

**INFLUENCE OF BIOMECHANICAL CONSTRAINTS ON ENDPOINT  
CONTROL, INTERLIMB COORDINATION, AND LEARNING**

A Dissertation

by

TIFFANY MICHELLE RODRIGUEZ

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

DOCTOR OF PHILOSOPHY

May 2009

Major Subject: Kinesiology

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**ABSTRACT**

Influence of Biomechanical Constraints on Endpoint Control, Interlimb Coordination,  
and Learning.

(May 2009)

Tiffany Michelle Rodriguez, B.S., Texas A&M University

Chair of Advisory Committee: Dr. John J. Buchanan

A number of movements produced in everyday life require not only coordination of joints within a limb, but also coordination between one or more limbs. The aim of this dissertation was to examine the influence of biomechanical constraints on intralimb coordination, interlimb coordination, and learning. Experiment 1 sought to determine if principles of the Leading Joint Hypothesis, when applied to a multijoint bimanual coordination task, could provide insight into the contribution of intralimb dynamics to interlimb coordination. Participants repetitively traced ellipse templates in an asymmetrical coordination pattern (i.e. both limbs moving counter-clockwise). Kinematic data of the upper limbs were recorded with a VICON camera system. Ellipse templates were oriented either tilted right or tilted left; yielding a total of four left arm-right arm leading joint combinations. The findings indicated that stability of interlimb coordination patterns were found to be influenced by whether arm movements were produced with similar or different leading joints. Bimanual asymmetric ellipse-tracing produced with similar leading joints were more stable than patterns produced with

different leading joints. For example, asymmetric coordination patterns produced with similar leading joints exhibited less transient behavior than coordination patterns produced with different leading joints ( $p < .01$ ). Experiment 2 expanded on these findings by employing a similar task and incorporating a learning component to assess how intralimb dynamics are tuned with practice of a novel coordination pattern.

Participants were randomly assigned to one of three groups. One group practiced tracing a pair of ellipse templates that were oriented in such a way that required similar leading joints while the other two groups practiced tracing ellipse templates that required different leading joints. Early in practice, the group learning the coordination pattern with similar leading joints exhibited greater interlimb stability than the two groups learning with different leading joints. However, following two days of practice, performance of the groups learning with different leading joints improved to match that of the group learning with similar leading joints. The findings suggest that initial biomechanical constraints can be overcome with practice, resulting in similar performance regardless of whether being produced with similar or different leading joints.

## **DEDICATION**

To my Mother, Father, and Brother.

## ACKNOWLEDGEMENTS

First and foremost, I would like to express my sincere gratitude to my parents, Velma and Raul Rodriguez, for their unending support throughout my life and particularly during this journey. Thank you for lending me your strong shoulders and patient ears throughout this endeavor. Your reassurances inspired me to emulate from your determination and faith in God. To my brother, Ryan, with any obstacle I encountered along the way, I always turned to you first. You lessened any burden I had, gave me perspective on what is important in life, and showed me how to live life to the fullest.

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**NOMENCLATURE**

CNS	Central Nervous System
EL	Elbow Leading
IT	Interactive Torque
LH	Left Hand
LJH	Leading Joint Hypothesis
LT	Left Tilt
MT	Muscle Torque
NT	Net Torque
RH	Right Hand
RT	Right Tilt
SL	Shoulder Leading

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## CHAPTER I

### INTRODUCTION

#### **Bimanual Coordination**

Identifying the role of pattern stability in interlimb coordination patterns has been the focus of an extensive amount of research on bimanual coordination (Carson, Thomas, Summers, Walters, & Semjen, 1997). Initial bimanual coordination studies examined interlimb stability using tasks requiring single-joint movements such as, index finger abduction-adduction (Kelso & Scholz, 1985), flexion-extension (Haken, Kelso, & Bunz, 1985; Kelso, 1984; Scholz & Kelso, 1990; Schöner, Haken, & Kelso, 1986), and hand tapping (Ibbotson & Morton, 1981). Out of these initial single-joint bimanual coordination studies emerged a number of consistent findings with regard to the relative phasing between limb. First, there exist two stable modes of coordination that can be produced without practice: 1) symmetric (also referred to as in-phase) and 2) asymmetric (also referred to as anti-phase). Second, asymmetric coordination patterns are less stable than symmetric coordination patterns. Moreover, at high movement rates, asymmetric coordination patterns are particularly unstable and can exhibit a spontaneous pattern change that gives rise to the symmetric coordination pattern. These spontaneous pattern changes (always from the less stable asymmetric pattern to the more stable symmetric pattern) are termed phase transitions and indicative of a loss of stability in the relative phase relationship between the arms

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This dissertation follows the style of *Journal of Motor Behavior*.

(Kelso, 1984; Schöner et al., 1986). Just prior to a phase transition, an increase in relative phase variability is often observed and then following the transition into a symmetric pattern, a decrease in relative phase variability is also observed. This increase in variability represents critical fluctuations in the coordinative pattern, a key indicator that loss of stability drove the phase transitions from asymmetric to symmetric coordination (Schöner et al., 1986). Lastly, when changes in coordination pattern are observed, it is usually in the form of the non-dominant limb speeding-up, slowing-down, or exhibiting a movement reversal (Byblow, Lewis, Stinear, Austin, & Lynch, 2000; Byblow, Summers, Semjen, Wuyts, & Carson, 1999; de Poel, Peper, & Beek, 2006). The previously outlined literature on bimanual single-joint coordination studies provides a foundation for understanding stability of interlimb coordination. However, a number of daily tasks require not only coordination between limbs but also the coordination of multiple joints within a limb.

Semjen, Summers, and Cattaert (1995) introduced a bimanual circle-tracing task to examine the stability of interlimb coordination patterns during tasks requiring the coordination of multiple intralimb (shoulder and elbow of both arms) joints. Participants were required to trace (in the horizontal plane) circle templates (10 cm diameter) in either a symmetric (i.e., one hand tracing clockwise and the other counter-clockwise) or in an asymmetric (i.e., both hands tracing clockwise or counter-clockwise) coordination pattern at their preferred rate and at their maximum rate. The relative phasing between hands was found to be less stable during asymmetric circle tracing compared with symmetric circle tracing in both the preferred rate and

maximum rate conditions. On average, cycling frequencies averaged 1.32 Hz during the preferred rate movement condition and during the maximum rate condition cycling frequencies were near 2.53 Hz. This finding is consistent with the previously mentioned single-joint abduction-adduction bimanual work (Buchanan, Kelso, & de Guzman, 1997). Furthermore, when tracing circles in the maximum speed condition with an asymmetric coordination pattern, movement reversals and distortions in the trajectory of the non-dominant hand were observed. In contrast, during symmetric circle tracing, the relative phase between hands was stable for both frequency rate conditions. Based on these findings, the authors concluded that movement frequency influences the stability of interlimb coordination during bimanual circle tracing.

Carson, Thomas, Summers, Walters, and Semjen (1997) argued that an experimental design which employed a continuous variation in movement frequency would be needed in order to conclude definitively that movement frequency was influencing stability of interlimb coordination during bimanual circle tracing in a manner consistent with the single-joint work. Thus, Carson and colleagues (1997) performed a study which added a frequency scaling component to the same bimanual circle (10 cm diameter) tracing patterns used by Semjen et al. (1995). Participants synchronized movements to an auditory signal that increased from 1.50 Hz to 3.00 Hz. The movement frequency increase coincided to an increase in speed from 47.1 cm/s (1.50 Hz) to 94.3 cm/s (3.0 Hz), if speed remained constant when tracing the circles. Overall, the findings were consistent with the results of Semjen et al. (1995). For example, the asymmetric coordination pattern was less stable than the symmetric

pattern. Moreover, movement reversals and distortions in the trajectory of the non-dominant hand occurred consistently in the asymmetric condition as movement frequency was increased. In contrast to previous findings of phase transitions observed during single-joint movements, this study and other bimanual circle drawing studies did not find departures in coordination to be sustained in the form of a phase transition (Byblow et al., 1999; Carson et al., 1997; Semjen et al., 1995; Wuyts, Summers, Carson, Byblow, & Semjen, 1996). Additionally, analysis of the aspect ratio of the produced circle indicated that increasing movement frequency during the asymmetric coordination pattern resulted in an increase in the variability of spatial error, suggesting that accuracy might have been forfeit as a means of maintaining the asymmetric coordination pattern. Furthermore, movement frequency error values indicated that participants did not keep pace with the metronome at higher frequencies (3.0 Hz). The previously mentioned studies replicated the stability findings so common in many single-joint (index fingers, elbows, forearms, wrists) bimanual studies, but did not attempt to identify the contribution of intralimb joint control processes regarding bimanual stability, which is the goal of this dissertation.

While a large majority of previous bimanual work focused on the stability of coordination patterns, recent attempts have been made to understand intralimb coordination and its contribution to observed changes in the stability of multijoint interlimb coordination patterns (Buchanan & Ryu, 2005, 2006; Tseng & Scholz, 2005; Tseng, Scholz, & Valere, 2006). Ryu and Buchanan (2004) examined the influence of amplitude scaling on the stability of interlimb and intralimb coordination by scaling the

diameter of circles within a trial. The findings highlighted the influence of joint amplitude on the stability of interlimb coordination by demonstrating that as circle diameter increased, the probability of having a transition from asymmetric coordination to symmetric coordination decreased and that as circle diameter decreased, the probability of having a similar transition increased. Moreover, tracing smaller circles resulted in more variable asymmetric and symmetric coordination patterns compared with tracing larger circles. The findings suggest that increased joint amplitude can help stabilize asymmetric coordination patterns during bimanual circle tracing. More recently, a study by Tseng, Scholz, and Valere (2006) revealed a link between the variability of elbow interaction torque impulse and cycle-to-cycle variability of the non-dominant hand's path. The Tseng study demonstrated that previously reported frequency-related changes in multijoint (shoulder-elbow) interlimb coordination tasks (Carson et al., 1997; Semjen et al., 1995) could be related to differences in the selective use of joint configuration solutions. The recent consideration of intralimb coordination dynamics and its influence on the stability of multijoint bimanual coordination expand on our understanding of factors contributing to the stabilization of interlimb coordination patterns during multijoint movements.

Much of the bimanual work that has considered intralimb coordination dynamics has done so by examining bimanual circle drawing. However, when tracing a circle, cycling frequency tends to remain constant throughout; with relatively similar contributions of shoulder and elbow joint amplitudes between the limbs. Yet we know that a number of daily tasks require coordination of limbs comprised of varying joint



configurations and joint amplitudes. For this reason, this dissertation will examine the influence of coordinating two limbs wherein the initial task constraints requires the regulation of unequal joint amplitudes within and between limbs.

### **Joint Torques as the Basis for Models of Multijoint Control**

It is important to understand and consider movements at a joint torque level since a number of our daily tasks require the coordination of joints and the ability to coordinate intersegmental dynamics is a key feature in controlling multijoint movements (Ghez & Sainburg, 1995; Ketcham, Dounskaia, & Stelmach, 2004b; Sainburg, Ghilardi, Poizner, & Ghez, 1995). Ketcham, Dounskaia, and Stelmach (2004b) outlined the benefits of considering the influence of intersegmental dynamics. The authors emphasized that considering interaction torques during experimental design and interpretation of data can allow for more of a multi-level approach and broaden our understanding of neural control and movement control.

