are activated simultaneously during symmetric bimanual movements because similar neural networks in the left and right hemispheres are activated (Carson, 2005; Hallet, 2001).

Given that cross education research has shown that muscle contractions using a high level of force with one limb led to strength gains in contralateral homologous muscles (see Lee & Carroll, 2007 for a review), it stands to reason patients with hemiplegia may benefit from rehabilitation protocols that utilize unimanual strength training with the unaffected limb as well as bimanual training utilizing force control with both limbs. However, future research is needed to more fully understand the influence of neural crosstalk on bimanual coordination in the general population before rehabilitation protocols can more fully exploit neural crosstalk effect.

Future Directions

Future research should address the influence of neural crosstalk on bimanual force control in left limb dominant individuals, children, older adults and special populations such as stroke patients and individuals with Cerebral Palsy. In addition, this line of research can be extended to include a variety of bimanual coordination patterns. For example, is it possible to predict when and where interference occurs in a 1:3 coordination pattern based upon the pattern of results from a 1:2 bimanual coordination pattern? Furthermore, it may be possible to increase the understanding of inherent constraints on the coordination dynamics by extending this line of research to include the passive movements of one limb (one limb is driven by a torque motor) and social coordination dynamics (two individuals coordinate the multi-frequency pattern). Finally, by including measures such as EMG or EEG it may be possible to identify and provide physiological conformation of when neural crosstalk influences coordinated behavior.

Summary

Three experiments were conducted to better understand the influence of neural crosstalk on bimanual coordination by investigating how and when the forces produced in one limb affect the forces produced in the contralateral limb. Lissajous feedback was provided to reduce the perceptual and attentional constraints. Participants in all three experiments were able to quickly perform the multi-frequency coordination tasks when provided Lissajous feedback. Despite the success of this type of feedback, distortions consistent with neural crosstalk were observed in all three experiments. The results from Experiment I indicated distortions in the force produced by the left limb that were associated with the force produced by the right limb in both homologous and non-homologous muscle conditions. However, distortions were not observed in the force produced by the right limb that could be associated with the force produced in the left limb.

Replicating the results of Experiment I, the results for Experiment II indicated distortions in the left limb that could be attributed to the production of force by the right limb during a 1:2 coordination task. However, identifiable distortions were observed in the force produced by both the left and right limb in the 2:1 coordination task. Observed distortions in the left limb, when assigned the faster rhythm indicated that the source of interference is not limited to limb assignment but also a function of limb dominance. The results for Experiment III also indicated consistent distortions in the force produced by the left limb that could be associated with the force produced by the right limb were observed. This was regardless of whether both limbs were required to produce the same force load or whether the left or right limb had to produce more force than the contralateral limb to perform the goal coordination pattern. Interestingly, however, distortions in the right limb were observed when the left limb was required to produce more force than the right limb to perform the goal coordination pattern. This result is consistent with the notion that neural crosstalk affects both limbs (symmetric influence); however, it manifests differently (asymmetric influence) depending upon the force requirements of the task.

REFERENCES

Amazeen PG, Amazeen EL, Turvey MT (2004a) Breaking the reflectional symmetry of interlimb coordination dynamics. J Motor Behav 30: 199-216

Amazeen PG, Amazeen EL, Turvey MT (2004b) Symmetry and the devil. J Motor Behav 36: 371-372

Amazeen EL, Amazeen PG, Treffner PJ, Turvey MT (1997) Attention and handedness in bimanual coordination dynamics. J of Exp Psychol-Hum Percept Performan 23: 1552-1560

Aramaki Y, Honda R, Okada T, Sadato N (2006) Neural correlates of the spontaneous phase transition during bimanual coordination. Cereb Cortex 16: 1338-1348

Aramaki Y, Osu R, Sadato N (2010) Resource-demanding versus cost-effective bimanual interaction in the brain. Exp Brain Res 203: 407-418

Armatas CA, Summers JJ (2001) The influence of task characteristics on the intermanual asymmetry of motor overflow. J Clin Exp Neuropsychol 23: 557–567

Baechle, T.R., Earle, R.W., & National Strength & Conditioning Association (U.S.). (2000). Essentials of strength training and conditioning. Champaign, Ill: Human Kinetics.