Different approaches have been used to understand how multijoint movements are controlled. In general, the different perspectives tend to fall into one of two categories, those that view the regulation of intersegmental dynamics as a byproduct of a control strategy and those that regard intersegmental dynamics as being purposefully used. Much of this work has viewed interaction torques as a byproduct of a control strategy. An example of this type of approach is the Equilibrium Point Hypothesis, which proposes that interaction torques result from the processes of transitioning a limb from one equilibrium point to the next (Bizzi, Mussa-Ivaldi, & Giszter, 1991;

Feldman, 1986). Additionally, the perspective of optimal control suggests that interaction torque is a secondary phenomenon of cost-function optimization (Todorov, 2004). Another example includes the inverse dynamics approach, which proposes that interaction torques emerge from movement kinematics (Hollerbach & Flash, 1982). In this approach, movement control is examined in terms of sensorimotor transformation. Specifically, task parameters are transformed into neural commands while at the same time integrating properties of the motor system to produce coordinated joint torque patterns (Kawato, Maeda, Uno, & Suzuki, 1990; Lacquaniti, 1989; Soechting & Flanders, 1991). In contrast, the force control approach proposes that neural representation of intersegmental dynamics is used to specify muscular force (Hollerbach & Flash, 1982). In other words, descending control signals are adapted to the musculo-skeletal limb dynamics (Gribble & Ostry, 1999; Koshland, Galloway, & Nevoret-Bell, 2000; Sainburg, Ghez, & Kalakanis, 1999).

The Leading Joint Hypothesis (LJH) as a model of torque control differs from the other perspective in its interpretation of the regulation of intersegmental dynamics, and in particular, interaction torque. Specifically, the LJH suggests that interaction torque is purposefully generated to exploit the specific biomechanical properties of human limbs for movement production (Dounskaia, 2005).

### **Leading Joint Hypothesis - Multijoint Coordination**

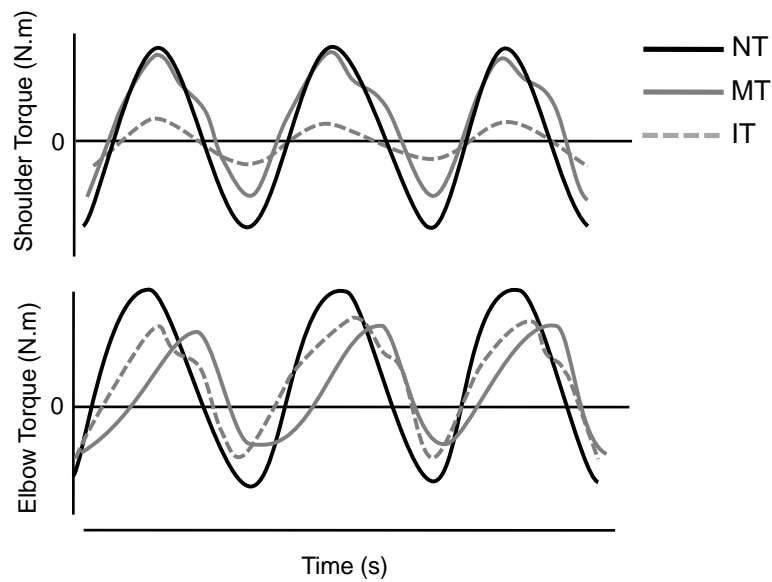
The Leading Joint Hypothesis is a strategy of multijoint control that takes into account intralimb biomechanical properties and proposes a simplified hierarchical

control structure by decomposing multijoint movements into two components, a leading joint and a subordinate joint (for review, see Dounskaia, 2005). Each joint is thought to play a specific role within the multijoint chain of the limb. By definition, control of the *leading* joint generates motion at that joint, which in turn generates large interaction torques at the subordinate joint. These large interaction torques can actually result in significant motion of the subordinate joint which in turn leads to motion of the end-effector. Thus, control of the leading joint generates the dynamic foundation of the entire multijoint chain of the limb. In contrast, the *subordinate* joint is controlled in a manner to regulate the imposed interaction torques from the leading joint. In doing so, the resultant net torque at the subordinate joint generates appropriate (task-specific) end-effector motion.

During multijoint arm movements, the net torque (NT) at a joint can be partitioned into two different components, muscle torque (MT) and interaction torque (IT). The significance of NT is that it is proportional to the joint's angular acceleration. MT is considered *active* torque, because it takes into account the active component due to muscle contraction and the viscoelastic properties of muscles, tendons, ligaments, and other periarticular tissues at the joint. IT is considered *passive* torque because it originates from the motion of the adjacent limb segments. Thus, IT is dependent on motion at both joints.

One of the benefits of the LJH is that by identifying the leading and subordinate joints of a particular movement, categories of movements can be distinguished. The identification of various movement types or categories, allows for the detection of

features that can be generalized across multiple movement directions and/or joint motion combinations. The LJH suggests that different torque profiles that emerge at each joint result from a control strategy that designates different functions at each joint to produce the entire movement. For example, motion at the leading joint is characterized by a significantly larger contribution of MT to NT in comparison to the subordinate joint, with little influence from IT. Furthermore, motion of the leading joint imposes IT at the subordinate joint. This supports the idea that the leading joint's role is to generate the dynamic foundation of the entire movement. The benefit of this is that a simplified control strategy may be used at the leading joint to produce acceleration and deceleration of the entire limb. As a result, motion of the subordinate joint is characterized by a significantly larger contribution of IT with regard to net acceleration in comparison to the leading joint, with this larger contribution of IT regulated by the subordinate joint's MT. Figure 1 portrays how the role of each joint can be identified by examining the torque components at each joint during a multijoint movement. The figure is intended to depict a fragment of an individual torque profile at the shoulder and elbow joints during a circle-tracing task. The top panel demonstrates that shoulder NT (solid black), and thus shoulder acceleration, was primarily due to MT (solid grey) with relatively little influence from IT (dashed grey). This may be seen in that the NT and MT profiles are nearly identical for the shoulder, and therefore, the role of shoulder MT was to accelerate the joint. As a result, the shoulder joint is identified as the *leading joint*.



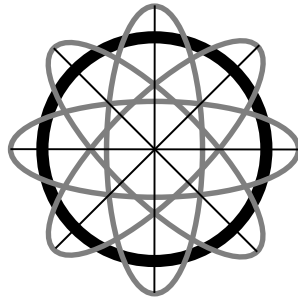
**Figure 1. Sample Torque Profile**

Fragment of individual torque profiles at the shoulder joint (top panel) and elbow joint (bottom panel) during continuous tracing of a circle (horizontal plane). Positive values correspond to flexing torque and negative values correspond to extending torque. Because (net torque) NT is a sum of (muscle torque) MT and (interaction torque) IT, the top panel shows that NT was defined largely by MT at the shoulder, whereas both IT and MT significantly contributed to NT at the elbow (Data developed based on Dounskaia et al., 2002a).

However, at the elbow, the role of MT is different due to the contribution of IT. At the elbow joint, IT contributed significantly to elbow joint acceleration, as evident by the three torque components at the elbow exhibiting similar frequency and amplitude. Thus, elbow MT worked in conjunction with IT to regulate joint acceleration. As a result, the elbow joint is identified as the *subordinate joint*. When the role of the two joints are considered collectively, with the shoulder acting as the leading joint and the elbow acting as the subordinate joint, this particular example of circle tracing would be categorized as a *shoulder-leading* movement. Thus, shoulder joint motion not only contributed to flexion and extension of the upper limb, but it also resulted in motion of the forearm (via elbow IT) to produce the desired circular shape.

Torque profiles can be quantitatively examined with two measures, torque sign and torque impulse. Analysis of torque sign assesses the *temporal* distribution of torque components and provides the means by which the leading and subordinate joints are identified. The joint with the largest torque sign value regarding the contribution of MT to NT is labeled as the leading joint. However, torque sign as a measure does not offer information about the *magnitude* of the contribution of MT and IT to NT.

In order to take into account the contribution of MT and IT to NT regarding the leading and subordinate joint roles, analysis of torque impulses must also be performed. Dounskaia and colleagues (2002a) examined single-limb multijoint arm movements in which subjects continuously traced nine different shapes: a circle, four ellipses (oriented in different directions), and four lines (oriented in different directions) (Figure 2).



Circle Diameter- 18 cm  
Ellipse Diameter-  $25/12$  cm  
Line Length- 25 cm

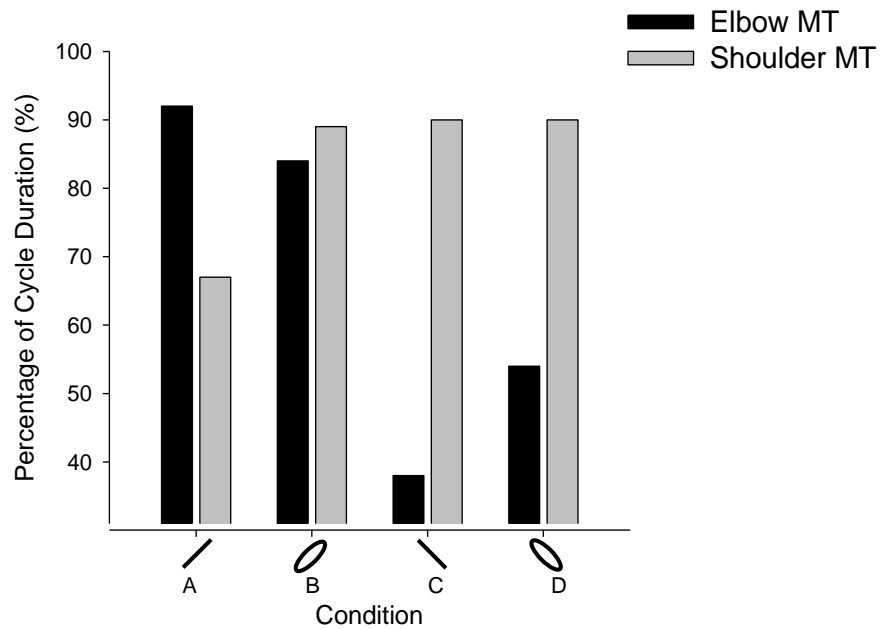
**Figure 2. Shape Templates**

A total of nine shapes were traced: one circle, four ellipses, and four lines. Ellipse and line shapes were oriented in one of four possible directions: vertical, horizontal, tilted left, and tilted right.

Shape templates were traced on a table-top surface, using the index finger, at a cycling frequency of 1.50 Hz. A torque sign analysis and impulse analysis were performed and two leading joint control categories were identified; shoulder-leading and elbow-leading, with eight out of the nine shapes classified as shoulder-leading. Only the line slanted right was classified as an elbow-leading joint strategy, due to evidence of a significant contribution of elbow MT to elbow NT.

For the eight remaining shapes, seven were clearly linked to a shoulder leading strategy, torque sign analysis indicated that shoulder MT functioned to produce motion at the elbow joint, while at the elbow joint, MT and IT shared control. In other words, during some intervals elbow MT accelerated the joint and during other intervals, it regulated the effect of the shoulder's motion. Specifically, conditions B-C (Figure 3) are shoulder-leading as evident by the greater contribution of shoulder MT (than elbow MT) to NT. Conversely, condition A (Figure 3) demonstrates greater contribution of elbow MT (than shoulder MT) to NT and thus indicates elbow-leading control. The contribution of elbow MT and IT varied across shapes. Of the eight remaining shapes (Figure 3, only four shown), only the ellipse slanted right was characterized by a tendency to have a greater contribution of elbow MT to NT, possibly reflecting elbow-leading control similar to that of tracing a line slanted right; but clearly less conclusive. The authors proposed that the consistency of findings across shapes suggests that the differences in shoulder and elbow joint control are indicative of how IT might be exploited to simplify control.





**Figure 3. Percentage of Cycle Duration Example**

Mean percentage of cycle duration for the shoulder (grey) and elbow (black) during which the MT and NT coincided in sign. Data are shown for right tilted line and ellipse conditions (left side) and left tilted line and ellipse conditions (right side) (Data reproduced based on Dounskaia et al., 2002a).

This highlights a distinguishing feature of the LJH in that as a model of multijoint limb control it suggests that IT is controlled in a purposeful manner, and is not just a mere byproduct of the mechanical linkage. One advantage of this type of multijoint control strategy is that it allows for a partial substitution of active control for passive effects and thereby reduces computational complexity associated with producing multijoint movements.

The Leading Joint Hypothesis has been discussed in the context of a variety of single-limb multijoint coordination tasks (Buchanan, 2004; Buchanan, Zihlman, Ryu, & Wright, 2007; Dounskaia, 1998, 2005; Dounskaia et al., 2002a; Ketcham, Dounskaia, & Stelmach, 2004a). However, the LJH has yet to be expanded to a multijoint bimanual task which requires not only the control of intralimb coordination but also interlimb coordination. The additional task of interlimb control in conjunction with manipulation of initial joint configurations provides a platform for evaluating the organization of control when different leading joint strategies are employed to drive the motion of the two limbs.

Experiment 1 will attempt to link principles of the LJH and multijoint intralimb control to bimanual interlimb coordination by employing an ellipse-tracing task requiring participants to trace ellipse template pairs at varying orientations and preset frequencies. In this task, the ellipse templates are larger than those used in previous studies (Dounskaia et al., 2002a; Ketcham et al., 2004a, 2004b) in order to induce more joint motion and possibly find more conclusive evidence for the elbow as a leading joint. The purpose of the ellipse orientation and cycling frequency manipulations was

to alter the relationship between the coordination of joint rotations and the required compensation of IT (Dounskaia et al., 2002a; Ketcham et al., 2004a). Previous reports from intralimb coordination studies have documented a breakdown in IT regulation with increasing cycling frequency (Dounskaia, Ketcham, & Stelmach, 2002b; Ketcham et al., 2004a). A number of studies on bimanual coordination have reported a loss of stability at faster cycling frequencies, particularly during asymmetric circle tracing (Carson et al., 1997; Lee, Swinnen, & Verschueren, 1995). For these reasons, two cycling frequencies were chosen for experiment 1, 1.50 Hz and 2.50 Hz. The combination of producing movements in an asymmetric coordination mode and at the cycling frequency of 2.50 Hz was expected to push the stability of system while not resulting in a lot of transient behavior. The cycling frequency of 1.50 Hz was introduced to serve as a slower baseline condition to make comparisons against, as it has been shown to be relatively more stable (Carson et al., 1997).

The ellipse orientation manipulation described next was intended to develop conditions with varying levels of complexity in the control of individual limbs and coordination between limbs based on initial task constraints. Ellipse templates were oriented in one of two directions; either right tilted (RT) or left tilted (LT). Each ellipse orientation was paired to form four left arm-right arm ellipse-tracing conditions. Based on previous work (Dounskaia et al., 2002a; Ketcham et al., 2004a), it was predicted that when the right limb traced an ellipse slanted left it would result in a shoulder-leading control strategy; whereas, when the right limb traced an ellipse slanted right it would result in a control strategy that reflected elbow-leading control.

The exact opposite was predicted for the left limb. As a result, there would be four conditions of left arm-right arm control strategies; two requiring similar leading-joint control strategies for the left and right limbs and two conditions requiring different leading-joint control strategies for the left and right limbs. Of the two conditions requiring similar leading-joint control strategies, it is predicted that one condition would exhibit shoulder-leading control for both limbs; while the other condition would exhibit elbow-leading control for both limbs. Of the two conditions requiring different leading-joint control strategies, it is predicted that one condition would exhibit elbow-leading control of the left limb and shoulder-leading control of the right limb; while the other condition would exhibit shoulder leading control of the left limb and elbow-leading control of the right limb. A main issue will be whether or not bimanual coordination patterns are more stable when the two arms are controlled by the same leading joint combination compared to the different leading joint combinations.

### **Leading Joint Hypothesis - Acquisition of Novel Motor Skills**

Experiment 2 focuses on the impact of similar and mixed leading joint control on the acquisition of a novel bimanual coordination pattern. Based on the principles of the LJH, two hypotheses pertaining to the acquisition of a novel joint coordination pattern have been proposed. The first prediction is that the acquisition of a novel joint coordination pattern is influenced by the biomechanical properties of a limb when producing a multijoint movement. An example of a biomechanical property is the notion that proximal segments (within a multi-segment linkage) have more massive

musculature and higher inertia than distal segments. As a result, the mechanical influence of the proximal segment motion on to the distal segment is often greater than the influence of distal segment motion on to proximal segments. The LJH is rooted in the idea that the mass and inertial properties of human limbs may constrain multijoint movement control and influence the acquisition of novel coordination patterns.

The second prediction is that the process of acquiring a novel motor skill occurs in a two-step manner. First, during the initial stage of acquisition, motion at the leading joint is developed. This is followed by a second stage, during which motion of the subordinate joint is tuned. The predictions are based on the idea that leading joint control is relatively simple, as its motion is independent of the subordinate joint's motion. As a result, fewer parameters of the leading joint must be specified. For example, muscular control at the leading joint must specify only gross parameters such as magnitude and direction rather than torque values for every moment in time (Dounskaia et al., 2002a). This type of (leading joint) control has been likened to that of single joint control which is characterized by reciprocal activity of antagonistic muscles (Berardelli et al., 1996; Gottlieb, 1998). In other words, leading joint muscle activity directly causes movement at the leading joint and indirectly causes movement at the subordinate joint. In contrast, subordinate joint muscle activity must be continuously modulated to regulate the imposed passive motion, presumably to adjust endpoint movement to meet task demands.

Presently, the predictions put forth by the LJH regarding the acquisition of novel motor skills have not been tested; however, there exists evidence from previous

studies which offer support for the predictions. Evidence for the first prediction comes from a study by Buchanan (2004). Participants were required to learn a  $90^\circ$  relative phase coordination pattern between the elbow and wrist. Joint motion was constrained to flexion-extension of the elbow and wrist joints in the sagittal plane; with the arm in a supine position. Results showed that all but one of the participants spontaneously produced a wrist-lagging (wrist motion lagged elbow motion) coordination pattern rather than a wrist-leading (wrist motion lead elbow motion) pattern, during learning of the continuous  $90^\circ$  intralimb relative phase pattern. The authors offer the explanation that the wrist-lagging pattern might have emerged as a result of the central nervous system (CNS) exploiting interactive torques by transferring angular momentum from the elbow to the wrist as the elbow rotated up and down. The findings shed light on the influence of interactive torque during elbow-wrist coordination and the role of IT as a mechanical constraint on the selection of intralimb coordination strategies during learning. If the data are considered in terms of the LJI principles, then it would be predicted that the elbow joint was functioning as the leading joint, which imposed interactive torques onto the wrist, which was acting as the subordinate joint.

Indirect support for the second prediction comes from a developmental longitudinal study by Konczak and Dichgans (1997) which examined reaching movements from infancy until 3 years of age. By two years of age, the children exhibited shoulder movement patterns similar to that of adults. However, not until 3 years of age did elbow movement patterns represent those of adults. Additionally, Shimansky and colleagues (2004) studied the adaption of reaching movements to

external perturbations in cats and found that adaptive changes in shoulder control occurred earlier in practice; whereas, adaptation of the distal joint's motion occurred later in practice. When the data are considered in the context of the LJH predictions regarding differential time scales of leading and subordinate joint tuning, it can be predicted that the early tuning of the shoulder joint (both children and cats) was indicative of its role as the leading joint and the later elbow joint tuning was indicative of its role as the subordinate joint.

Previous research examining the adaptation processes associated with changes in limb dynamics (Lackner & Dizio, 1994; Sainburg et al., 1999; Shadmehr & Mussa-Ivaldi, 1994) has predominantly focused on how learning affects motion of the arm's endpoint path with less consideration for changes in joint motion. Furthermore, the majority of the bimanual learning work has focused on single joint arm movements with less attention given to bimanual multijoint movements (Walter, Swinnen, & Dounskaia, 2002). Experiment 2 employed a multijoint bimanual ellipse-tracing task in order to establish a link between intralimb control processes, endpoint accuracy, and the stability of interlimb coordination patterns within a motor skill learning context. Experiment 2 was designed to test the predictions put forth by the LJH regarding the acquisition of a novel motor skill. It was predicted that the adaptation processes would evolve differently at the leading and subordinate joints, based on whether movements were produced with similar leading joints or with different leading joints.

Learning a novel coordination pattern (one not inherent to the system) requires the use of specific environment information to characterize the to-be-learned

coordination pattern (spatio-temporal relationship between components). Examples of types of information used to characterize the to-be-learned coordination pattern include flashing lights with time delays to represent various relative phase patterns between the index fingers (Zanone & Kelso, 1992, 1997) and angle-angle plots to specify coordination patterns between joints and limbs (Buchanan, 2004; Fontaine, Lee, & Swinnen, 1997; Lee et al., 1995). For the angle-angle plots, a  $45^\circ$  positively sloped line can represent an in-phase coordination pattern; and a  $45^\circ$  negatively sloped line can represent an anti-phase coordination pattern (Fontaine et al., 1997; Lee et al., 1995). Additionally, a  $90^\circ$  relative phase between the arms can be represented as a circle (Lee et al., 1995). Many of these studies employed a scanning procedure to identify the systems so-called intrinsic dynamics, in other words, what patterns can an individual produce without practice. Collectively, prior research has found two consistent results (Fontaine et al., 1997; Lee et al., 1995; Zanone & Kelso, 1992, 1997): 1) in phase ( $0^\circ$ ) and anti phase ( $180^\circ$ ) bimanual coordination patterns are intrinsically stable and present in our motor repertoire, and 2) a  $90^\circ$  relative phase bimanual pattern is inherently unstable and requires extensive practice to develop an internal representation in order to produce without salient feedback. However, with extensive practice the  $90^\circ$  relative phase pattern can be learned and reproduced in a stable manner up to two weeks after the last practice session (Buchanan, 2004; Zanone & Kelso, 1997).

The LJIH predictions pertaining to learning are for the acquisition of a *novel* intralimb coordination pattern. For this reason, a  $90^\circ$  relative phase bimanual pattern



was chosen as the goal interlimb pattern since this pattern may require intralimb adjustments to achieve the bimanual goal. This task may provide an opportunity to link intralimb control based on the LJH to bimanual control based on pattern stability. The LJH hypothesizes that learning is influenced by biomechanical properties of the limb. The LJH also hypothesizes that intralimb learning involves two stages, first (early in practice) the leading joint is tuned and second (later in practice) the subordinate joint is tuned. Based on these hypotheses, it is predicted that a group learning the 90° relative phase pattern with similar leading joints will achieve the target relative phase earlier in practice than the group learning the phase pattern with different leading joints. This is based on the notion that the group learning the pattern with similar leading joints will have the advantage of tuning similar leading joints at the same time. For example, early in practice it is expected that for a group learning the 90 relative phase pattern with the shoulder the leading joint for both arms etc. the similar leading joint group (SL-SL) tuning of the shoulder joints (leading joint) would occur for both resulting in less complex planning demands relative to the group learning with different leading joints (EL-SL). For these groups (EL-SL RH lead and LH lead), early in learning the left limb would require tuning of the elbow joint while the right limb would require tuning of the shoulder joint.