Barral J, Debû B, Rival C (2006) Developmental changes in unimanual and bimanual aiming movements. Dev Neuropsychol 29: 415-29

Barral J, De Pretto M, Debû B, Hauert CA (2010) Activation and inhibition of bimanual movements in school-aged children. Human Physiol 36: 47-57

Beets IAM, Gooijers J, Boisgontier MP, Pauwels L, Coxon, JP, Wittenberg G, Swinnen, SP (2015). Reduced neural differentiation between feedback conditions after bimanual coordination with and without augmented feedback. Cereb Cortex 25: 1958-1969

Bingham GP, Schmidt RC, Zaal FT (1999). Visual perception of the relative phasing of human limb movements. Percept Psychophys 61: 246-258

Boyles J, Panzer S, Shea CH (2012) Increasingly complex bimanual multi-frequency coordination patterns are equally easy to perform with on-line relative velocity feedback. Exp Brain Res 216: 515-525

Buchanan JJ, Kelso JAS (1993) Posturally induced transitions in rhythmic multijoint limb movements. Exp Brain Res 94: 131-142

Buchanan JJ, Park JH, Shea CH (2006) Target width scaling in a repetitive aiming task: switching between cyclical and discrete units of action. Exp Brain Res 175: 710-725

Buchanan JJ, Ryu YU (2006) One-to-one and polyrhythmic temporal coordination in bimanual circle tracing. J Mot Behav 38: 163-184

Buchanan JJ, Ryu YU (2012) Scaling movement amplitude: adaptation of timing and amplitude control in a bimanual task. J Motor Behav 44: 135-147

Byblow WD, Bysouth-Young D, Summers JJ, Carson RG (1998) Performance asymmetries and coupling dynamics in the acquisition of multifrequency bimanual coordination. Psychol Res 61: 56-70

Byblow WD, Goodman D (1994) Performance asymmetries in multifrequency coordination. Hum Movement Sci 13: 147-174

Cardoso de Oliveira S (2002) The neuronal basis of bimanual coordination: Recent neurophysiological evidence and functional models. Acta Psychol 110: 139-159

Carson RG (1995) The dynamics of isometric bimanual coordination. Exp Brain Res 105: 465-476

Carson RG (2005) Neural pathways mediating bilateral interactions between the upper limbs. Brain Res Rev 49: 641-662

Carson RG, Byblow WD, Abernethy B, Summers JJ (1996) The contribution of inherent and incidental constraints to intentional switching between patterns of bimanual coordination. Hum Movement Sci 15: 565-589

Carson RG, Kelso JAS (2004) Governing coordination: behavioural principles and neural correlates. Exp Brain Res154: 267-274

Carson RG, Riek CJ, Smethurst JF, Lison Parraga JF, Byblow WD (2000) Neuromuscular-skeletal constraints upon the dynamics of unimanual and bimanual coordination. Exp Brain Res 131: 196-214

Carson RG, Thomas J, Summers JJ, Walters MR, Semjen A (1997) The dynamics of bimanual circle drawing. Q J Exp Psychol A 50: 664-683

Cattaert D, Semjen A, Summers JJ (1999) Simulating a neural cross-talk model for between-hand interference during bimanual circle drawing. Biol Cybern 81: 343-358

Cincotta M, Giovannelli F, Borgheresi A, Balestrieri F, Vanni P, Ragazzoni A, … Ziemann U (2006). Surface electromyography shows increased mirroring in Parkinson's disease patients without overt mirror movements. Movement Disord 21: 1461-1465

Cohen L (1971) Synchronous bimanual movements performed by homologous and non-homologous muscles. Percept Motor Skill 32: 639–644

de Poel HJ, Peper CE, Beek, PJ (2006) Laterally focused attention modulates asymmetric coupling in rhythmic interlimb coordination. Psychol Res 72: 123-137

de Poel HJ, Peper CE, Beek, PJ (2007) Handedness-related asymmetry in coupling strength in bimanual coordination: furthering theory and evidence. Acta Psychol 124: 209-237

Deutsch D (1983) The generation of two isochronous sequences in parallel. Percept Psychophys 34: 331–337

Diedrichsen J, Hazeltine E, Nurss WK, Ivry RB (2003)The role of the corpus callosum in the coupling of bimanual isometric force pulses. J Neurophysiol 4: 2409-2418

Dragert K, Zehr EP (2011) Bilateral neuromuscular plasticity from unilateral training of the ankle dorsiflexors. Exp Brain Res 208: 217-227

Dragert K, Zehr EP (2013) High-intensity unilateral dorsiflexor resistance training results in bilateral neuromuscular plasticity after stroke. Exp Brain Res 225: 93-104

Febert A, Priori A, Rothwell JC, Day BL, Colebatch, JG, Marsden CD (1992) Interhemispheric inhibition of the human motor cortex. J Physiol 453: 525-546

Fraisse P(1946) Contribution a etude du rythme en tant que forme temporelle. J Psychol Norm Pathol (Paris) 39: 283-304

Franz EA, Eliassen JC, Ivry RB, Gazzaniga MS (1996) Dissociation of spatial and temporal coupling in the bimanual movements of callosotomy patients. Psychol Sci 7: 306-310

Gooijers J, Caeyenberghs K, Sisti H, Geurts M, Heitger MH, Leemans A, Swinnen SP (2013) Diffusion tensor imaging metrics of the corpus callosum in relation to bimanual coordination: Effect of task complexity and sensory feedback. Hum Brain Mapp 34: 241-252

Gordon Y, Ghez C (1984) EMG patterns in antagonist muscles during isometric contraction in man: relations to response dynamics. Exp Brain Res 55:167-171

Guiard Y (1993) On Fitts's and Hooke's laws: simple harmonic movement in upper-limb cyclical aiming. Acta Psychol 82: 139-159

Haken H, Kelso J A, Bunz H (1985) A theoretical model of phase transitions in human hand movements. Biol Cybern 51: 347-356

Hallett M (2001) Plasticity of the human motor cortex and recovery from stroke. Brain Res Rev 36: 169-174

Helmuth LL, Ivry RB (1996) When two hands are better than one: reduced timing variability during bimanual movements. J Exp Psychol Hum Percept Perform 22: 278-293

Hessler EE, Gonzales LM, Amazeen PG (2010) Displays that facilitate performance of multifrequency ratios during motor-respiratory coordination. Acta Psychol 133: 96–105

Heuer H, Kleinsorge T, Spijkers W, Steglich W (2001) Static and phasic cross-talk effects indiscrete bimanual reversal movements. J Mot Behav 33: 67–85

Heuer H, Spijkers W, Steglich C, Kleinsorge T (2002) Parametric coupling and generalized decoupling revealed by concurrent and successive isometric contractions of distal muscles. Acta Psychol 136: 205–242

Houweling S, Beek PJ, Daffertshofer A (2010) Spectral changes of interhemispheric crosstalk during movement instabilities. Cereb Cortex 20: 2605-2613

Hu X, Newell KM (2011). Visual information gain and task asymmetry interact in bimanual force coordination and control. Exp Brain Res 212: 497-504

Hu X, Loncharich M, Newell KM (2011) Visual information interacts with neuromuscular factors in the coordination of bimanual isometric force. Exp Brain Res 209: 129-138

Hu X, Newell KM (2012) Asymmetric interference associated with force amplitude and hand dominance in bimanual constant isometric force. Motor Control 16: 297-316

Ivry RB, Richardson TC (2002) Temporal control and coordination: the multiple timer model. Brain Cogn 48:11-132

Kagerer FA, Summers JJ, Semjen A (2003) Instabilities during antiphase bimanual movements: are ipsilateral pathways involved? Exp Brain Res 151: 489-500