## CHAPTER II

### EXPERIMENT 1

#### **Objective**

The purpose of this study was to determine if principles of the Leading Joint Hypothesis, when applied to a multijoint bimanual coordination task, can provide additional insight into the influence of intersegmental dynamics on endpoint control and stability of interlimb coordination patterns.

#### **Methodology**

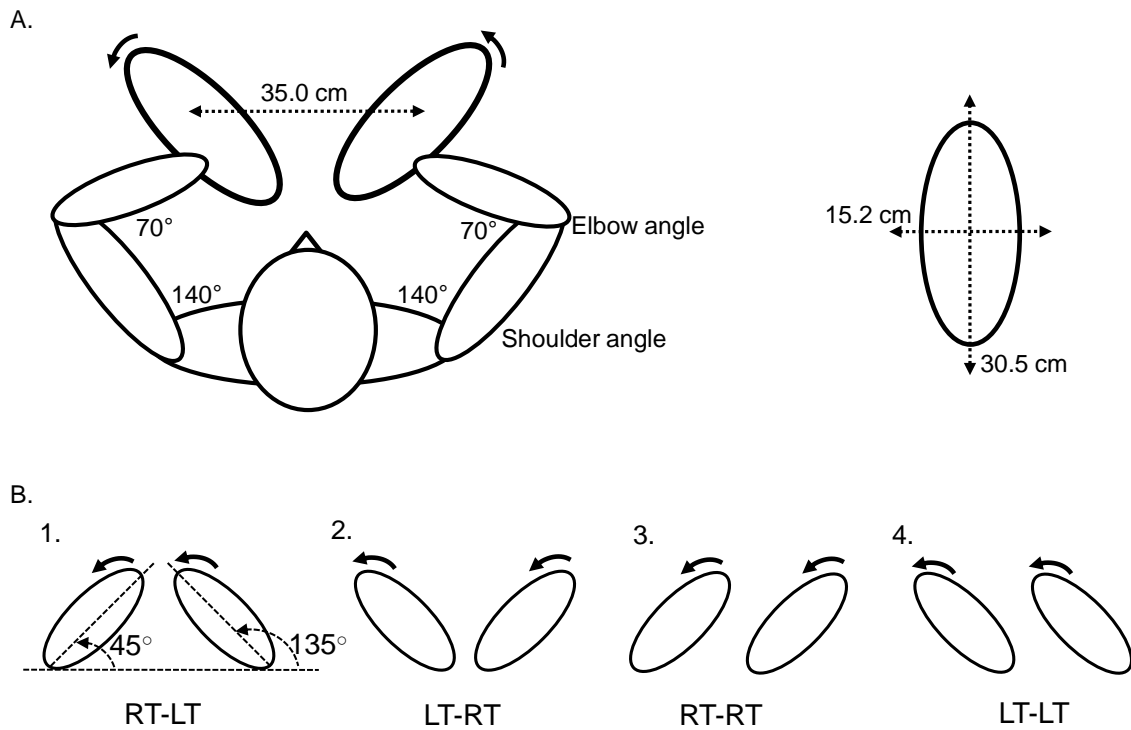
##### *Participants and Procedures*

Eight right-handed (self reported) young adults ( $23.4 \pm 3.4$  yrs) participated in this study. All subjects received a brief explanation of the experiment before reading and signing a consent form approved by the local Institutional Review Board at Texas A&M University.

Participants were seated at a table with the chair height adjusted such that when the arms rested on the table; both the upper and lower arms were parallel with the table surface. Subjects performed bimanual arm movements in the horizontal plane by repetitively tracing a pair of ellipse templates projected (via NEC light projector) from below up to a Plexiglas<sup>®</sup> surface. The trunk, wrists, and index fingers were immobilized and the templates were traced using the index finger tips. Starting positions were individually adjusted to the position of the subjects' index fingers with

their shoulder joints angled at  $140^\circ$  and elbow joints at  $70^\circ$  (Figure 4A). An auditory cue indicated the start of each trial. A wrist brace and finger splint were worn. Motion of the distal interphalangeal and proximal interphalangeal joints of the index finger was reduced by wrapping them in tape. The tape also served to reduce friction when sliding the index finger across the Plexiglas<sup>®</sup>.

Ellipse template size was 30.5 cm (major axis) and 15.2 cm (minor axis). The distance between the centers of the ellipses was fixed at 35.0 cm. Each ellipse template was oriented in one of two directions: 1) right tilted with the major axis at a  $45^\circ$  angle or 2) left tilted with the major axis at a  $135^\circ$  angle. The two ellipse orientations were paired to form four ellipse-tracing conditions (Figure 4B). Subjects traced each ellipse pair at 1.5 Hz and 2.5 Hz. Tracing frequency was controlled by an auditory metronome. The ellipses were always traced with an asymmetrical coordination pattern as the initial tracing pattern (both limbs moving counter-clockwise). Subjects performed three trials of each set of templates at each cycling frequency. A trial lasted 10 seconds in duration. The order of template pairs and cycling frequency were counterbalanced across subjects so that each participant had a different initial template-cycling frequency combination.



**Figure 4. Experiment 1 Setup and Design**

A) Schematic representation of the experimental setup. Ellipse diameters remained constant throughout the experiment. B) Ellipse-tracing conditions. Each ellipse template was oriented in one of two directions: 1) right tilted (RT) or 2) left tilted (LT). The two ellipse orientations were paired to form four ellipse-tracing conditions: 1) RT-LT, 2) LT-RT, 3) RT-RT, and 4) LT-LT.

### *Data Recording and Analysis*

A VICON four camera system (120 Hz sampling frequency) recorded movement from near-infrared reflective markers that were attached with adhesive tape to the skin above the following landmarks: 1) sternal notch; 2) left and right upper limbs' lateral edge of acromion process; 3) left and right limbs' lateral epicondyle of the humerus; and 4) left and right distal end of the index fingers. The four cameras were located on the opposite side of the table from where the subjects were sitting. Cameras were raised approximately three feet above the table facing the subjects. The extraction of all dependent measures was performed with routines written in Matlab 7.0 (The Mathworks, Inc.).

### *Torque Analyses*

The purpose of the torque analyses was to determine the classification of movements based on principles of the L<sub>JH</sub> by revealing the role of torque components in the production of movement at each joint. Elbow and shoulder joint angular displacements were used to compute joint torques. Segment masses, locations of center of mass, and moments of inertia about the transverse axes passing through the joint centers were determined based on a subject's height, weight, and statistically based anatomical data (Chaffin & Anderson, 1984). The torque components at each joint are defined as follows (Dounskaia et al., 2002a): NT is proportional to angular acceleration at the joint and is comprised of two components, MT and IT. MT takes into account the active component due to muscle activation and the passive component

due to viscoelastic properties of muscles, tendons, ligaments, and other periarticular tissues at the joint. IT comes from motion at the joint and from motion of any adjacent joint in the multilink system. Accordingly, torque components are bounded by the following relationship:  $NT = MT + IT$ .

The torque time series were used to compute measures in order to identify leading and subordinate joints. The first measure is that of torque sign which estimates the portion of cycle duration where the sign of MT coincides with the sign of NT for each joint (Dounskaia, 1998; Sainburg et al., 1995). Torque sign values close to 100% of cycle duration indicate that MT played a dominant role in joint acceleration. Based on the LJH, the joint in a multijoint link like the arm that has the largest torque sign is taken as the *leading* joint. i.e., the joint that forms the dynamic base for the entire movement. The second measure is that of torque impulse and this measure determines the magnitude of MT and IT contributions to NT at each joint (Sainburg & Kalakanis, 2000). The positive impulse of a torque component was calculated as the torque integral during intervals where the torque component acted in the same direction as NT. The negative impulse of a torque component was calculated during the intervals where the torque component acted in the opposite direction of NT. For each torque component, positive and negative impulses were summed for each cycle and the portion of NT produced by MT was determined. Positive values of torque impulse correspond to the torque that predominately had the same sign as the NT. In contrast, when MT or IT was predominately opposite in sign to NT, its impulse was negative

(Dounskaia et al., 2002a; Sainburg & Kalakanis, 2000). One of the characteristics of subordinate joint control is that IT substantially contributes to NT.

### *Kinematic Analysis*

*Cycling Frequency.* The x,y time series of each end-effector marker were used to compute cycling frequency; points of maximum angular displacement were delineated for each movement cycle using a ‘peak picking’ algorithm to estimate cycling frequency and amplitude. Cycling frequency was computed on a cycle to cycle basis.

*Interlimb Relative Phase.* Interlimb relative phase was computed as a continuous relative phase ( $\varphi_c$ ) using the left limb ( $l$ ) as the target, and the right limb ( $r$ ) as the reference. For each end-effector marker, the x,y time series were fitted by an ellipse and rotated by  $45^\circ$  on a cycle-to-cycle basis (Beek & Beek, 1988). Following the rotation, the tangential angle ( $\theta$ ) associated with the x,y trajectory of each end-effector marker was computed (Carson et al., 1997) and the continuous relative phase was computed as  $\varphi_c = \theta_r - \theta_l$ , and circular statistics were applied (Mardia, 1972). Interlimb relative phase error ( $\varphi_{err}$ ) was computed as the constant error of the continuous mean relative phase ( $\varphi_c$ ) relative to the required relative phase ( $\varphi_{req} = 180^\circ$ ) ( $\varphi_{err} = \varphi_c - \varphi_{req}$ ), with a negative value indicating a right limb lead and a positive value indicating a left limb lead.

Stability of coordination patterns were quantified by examining the interlimb relative phase variability, assessed by means of a transformed circular variance that

captures the uniformity (circular dispersion) of the relative phasing between two components (Burgess-Limerick, Abernethy, & Neal, 1991; Semjen & Summers, 2002). Specifically, a uniformity value of 1 represents no variance and a uniformity value of 0 represents no central tendency. Another way to examine the stability of a coordination pattern is to identify whether or not some form of transient behavior (movement reversals, phase wrapping, phase transition) occurs within a trial. A movement reversal occurs when the direction of movement of one of the arms switches from the required counter-clockwise motion to clock-wise motion, and then back to counter-clockwise motion. Movement reversals were identified for individual limbs. Phase wrapping in the current experiment was identified as sustained drift in the relative phase between limbs of greater than  $30^\circ$  within a trial. A phase transition was a switch from the required asymmetric coordination pattern to a sustained (end of the trial) symmetric coordination pattern. Both phase wrapping and phase transitions were identified for individual trials. Less than 1% of all trials included a phase transition. The relative phase analysis was performed to determine if the stability of bimanual coordination is influenced by whether or not the end-effector motion is being driven by the same or different leading joints across the arms.

*Diameter Ratio.* The x,y time series of the end-effector markers were used to compute the major and minor axis diameters of each ellipse traced by each arm on a cycle to cycle basis. The ratio of major axis diameter to minor axis diameter was determined. Diameter ratio is a measure of trajectory distortion. For the current study,



the required diameter ratio ( $DR_{req}$ ) was 0.5. A constant error was computed ( $CE = DR_{obs} - DR_{req}$ ) to determine the mean diameter ratio directional bias.