Kasuga S, Nozaki D (2011) Cross talk in implicit assignment of error information during bimanual visuomotor learning. J Neurophys 106: 1218-1226

Kato K, Muraoka T, Higuchi T, Mizuguchi N, Kanosue K (2014) Interaction between simultaneous contraction and relaxation in different limbs. Exp Brain Res 232:181-189

Kelso JAS (1981) On the oscillatory nature of movement. Bull Psychon Soc 18: 63

Kelso JAS (1984) Phase-Transitions and Critical-Behavior in Human Bimanual Coordination. Am J of Phys 246:1000-1004

Kelso JAS (1994) The informational character of self-organized coordination dynamics. Hum Mov Sci 13: 393-413

Kelso JAS (1995) Dynamic patterns: the self-organization of the brain and behavior. Cambridge, MA: MIT Press

Kelso JAS, Buchanan JJ, Wallace SA (1991) Order parameters for the neural organization of single, multi-joint limb movement patterns. Exp Brain Res 85: 432-444

Kelso JAS, deGuzman GC (1988) Order in time: how cooperation between the hands informs the design of the brain. In H. Haken (Ed) Neural and synergetic computers (180-196) Berlin, Germany: Springer-Verlag

Kelso JAS, Fink PW, DeLaplain CR, Carson RG (2001) Haptic information stabilizes and destabilizes coordination dynamics. P Roy Soc Lond B Bio 268: 1207-1213

Kelso JAS, Scholz JP, Schoner G (1986) Nonequilibrium phase-transitions in coordinated biological motion - Critical fluctuations. Phys Letters A 118: 279-284

Kennedy DM, Boyle JB, Shea CH (2013a) The role of auditory and visual models in the production of bimanual tapping patterns. Exp Brain Res 224: 507-518

Kennedy DM, Boyle JB, Rhee J, Shea CH (2015) Rhythmical bimanual force production: homologous and non-homologous muscles. Exp Brain Res 233: 181-195

Kennedy DM, Boyle JB, Wang C, Shea CH (In Press) Bimanual force production: cooperation and interference. Psychol Res: DOI 10.1007/s00426-014-0637-6

Kennedy DM, Wang C., Shea CH (2013c) Reacting while moving: influence of right limb movement on left limb reaction. Exp Brain Res 230: 143-152

Kennerley SW, Diedrichsen J, Hazeltine E, Semjen A, Ivry RB (2002) Callosotomy patients exhibit temporal uncoupling during continuous bimanual movements. Nat Neurosci 5: 376-381.

Kirk RE (1968) Experimental design procedures for behavior sciences. Belmont, CA: Wadsworth

Kovacs AJ, Buchanan JJ, Shea CH (2009a) Bimanual 1:1 with 90 degrees continuous relative phase: difficult or easy! Exp Brain Res 193: 129-136

Kovacs AJ, Buchanan JJ, Shea CH (2009b) Using scanning trials to assess intrinsic coordination dynamics. Neurosci Lett 455: 162-167

Kovacs AJ, Buchanan JJ, Shea CH (2010a) Impossible is nothing: 5:3 and 4:3 multi-frequency bimanual coordination. Exp Brain Res 201: 249-259

Kovacs AJ, Buchanan JJ, Shea CH (2010b) Perceptual and attentional influences on continuous 2:1 and 3:2 multi-frequency bimanual coordination. J Exp Psychol Hum Percept Perform 36: 936-954

Kovacs AJ, Shea CH (2011) The learning of 90 degrees continuous relative phase with and without Lissajous feedback: External and internally generated bimanual coordination. Acta Psychol 136: 311-320

Kugler PN, Turvey M (1987) Information, natural law, and the self-assembly of rhythmic movement. New Jersey: Lawrence Erlbaum Associates

Latash ML (2010) Motor synergies and the equilibrium-point hypothesis. Motor Control 14: 294-322

Lee M, Carroll TJ (2007) Cross education: possible mechanisms for the contralateral effects of unilateral resistance training. Sports Med 37: 1-14

Levin O, Suy E, Huybrechts J, Vangheluwe S, Swinnen S P (2004) Bimanual coordination involving homologous and heterologous joint combinations: When lower stability is associated with higher flexibility. Behav Brain Res152: 437-445

Li Y, Levin O, Carson RG, Swinnen SP (2004) Bimanual coordination: constraints imposed by the relative timing of homologous muscle activation. Exp Brain Res 217: 1-5.

Liuzzi G, Hörniss V, Zimerman M, Gerloff C, Hummel FC (2011) Coordination of uncoupled bimanual movements by strictly timed interhemispheric connectivity. J Neurosci 31: 9111-9117

Lodha N, Coombes SA, Cauraugh JH (2012) Bimanual isometric force control: asymmetry and coordination evidence post stroke. Clin Neurophysiol 123: 787-795

Mai JK, Paxinos G (eds). (2011). The Human Nervous System (3rd ed.) New York, NY: Academic Press

Maki Y, Wong KFK, Sugiura M, Ozaki T, Sadato N (2008) Asymmetric control mechanisms of bimanual coordination: an application of directed connectivity analysis to kinematic and functional MRI data. Neuroimage 42: 1295-1304

Marteniuk RG, Mackenzie CL, Baba DM (1984) Bimanual movement control – information-processing and interaction effects. Q J Exp Psychol 36: 335-365

Mechsner F, Kerzel D, Knoblich G, Prinz W (2001) Perceptual basis of bimanual coordination. Nature 414: 69-73

Mechsner F, Knoblich G (2004) Do muscles matter for coordinated action? J Exp Psychol Hum Percept Perform 30: 490-503

Murian A, Deschamps T, Temprado JJ (2008) Effects of force production and trial duration on bimanual performance and attentional demands in a rhythmic coordination task. Motor Control 12: 21-37

Nathan PW, Smith MC, Deacon P (1990) The corticospinal tracts in man: course and location of fibres at different segmental levels. Brain 113: 303-324

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9: 97-113

Oullier O, de Guzman GC, Jantzen KJ, Lagarde J, Kelso JAS (2008) Social coordination dynamics: measuring human bonding. Soc Neurosci 3: 178-192

Park S, Dijkstra TMH, Sternad D (2013) Learning to never forget – time scales and specificity of long-term memory of a motor skill. Front Comput Neurosci 7: 1-13

Peper CE, Beek, PJ (1998) Distinguishing between the effects of frequency and amplitude on interlimb coupling in tapping a 2:3 polyrhythm. Exp Brain Res 118: 78-92

Peper CE, Beek PJ, van Wieringen PCW (1995a) Coupling strength in tapping a 2/3 polyrhythm. Hum Movement Sci 14: 217-245

Peper CE, Beek PJ, van Wieringen PC (1995b) Frequency-induced phase transitions in bimanual tapping. Biol Cybern 73:301-309

Peper CE, Beek PJ, van Wieringen PC (1995c) Multifrequency coordination in bimanual tapping: asymmetric coupling and signs of supercriticality. J Exp Psychol Hum Percept Perform 21:1117-1138

Peters M (1980) Why the preferred hand taps more quickly than the non-preferred hand: Three experiments on handedness. Can J Psycho 34:62-71

Peters M (1985) Constraints on the coordination of bimanual movements and their expression in skilled and unskilled subjects. Q J Exp Psychol (A) 37: 171-196

Peters M (1987) A nontrivial motor performance difference between right-handers and left-handers: attention as intervening variable in the expression of handedness. Can J Psychol 41: 91-99

Peters M (1994) Does handedness play a role in the coordination of bimanual movements? In SP Swinnen, J Heuer, J Massion, P Casaer (eds) Interlimb coordination: neural, dynamical, and cognitive constraints. San Diego, CA: Academic Press

Peters M, Schwartz S (1989) Coordination of the two hands and effects of attentional manipulation in the production of a bimanual 2:3 polyrhythm. Aust J Psychol 41: 215-224

Puttemans V, Wenderoth N, Swinnen SP (2005) Changes in brain activation during the acquisition of a multifrequency bimanual coordination task: from the cognitive stage to advanced levels of automaticity. J Neurosci 25: 4270-4278