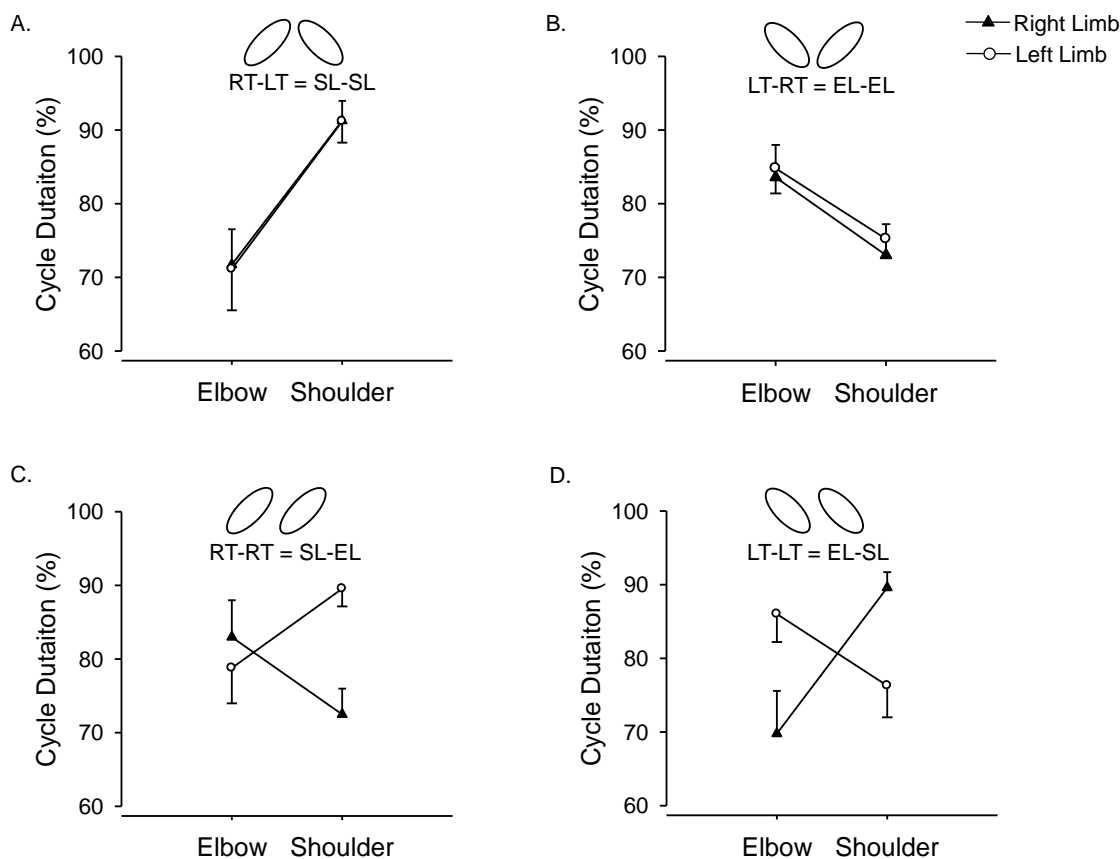
### **Statistics**

Three different ANOVA models were used to analyze data. The torque variables were analyzed with a 4 Condition (RT-LT, LT-RT, RT-RT, LT-LT) x 2 Cycling Frequency (1.5, 2.5 Hz) x 2 Limb (left, right) x 2 Joint (shoulder, elbow) ANOVA with repeated measures on Condition, Frequency, Limb, and Joint. The relative timing variables were analyzed with a 4 Condition (RT-LT, LT-RT, RT-RT, LT-LT) x 2 Cycling Frequency (1.5, 2.5 Hz) ANOVA with repeated measures on Condition and Frequency. The cycling frequency, transient behavior, and diameter ratio data were analyzed with a 4 Condition (RT-LT, LT-RT, RT-RT, LT-LT) x 2 Frequency (1.5, 2.5 Hz) x 2 Limb (Left, Right) ANOVA with repeated measures on Condition, Frequency, and Limb. Post-hoc analyses were performed when needed to delineate main effects and interaction effects. All post-hoc comparisons were conducted using Tukey's HSD test. The Greenhouse-Geisser corrected degrees of freedom were used when sphericity violations occurred. All statistical analyses were performed with SPSS software (SPSS version 15.0). The alpha level for all statistical tests was 0.05. Data are reported as means  $\pm$  standard error within the text and in the figures.

## Results

### *Torque Signs*

According to the LJM, the joint characterized by the largest torque sign is acting as the leading joint in a multijoint link. The torque sign data provided compelling evidence that both the elbow and shoulder can be designated as leading joints based on initial task conditions. Analysis of torque sign cycle duration yielded a significant Joint main effect ( $F_{1,7} = 23.6, p < .01$ ), Limb main effect ( $F_{1,7} = 20.9, p < .01$ ), Frequency main effect ( $F_{1,7} = 11.9, p < .05$ ), and Condition main effect ( $F_{3,21} = 5.48, p < .01$ ). There was also a significant Condition x Limb x Joint interaction ( $F_{1,10} = 47.6, p < .001$ ). Post-hoc ( $p < .05$ ) analysis indicated that the portion of cycle duration when MT acted to accelerate the joint was significantly different for the shoulder and elbow depending on the condition. Figure 5A shows the condition (RT-LT) in which the left and right shoulders exhibited a greater contribution of MT to NT compared to the elbow. Figure 5B depicts the condition (LT-RT) in which the left and right elbows exhibited a greater contribution of MT to NT compared to the shoulders. Figures 5C and D depict the conditions which resulted in *different* control strategies for the left and right limbs. The bottom left panel (Figure 5C) portrays the condition (RT-RT) in which the left limb had a greater contribution of shoulder MT (than elbow MT) to NT; while the right limb had a greater contribution of elbow MT (than shoulder MT) to NT. The bottom right panel (Figure 5D) depicts the condition (LT-LT) in which the left limb had a greater contribution of elbow MT (than shoulder MT) to NT; while the right limb had a greater contribution of shoulder MT (than elbow MT) to NT.



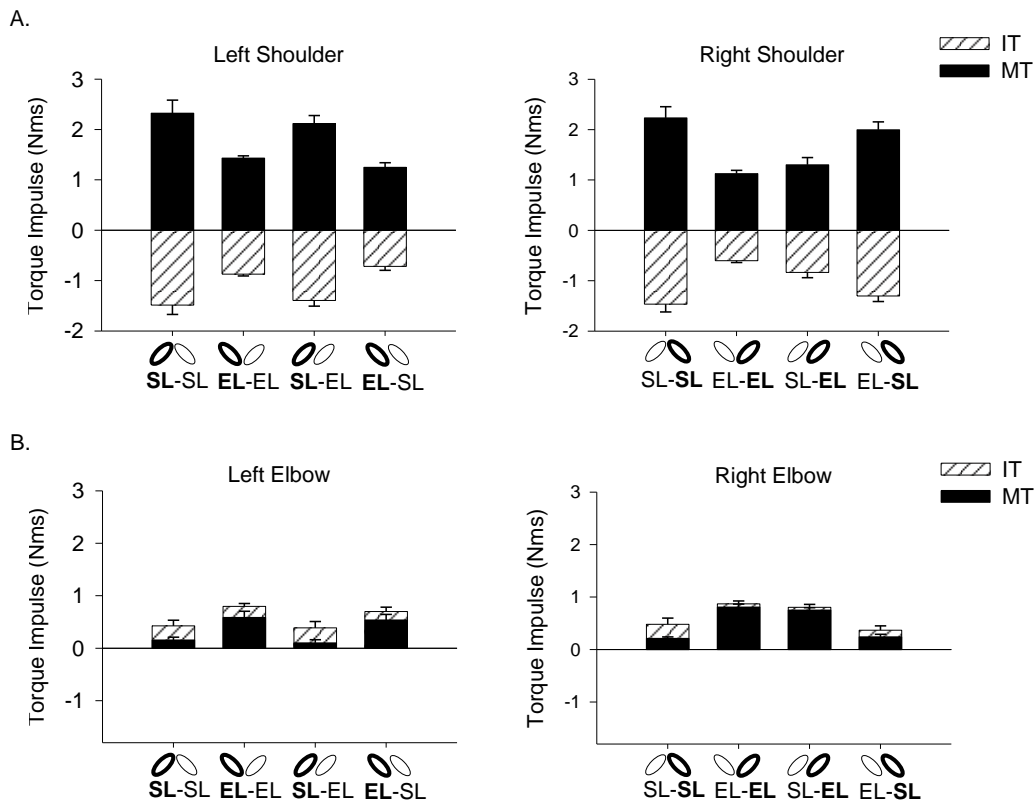
**Figure 5. Torque Signs**

Mean percentages of cycle duration for the elbow and shoulder during which the sign of MT and the sign of NT coincided for the left limb (open circle) and right limb (solid-filled triangle) averaged across cycling frequencies. A-B) Mean percentages (and standard error) of torque sign cycle duration for elbow MT and shoulder MT during *similar* left arm-right arm leading joint condition (left panel: SL-SL; right panel: EL-EL). C-D) Mean percentages (and standard error) of torque sign cycle duration for elbow MT and shoulder MT during *different* left arm-right arm leading joint conditions (left panel: SL-EL; right panel: EL-SL).

### *Torque Impulses*

Torque impulse at each joint was computed to determine the magnitude of the contribution of MT and IT to a joint's NT. The torque impulse values, especially MT, varied in a manner consistent with the torque sign data that indicated different leading joint combinations as function of initial ellipse orientation.

Analysis of the MT impulse data yielded a significant Condition main effect ( $F_{3,21} = 3.84, p < .05$ ) and Joint main effect ( $F_{1,7} = 75.1, p < .001$ ). The Joint x Condition interaction ( $F_{3,21} = 14.8, p < .01$ ) and Limb x Condition interaction ( $F_{3,21} = 6.63, p < .01$ ) were significant. The Joint x Limb x Condition interaction ( $F_{3,21} = 19.9, p < .001$ ) was also significant (Figure 6) and further post-hoc tests were performed to locate the factors contributing to the interaction. On average, both shoulder MTs and both elbow MTs positively contributed to NT. Post-hoc analysis ( $p < .05$ ) indicated that the contribution of MT to NT was significantly different for both the shoulder and elbow depending on the condition. Take for example shoulder MT (solid-filled bars). For the left limb, shoulder MT was larger (greater contribution to NT) when tracing an ellipse tilted right compared to when it was tracing an ellipse tilted left. Conversely, for the right limb, shoulder MT was smaller (less contribution to NT) when tracing an ellipse tilted right compared to when it was tracing an ellipse tilted left. In contrast, for the left limb, elbow MT was larger (greater contribution to NT) when tracing an ellipse tilted left (LT-RT: EL-EL, LT-LT: EL-SL).



**Figure 6. Torque Impulses**

A) Mean (and standard error) shoulder MT (solid-filled bars) and shoulder IT (pattern-filled bars) impulses for each limb across each left arm-right arm leading joint combination and averaged across frequencies. B) Mean (and standard error) elbow MT (solid-filled bars) and elbow IT (pattern-filled bars) impulses for each limb across each left arm-right arm leading joint combination and averaged across frequencies. A positive impulse demarks the torque component that predominantly had the same sign as NT; while a negative impulse indicates the torque component that had the opposite sign as NT.