Ridderikhoff A, Peper CL, Beek PJ (2005) Unraveling interlimb interactions underlying bimanual coordination. J Neurophysiol 94: 3112-3125

Riek S, Carson RG, Byblow WD (1992) Spatial and muscular dependencies in bimanual coordination. J Hum Movement Stud 23: 251-265

Rose DK, Winstein CJ (2004) Bimanual training after stroke: are two hands better than one? Top Stroke Rehabil 11: 20-30

Salesse R, Oullier O, Temprado JJ (2005) Plane of motion mediates the coalition of constraints in rhythmic bimanual coordination. J Motor Behav 37: 454-464

Salter JE, Wishart LR, Lee TD, Simon D (2004) Perceptual and motoric contributions to bimanual coordination. Neurosci Lett 363: 102-107

Schmidt RC, Carello C, Turvey MT(1990) Phase transitions and critical fluctuations in the visual coordination of rhythmic movements between people. J Exp Psychol Hum Percept Perform 16: 227–247

Scholz JP, Kelso JAS (1989) A quantitative approach to understanding the formation and change of coordinated movement patterns. J Motor Behav 21: 122-144

Schöner G, Kelso JAS (1988) Dynamic pattern generation in behavioral and neural systems. Science 239:1513–1520

Seidler RD (2010) Neural correlates of motor learning, transfer of learning, and learning to learn. Exercise Sport Sci R 38: 3-9

Semjen A, Summers JJ (2002) Timing goals in bimanual coordination. Q J Exp Psychol A 55: 155-171

Semjen A, Summers JJ, Cattaert D (1995) Hand coordination in bimanual circle drawing. J Exp Psychol Hum Percept Perform 21: 1139–1157

Serrien D (2009) Interactions between new and pre-existing dynamics in bimanual movement control. Exp Brain Res197: 269-278

Serrien DJ, Cassidy MJ, Brown P (2003) The importance of the dominant hemisphere in the organization of bimanual movements. Hum Brain Mapp 18: 296-305

Serrien DJ, Li Y, Steyvers M, Debaere F, Swinnen SP (2001) Proprioceptive regulation of interlimb behavior: interference between passive movement and active coordination dynamics. Exp Brain Res 140: 411-419

Serrien D, Swinnen SP (1997) Coordination constraints induced by effector combination under isofrequency and multifrequency conditions. J Exp Psychol Hum Percept Perform 23: 1493-1510

Shapkova EY, Shapkova AL, Goodman SR, Zatsiorsky VM, Latash ML (2008) Do synergies decrease force variability? A study of single-finger and multi-finger force production. Exp Brain Res 188: 411-425

Sherwood DE (2003) Hand preference, practice order, and spatial assimilations in rapid bimanual movements. J Mot Behav 26: 123-134

Sisti H M, Geurts M, Clerckx R, Gooijers J, Coxon JP, Heitger MH,… Swinnen SP (2011) Testing multiple coordination constraints with a novel bimanual visuomotor task. Plos One 6: e23619

Spijkers W, Heuer H (1995) Structural constraints on the performance of symmetrical bimanual movements with different amplitudes. Q J Exp Psychol 48: 716-740

Steglich C, Heuer H, Spijkers W, Kleinsorge T (1999) Bimanual coupling during the specification of isometric forces. Exp Brain Res 129: 302-316

Sternad D. Turvey MT, Saltzman EL (1999a) Dynamics of 1:2 coordination: generalizing relative phase to n:m rhythms. J Motor Behav 31: 207-223

Sternad D. Turvey MT, Saltzman EL (1999b) Dynamics of 1:2 coordination: sources of symmetry breaking. J Motor Behav 31: 224-235

Sternad D. Turvey MT, Saltzman EL (1999c). Dynamics of 1:2 coordination: temporal scaling, latent 1:1, and bistability. J Motor Behav 31: 236-247