Conditions with different leading joints exhibited the largest differences between left and right limb MT. For example, in the SL-EL (RT-RT) condition the left elbow produced relatively small MT (Figure 6B) and the right elbow produced relatively large MT. In contrast, within the SL-SL (RT-LT) condition, shoulder and elbow MT values of the left limb were similar to the shoulder and elbow MT values of the right limb. Thus, when torque sign indicates that one joint is assigned the leading role, MT contributes significantly more to NT in comparison to when that joint is acting in a subordinate role.

The analysis of the IT impulse data yielded a significant Condition main effect ( $F_{3,21} = 3.99, p < .05$ ) and Joint main effect ( $F_{1,7} = 64.9, p < .001$ ). There was also a significant Joint x Frequency interaction ( $F_{1,7} = 6.18, p < .05$ ), and Joint x Limb interaction ( $F_{1,7} = 10.3, p < .05$ ). The Joint x Condition interaction ( $F_{3,21} = 9.80, p < .05$ ) and Limb x Condition interaction ( $F_{3,21} = 6.79, p < .01$ ) were also significant. IT at the elbow and shoulder was differentially influenced by frequency. Elbow IT at the cycling frequency of 2.50 Hz was increased compared to 1.50 Hz, whereas shoulder IT did not differ at either cycling frequency. Similar to the muscle torque sign analysis, the Joint x Limb x Condition interaction ( $F_{3,21} = 22.7, p < .001$ ) was also significant. Overall, shoulder IT negatively contributed to NT and elbow IT positively contributed to NT.

Post-hoc analysis ( $p < .05$ ) indicated that the contribution of IT to NT was significantly different for the shoulder and elbow depending on the condition. For example, shoulder IT in the left limb was larger (greater contribution to NT) when

tracing an ellipse tilted right compared to when it was tracing an ellipse tilted left. Conversely, for the right limb, shoulder IT was smaller (less contribution to NT) when tracing an ellipse tilted right compared to when it was tracing an ellipse tilted right. Thus, when torque sign indicates that one joint is assigned the subordinate role, IT seems to contribute significantly more to NT in comparison to when that joint is acting in the leading role.

### *Cycling Frequency*

Analysis of cycling frequency yielded a significant Frequency main effect ( $F_{1,7} = 36.55, p < .001$ ) (1.5 Hz:  $1.53 \pm 0.03$  Hz; 2.5 Hz:  $2.39 \pm 0.09$  Hz) and Limb main effect ( $F_{1,7} = 12.94, p < .05$ ). The Frequency x Limb interaction approached significance ( $F_{1,7} = 9.02, p = .07$ ), hinting at a trend for differences between limbs for the 2.50 Hz cycling frequency (left:  $2.32 \pm 0.13$  Hz; right:  $2.44 \pm 0.06$ ). No statistical differences were found across the bimanual ellipse-tracing task conditions ( $p > .05$ ). All other interactions were not found to be statistically significant ( $p > .05$ ).

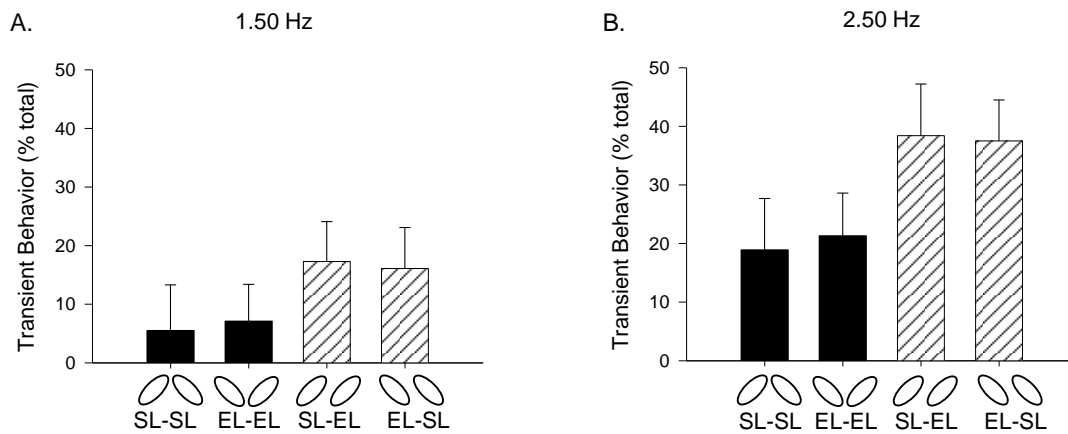
### *Interlimb Relative Phase: Transient Behavior*

The torque sign and torque impulse data indicated that the four ellipse-tracing conditions resulted in four distinct left arm-right arm leading joint combinations: two conditions with similar leading joints (SL-SL, EL-EL); and two conditions with different leading joints (SL-EL, EL-SL). The stability of interlimb coordination

patterns and endpoint variability were also found to be influenced by whether the tracing actions were produced with similar or different leading joints combinations.

The analysis of the number of transient behavior trials yielded a significant Condition main effect ( $F_{3,21} = 21.9, p < .001$ ), Frequency main effect ( $F_{1,7} = 43.4, p < .001$ ), and Limb main effect ( $F_{1,7} = 7.67, p < .05$ ). Figure 7 shows the percent of trials which exhibited transient behavior plotted as a function of condition and cycling frequency. Post-hoc analysis revealed that more transient behavior emerged for the different leading joint combinations (pattern-filled bars) compared to the similar leading joint combinations (solid-filled bars) ( $p < .05$ ). On average, the higher cycling frequency resulted in a greater number of transient behavior trials than the slower cycling frequency, with more transient behavior associated with the left arm (27%) compared to the right arm (13%). There was also a significant Frequency x Condition interaction ( $F_{3,21} = 4.14, p < .05$ ), and post-hoc analysis revealed more transient behavior trials with different leading joints (SL-EL and EL-SL) at the cycling frequency 2.5 Hz compared to the cycling frequency 1.5 Hz.





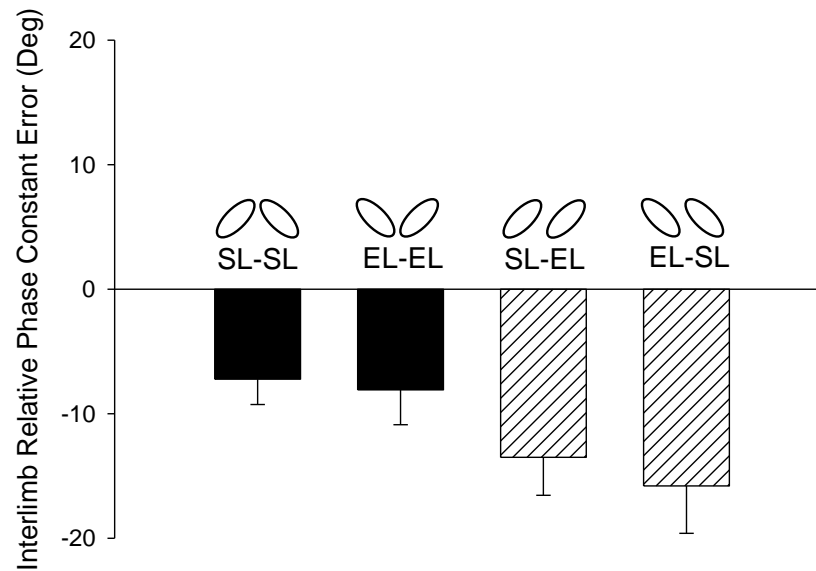
### Figure 7. Transient Behavior

Percent of trials exhibiting transient behavior for each left arm-right arm leading joint condition, SL-SL, EL-EL (similar, solid-filled) and SL-EL, EL-SL (different, pattern-filled) at cycling frequencies of 1.5 Hz (A) and 2.5 Hz (B).

All other interactions were not statistically significant ( $p > .05$ ). Of the trials containing transient behavior, approximately 56% contained a movement reversal, 43% exhibited phase wrapping, and less than 1% contained a phase transition. Trials containing transient behavior were removed from the remaining analysis.

#### *Interlimb Relative Phase: Performance Error*

Analysis of the interlimb relative phase error data yielded a significant Condition main effect ( $F_{3,21} = 13.2, p < .05$ ) and Frequency main effect ( $F_{1,7} = 28.4, p < .01$ ). Histogram plots of the relative phase data (constant error) are portrayed in Figure 8. A negative value indicated a right limb lead and a positive value indicated a left limb lead. Post-hoc analysis of the Condition main effect indicated that the condition requiring shoulder leading joint control for both limbs (SL-SL Figure 8, pattern-filled) resulted in significantly smaller error values in interlimb relative phase than the condition requiring elbow leading control for the left limb and shoulder leading control for the right limb (EL-SL Figure 8, pattern-filled). On average, movements produced at 1.50 Hz resulted in significantly smaller error values ( $-8.13^\circ$ ) than at 2.50 Hz ( $-14.2^\circ$ ). All other interactions were not statistically significant ( $p > .05$ ).



**Figure 8. Interlimb Endpoint Relative Phase**

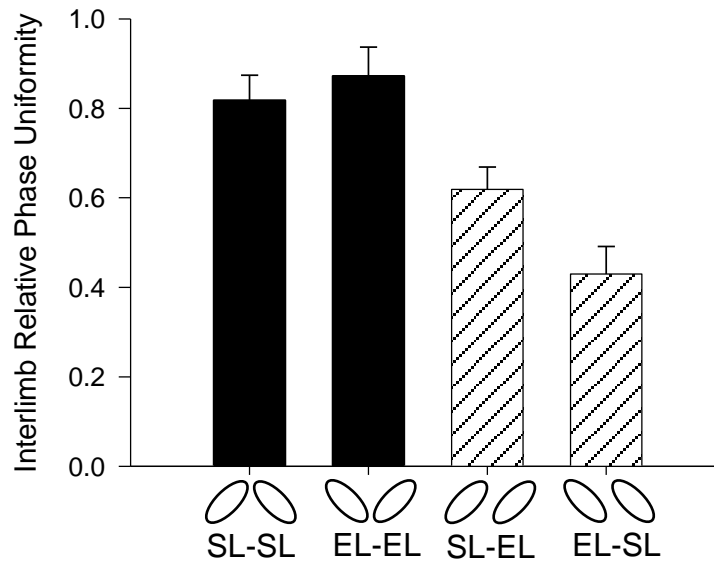
Mean (and standard error) interlimb endpoint relative phase constant error for each left arm-right arm leading joint condition: SL-SL, EL-EL (similar, solid-filled) and SL-EL, EL-SL (different, pattern-filled). Error values depicted are averaged across cycling frequencies.

*Interlimb Relative Phase: Pattern Stability (Uniformity)*

Analysis of the interlimb endpoint relative phase uniformity data yielded a significant Condition main effect ( $F_{3,21} = 7.97, p < .01$ ; Figure 9). Post-hoc analysis revealed larger interlimb endpoint relative phase uniformity values (indicating more stable performance) for bimanual asymmetric coordination patterns produced with the same leading joints (solid-filled bars) compared with bimanual asymmetric coordination patterns produced with different leading joints across limbs (solid-filled bars; Figure 9) ( $p < .05$ ). The Frequency main effect approached significance ( $F_{1,7} = 6.68, p = .07$ ). The data suggest that lower interlimb relative phase uniformity values in the 2.50 Hz cycling frequency condition (0.60) compared to the cycling frequency of 1.50 Hz (0.71). All other interactions were not found to be statistically significant ( $p > .05$ ).