Stewart KC, Cauraugh JH, Summers JJ (2006) Bilateral movement training and stroke rehabilitation: a systematic review and meta-analysis. J Neurol Sci 244: 89-95

Stinear JW, Byblow WD (2004) An interhemispheric asymmetry in motor cortex disinhibition during bimanual movement. Brain Res 1022: 81-87

Summers JJ, Davis AS, Byblow WD (2002) The acquisition of bimanual coordination is mediated by anisotropic coupling between the hands. Hum Movement Sci 21: 699-721

Summers JJ, Ford SK, Todd JA (1993a) Practice effects on the coordination of the 2 hands in a bimanual tapping task. Hum Movement Sci 12: 111-133

Summers JJ, Maeder S, Hiraga CY, Alexander JR (2008) Coordination dynamics and attentional costs of continuous and discontinuous bimanual circle drawing movements. Hum Movement Sci 27: 823-837

Summers JJ, Todd JA, Kim YH (1993b) The influence of perceptual and motor factors on bimanual coordination in a polyrhythmic tapping task. Psychol Res 55: 107-115

Swinnen SP (2002) Intermanual coordination: from behavioural principles to neural-network interactions. Nature Rev 3: 350-361

Swinnen SP, Dounskaia N, Duysens J (2002) Patterns of bimanual interference reveal movement encoding within a radial egocentric reference frame. J Cogn Neurosci 14: 463-471

Swinnen, SP, Dounskaia N, Levin O, Duysens J (2001) Constraints during bimanual coordination: the role of direction in relation to amplitude and force requirements. Behav Brain Res 123: 201-218

Swinnen SP, Dounskaia N, Walter CB, Serrien DJ (1997) Preferred and induced coordination modes during the acquisition of bimanual movements with a 2:1 frequency ratio. J Exp Psychol-Hum Percept Perform 23: 1087-1110

Swinnen SP, Wenderoth N (2004) Two hands, one brain: cognitive neuroscience of bimanual skill. Trends Cogn Sci 8: 18-25

Temprado JJ, Chardenon A, Laurent M (2001) Interplay of biomechanical and neuromuscular constraints on pattern stability and attentional demands in a bimanual coordination task in human subjects. Neurosci Lett 303: 127-131

Temprado JJ, Swinnen SP, Carson RG, Tourment A, Laurent M (2003) Interaction of directional, neuromuscular and egocentric constraints on the stability of preferred bimanual coordination patterns. Hum Movement Sci 22:339-363

Temprado JJ, Zanone PG, Monno A, Laurent M (1999) Attentional load associated with performing and stabilizing preferred bimanual patterns. J Exp Psychol-Hum Percept Perform 25: 1579–1594

Therrien AS, Lyons J, Balasubramaniam R (2013) Continuous theta-burst stimulation to primary motor cortex reveals asymmetric compensation for sensory attenuation in bimanual repetitive force production. J Neurophysiol 110: 872-882

Todor JI, Lazarus JA (1986) Exertion level and the intensity of associated movements. Dev Med Child Neurol 28: 205-212

Treffner PJ, Turvey MT (1993) Resonance constraints on rhythmic movement. J Exp Psychol-Hum Percept Perform 19: 1221–1237

Treffner PJ, Turvey MT (1995) Handedness and the asymmetric dynamics of bimanual rhythmic coordination. J of Exp Psychol-Hum Percept Perform 21: 318–333

Walter CB, Swinnen SP (1990) Asymmetric interlimb interference during the performance of a dynamic bimanual task. Brain Cogn 14: 185-200

Wang C, Kennedy DM, Boyle JB, Shea CH (2013) A guide to performing difficult bimanual coordination tasks: just follow the yellow brick road. Exp Brain Res 230: 31-40

Yamanishi J, Kawato M, Suzuki R (1980) Two coupled oscillators as a model for the coordinated finger tapping by both hands. Biol Cybern 37: 219-225

Zanone PG, Kelso JAS (1992) The evolution of behavioral attractors with learning: nonequilibrium phase transitions. J Exp Psychol Hum Percept Perform 18: 403–421