*Diameter Ratio*

Analysis of the error in the left and right arm's endpoint diameter ratios yielded a statistically significant Condition main effect ( $F_{3,21} = 9.89, p < .05$ ) and also a significant Limb main effect ( $F_{1,7} = 19.49, p < .001$ ). The Condition x Limb interaction was also found to be significant ( $F_{3,21} = 8.76, p < .05$ ).



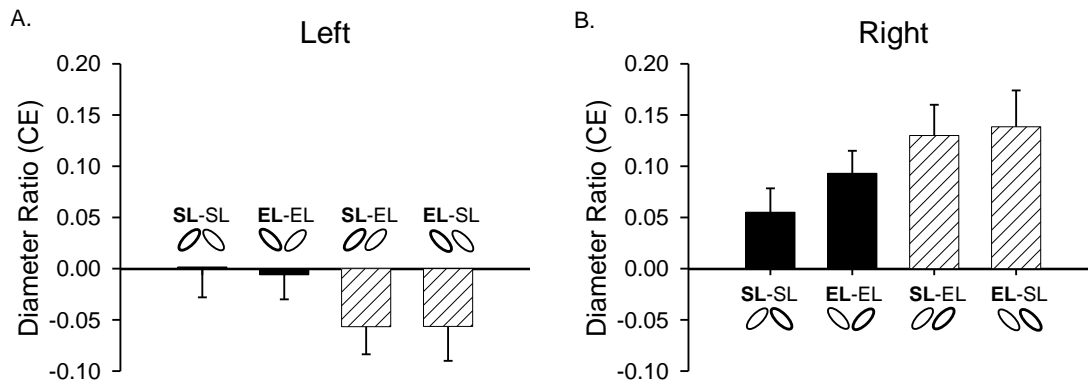
**Figure 9. Interlimb Endpoint Relative Phase Uniformity**

Mean (and standard error) of interlimb endpoint relative phase uniformity for each left arm-right arm leading joint condition: SL-SL, EL-EL (similar, solid-filled) and SL-EL, EL-SL (different, pattern-filled). Uniformity values depicted are averaged across cycling frequencies.

Post-hoc analysis of the Condition x Limb interaction revealed diameter ratio values closer to the target value for end-effector motion produced with similar leading joints (solid-filled bars) compared with end-effector motion produced with different leading joints (pattern-filled bars) for both arms (Figure 10). Overall, the directional bias of the diameter ratio error was different between the arms; with the largest difference in directional error occurring in the different leading joint conditions. The frequency main effects and all other interactions were not statistically significant ( $p > .05$ ).

### **Summary of Findings and Discussion**

The current study employed a bimanual ellipse-tracing task to examine the influence of biomechanical principles as defined by the LJH on the control of endpoint motion and the stability of interlimb coordination patterns. Similar to previous reports (Dounskaia et al., 2002a; Ketcham et al., 2004b), the findings from the current study demonstrate that the CNS exploits the biomechanical properties of the multi-jointed arm when performing drawing movements of various orientations, based on torque sign and impulse analysis.



**Figure 10. Diameter Ratio**

Mean (and standard error) diameter ratio constant error for each limb, in each left arm-right arm leading joint condition, SL-SL, EL-EL (similar, solid-filled) and SL-EL, EL-SL (different, pattern-filled). Separate plots are shown for the left limb (A) and the right limb (B).

The novel finding of the study was that categories of movements, defined by the pairing of leading joints, are constrained in different ways and associated with clear changes in endpoint control and stability of interlimb coordination patterns. More specifically, bimanual asymmetric coordination patterns produced with similar leading joints were more stable than asymmetric patterns produced with different leading joints. The findings expand on the growing body of literature which examines the influence of intralimb coordination dynamics on the stability of interlimb coordination (Buchanan & Ryu, 2005, 2006; Tseng & Scholz, 2005; Tseng et al., 2006).

#### *Identifying Leading Joints*

The LJH proposes that a leading joint is used to create the dynamic foundation of the entire movement; while the role of MT at the subordinate joint(s) is to regulate passive effects of the leading joint motion and thereby make adjustments to meet task demands (Dounskaia, 2005). Specifically, the leading joint develops the dynamic foundation by generating acceleration and deceleration at this joint and at the subordinate joint (via interactive torques). As a result of this control strategy, planning complexity is reduced due to a partial substitution of active control for passive effects.

Analysis of intersegmental dynamics was performed to determine the leading joints associated with each ellipse-tracing condition. Two categories of movements were identified; shoulder-leading and elbow-leading. By definition, motion at the leading joint was characterized by a significant contribution of MT to NT and was controlled in a manner that generated the dynamic foundation of the entire movement.



Motion at the subordinate joint differs from that of the leading joint in that both MT and IT contribute to NT and function to regulate the effect of the leading joint's motion. For example, during shoulder-leading movements, shoulder MT functioned to produce motion at this joint, whereas elbow MT and IT shared production of elbow motion. Similar movement categorizations have been previously reported for single-limb multijoint movements (Dounskaia et al., 2002a; Ketcham et al., 2004a).

For the current study, shoulder-leading control was observed when either the right limb traced an ellipse tilted left or when the left limb traced an ellipse tilted right. During shoulder-leading control, motion at the shoulder joint was predominately due to MT which resulted in imposed IT at the elbow joint. As a result, motion at the shoulder joint not only generated upper limb movement but also flexion and extension of the forearm (via elbow IT). Elbow-leading control occurred when either the right limb traced an ellipse tilted right or when the left limb traced an ellipse tilted left. During elbow leading control, motion at the elbow joint was predominately due to active control (MT) which in turn induced IT at the shoulder joint. As a result, elbow motion contributed to flexion and extension of the forearm and also flexion-extension motion of the upper limb (via shoulder IT).

The findings from the current study is the first to demonstrate that the shoulder and elbow can act as a leading joint within either arm, and be combined as leading joints across the arms to achieve an action goal. In addition, the findings also highlight the importance of identifying leading and subordinate joint control strategies of movements requiring the coordination of two limbs. For example, stability of

interlimb coordination patterns and endpoint variability was found to be influenced by whether the tracing actions were produced with similar or different leading joint combinations.

### *Endpoint Control and Stability of Interlimb Coordination*

Similar to previous reports (Carson et al., 1997; Tseng et al., 2006), the current study found that asymmetric coordination patterns were less stable when produced at the higher cycling frequency compared to asymmetric patterns produced at the slower frequency. At the higher cycling frequency, more transient behavior and increased variability in the relative phasing between limbs was observed.

Endpoint control was more accurate and the asymmetric coordination pattern was more stably produced when end-effector motion was driven by the same leading joints (SL-SL, EL-EL) compared to different leading joints (SL-EL, EL-SL). For example, movements produced with similar leading joints exhibited diameter ratio values closer to the target value compared with conditions produced with different leading joints. Furthermore, asymmetric coordination produced with similar leading joints exhibited fewer trials with transient behavior and less variability in the relative phase between limbs than asymmetric coordination produced with different leading joints. One possible explanation for different leading joint conditions exhibiting less stable coordination patterns is that different muscle groups are coordinated during the different leading joint conditions; whereas when both limbs are producing movements with similar leading joints, similar muscle groups are coordinated (Swinnen et al.,

1998). This is based on the notion of neural crosstalk in which studies have examined limitations in performance when the assigned task to each limb differs with respect to one or more parameters (i.e. timing, amplitude, force, direction) (Swinnen, 2002; Swinnen & Wenderoth, 2004). The neural crosstalk approach is related to pathways that give rise to neural interactions between command streams resulting in mutual patterns that interfere between limbs (Swinnen, 2002). These interactions are thought to occur at different levels of the CNS from cortex to spinal cord. With regard to bimanual coordination, the neural pathways are in reference to information transfer through the corpus callosum between the two hemispheres. Specifically, there are indirect and direct routes from the motor cortex to the spinal cord, namely the lateral and ventral corticospinal tracts. Take for example the ventral corticospinal tract, in this pathway axons run uncrossed through the brainstem and enter primarily in the medial aspect of the spinal cord with terminations ipsilaterally and contralaterally. These fibers control axial and proximal limb muscle groups. When considered in conjunction with distal control from the lateral corticospinal tract, each half of the brain has not only contralateral control of arm, hand, and finger movement, but also ipsilateral control of some aspects of arm movements (Swinnen, 2002).

A number of studies have examined differences in the stability of symmetric and asymmetric coordination patterns and demonstrated that asymmetric coordination is less stable overall, and particularly at higher frequencies (Carson et al., 1997; Semjen et al., 1995). Similarly, the current study also found that asymmetric coordination patterns produced at higher cycling frequencies were less stable; however,

we also found differences in stability among asymmetric patterns depending on the required combinations of leading joints. The findings not only provide support for recent reports (Tseng et al., 2006) demonstrating that intersegmental dynamics within a limb influence intralimb coordination; but they also show that particular joint coordination patterns will result in more stable interlimb coordination. The findings suggest a potential benefit for the CNS in selecting similar joint configurations and regulation of IT demands across limbs when performing bimanual coordination tasks. Furthermore, tasks requiring the CNS to coordinate limbs whose regulation of intersegmental dynamics are different from one another, and thus forcing the system to plan two different leading joint control strategies, can result in greater instability in overall interlimb coordination. The findings expand on our understanding of how the CNS can organize and assemble the many degrees of freedom contributing to a movement. This suggests that the ability of the CNS to select and coordinate leading joint combinations across limbs may provide greater flexibility and therefore, enhance the system's response to internal and external perturbations.

It should be noted that the current study found the non-dominant left-arm to have diameter ratio values which more closely matched the target diameter ratio relative to those of the dominant right-arm. While there are reports from previous work with bimanual circle drawing that did not find a similar effect of accuracy linked to the non-dominant left-arm (Ryu & Buchanan, 2004), there also exist reports from studies on discrete reaching that have demonstrated greater precision in endpoint control with the non-dominant left-arm (Gottlieb, 1996; Sainburg & Kalakanis, 2000).

There is evidence to suggest that attention could explain differences in diameter ratio values observed for different limbs. For example, Franz (2004) demonstrated that during bimanual circling when attention is directed to one of the limbs, movements of the attended limb exhibited larger excursion. Although attention was not manipulated in this experiment, the error values suggest that the right-handed participants may have directed more attention to their dominant arm, especially in the different leading joint conditions.

In summary, principles of the Leading Joint Hypothesis applied to a multijoint bimanual coordination task revealed insights into the influence of intralimb intersegmental dynamics on the coordination dynamics (i.e., stability, loss of stability, etc.) of interlimb coordination patterns. Collectively, the findings indicate that bimanual asymmetric coordination produced with similar leading joints is more stable than asymmetric coordination produced with different leading joints. There remain a number of unanswered questions pertaining to how leading and subordinate joints are tuned over time within a learning context. For example: Will practice of a novel bimanual pattern requiring the coordination of two limbs with different leading joints attain similar levels of stability compared to practicing the same novel bimanual pattern produced with similar leading joints? This is an important issue given the clear differences in pattern stability as a function of leading joint pairing as demonstrated in experiment 1. Or, how are the motions and torques of the individual joints within a limb tuned during the acquisition of a novel motor skill? The LJH has two predictions that relate to the acquisition of novel coordination patterns. The first prediction is that

biomechanical properties influence the acquisition of novel motor skills. For example, there might exist certain circumstances where differences in joint characteristics (i.e. joint amplitude, inertial resistance) lead to a biomechanical advantage which allows for a more rapid acquisition of a skill. The second prediction is that learning occurs in two stages: a) early in practice, motion of the leading joint is tuned first, and b) tuning of the subordinate joint occurs later in practice. One reason leading joint tuning would occur early in practice is because the mechanism of control at the leading joint is less complex than control mechanism of the subordinate joint. Additionally, acquiring leading joint control early on allows for generation of a close approximation of the required movement which later can be fine tuned with subordinate joint Experiment 2 aims to address the unanswered questions and learning predictions put forth by the LJM.

## CHAPTER III

### EXPERIMENT 2

#### Objective

The findings from experiment 1 led to the development of experiment 2. The previous experiment found stability of interlimb coordination patterns and endpoint variability to be influenced by whether the tracing actions were produced with similar or different leading joint combinations. Asymmetric coordination patterns produced with similar leading joints were more stably produced and characterized by more accurate endpoint control of individual limbs. Experiment 2 was designed to expand on the findings from experiment 1 by adding a learning component that would allow for the examination of learning predictions put forth by the LJH. The purpose of experiment 2 was to determine if the length of time of leading joint and subordinate joint tuning, when learning a novel coordination pattern, is different for movements produced with similar leading joints compared with movements produced with different leading joints.

It is predicted that early in practice the interlimb coordination of two groups learning with different leading joints (EL-SL RH lead and LH lead) will be less stable with decreased accuracy of endpoint control, than a group learning with similar leading joints (SL-SL). It is also predicted that, with practice, the performance of the groups learning the novel pattern with different leading joints will improve to reflect that of the group learning the pattern with similar leading joints; however the rate of learning

(tuning) will be slower. For example, the to-be-learned coordination pattern will be acquired by all three groups; however, the SL-SL group's performance will stabilize early in practice followed by stabilization of performance for both of the EL-SL groups. With regard to tuning of the individual joints, for the SL-SL group it is expected that early in practice the left shoulder and right shoulder joints (leading joints) would be tuned, followed by tuning of the left and right elbow joints (subordinate joints). In contrast, the EL-SL groups will tune the right shoulder and left elbow (leading joints) early in practice, followed by tuning of the right elbow and left shoulder (subordinate joints) later in practice.

## **Methodology**

### *Participants and Procedures*

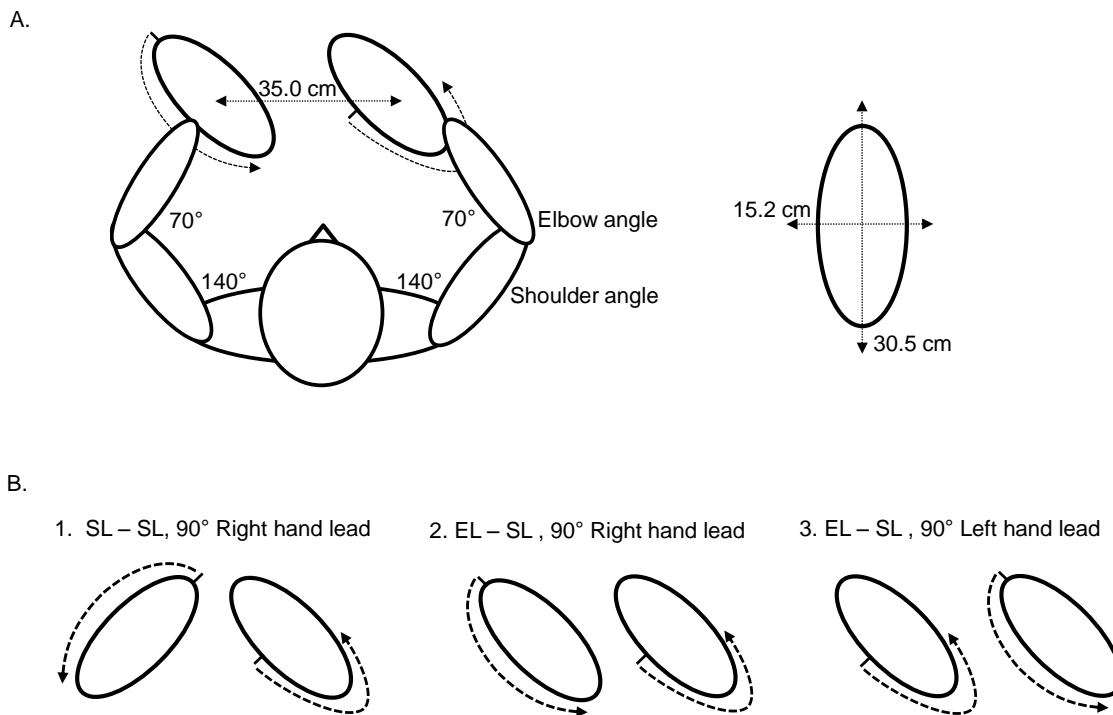
Thirty right-handed young adults ( $22.1 \pm 3.4$  yrs.) participated in this experiment. The Oldfield, (1971) handedness inventory questionnaire was used to screen participants for handedness (mean LQ = 89.8, SD = 9.01). Each participant received a brief explanation of the experimental procedures before reading and signing a consent form approved by the local Institutional Review Board at Texas A&M University.

Participants were seated at a table with the chair height adjusted such that when the arms rested on the table; both the upper and lower arms were parallel with the table surface. Subjects performed bimanual arm movements in the horizontal plane by repetitively tracing a pair of ellipse templates projected from below up to a Plexiglas<sup>®</sup>



surface (Figure 11A). Subjects were randomly assigned to one of three groups. One group traced a pair of ellipse templates that were oriented in such a way that required similar leading joints (SL-SL; Figure 11B1) while the other two groups traced a pair of ellipse templates that were oriented in such a way that required different leading joints (EL-SL; Figure 11B2 and 3). Ellipse template size was 30.5 cm (major axis) and 15.2 cm (minor axis). The distance between the centers of the ellipses remained fixed at 35.0 cm. Subjects traced each ellipse pair at a frequency of 1 Hz. Tracing frequency was controlled by an auditory metronome. Participants were required to trace the ellipses in an asymmetrical manner (i.e. both limbs moving counter-clockwise) and learn to produce a  $90^\circ$  relative phase offset between limbs (Groups 1 and 2: RH lead, Group 3: LH lead; Figure 11B).

Subjects performed six blocks of six trials for two days and then returned for a third day retention test of one block of six trials. Each trial lasted 16 seconds. Following each trial, subjects were given visual feedback of their interlimb endpoint relative phase performance. Angle-angle plots (or Lissajous plots) portraying the relative phasing between the limbs were displayed on a computer screen visible to the subject. Previous research has found Lissajous plots to be an effective means of portraying produced relative phase patterns in relation to the to-be-learned relative phase pattern (Buchanan, 2004; Fontaine et al., 1997; Lee et al., 1995).



**Figure 11. Experiment 2 Setup and Design**

A) Schematic representation of the experimental setup. Ellipse diameters remained constant throughout the experiment. B) Ellipse-tracing experimental groups: 1) SL-SL with a 90° RH lead, 2) EL-SL with a 90° RH lead, 3) EL-SL with a 90° LH lead.

In the current study, subjects were required to learn a  $90^\circ$  relative phase pattern. Prior to practice trials, subjects were informed that the to-be-learned  $90^\circ$  relative phase pattern was indicated by a perpendicular tick mark on each ellipse template. An asymmetric coordination pattern ( $180^\circ$ ) in which limbs synchronized at opposite points of max curvature on the ellipses would produce a slanted line with a negative slope in the Lissajous plot. However, the to-be-learned  $90^\circ$  relative phase offset would result in a circular shape in the Lissajous plot. Accordingly, following each trial a template of the to-be-learned  $90^\circ$  relative phase (represented as a circle) was plotted on the same graph with a Lissajous plot representing the relative phase relationship between the participant's hands. The Lissajous plot of the participants coordination was portrayed with the x-axis position of the left end-effector (index finger tip) plotted as a function of the x-axis position of the right end-effector.

#### *Data Recording and Analysis*

Data recording and analysis procedures were performed as described for experiment 1. See chapter II methods section for a detailed description of the computation of dependent variables. It should be noted that, unlike experiment 1, the current study calculates interlimb relative phase error of the  $90^\circ$  phase offset as an absolute error rather than a constant error. The dependent variables included in this experiment are: cycling frequency, diameter ratio, transient behavior, interlimb relative phase absolute error, interlimb relative phase uniformity, torque sign, torque

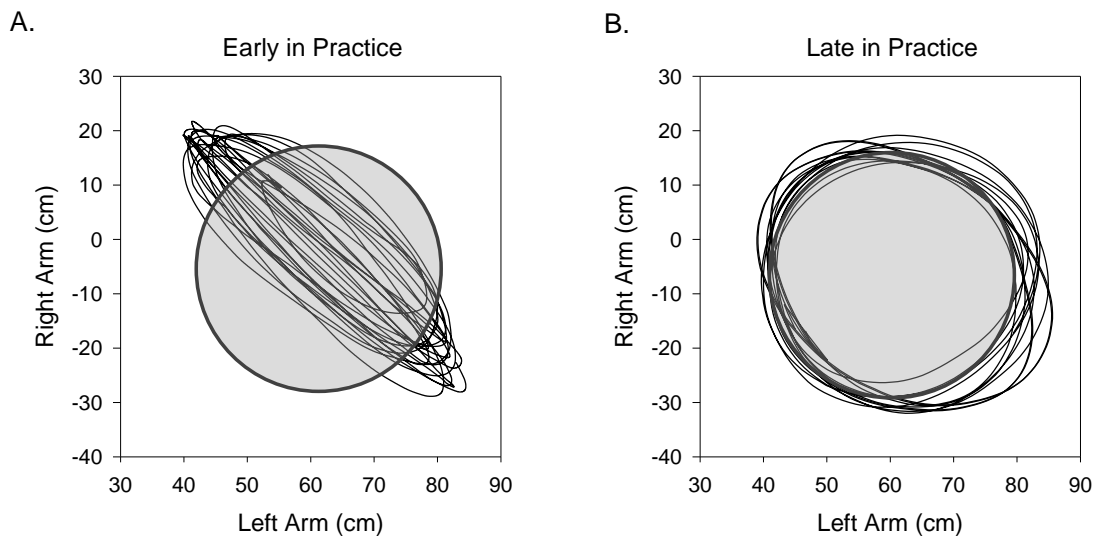
impulse, joint amplitude, joint amplitude angular deviation, and relative timing between MT and joint amplitude peaks.

### **Statistics**

Different ANOVA models were used to analyze the acquisition and retention data. Therefore, models are described individually for each variable in the following results section. Post-hoc analysis was performed to determine differences among significant Group and Practice Block main effects. All post-hoc comparisons were conducted using the Tukey's HSD test ( $\alpha = .05$ ). To determine differences between significant Day, Retention Block, Limb, and/or Joint main effects, t-tests were performed.

### **Results**

Figure 12 depicts sample representative data of the visual feedback of relative phase displacement plots early in practice and late in practice. The sample data demonstrates the general trend that early in practice, participants were drawn to producing an asymmetric coordination pattern (line with negative slope). The required 90° relative phase offset (circular shape) was not accurately produced until later in practice.



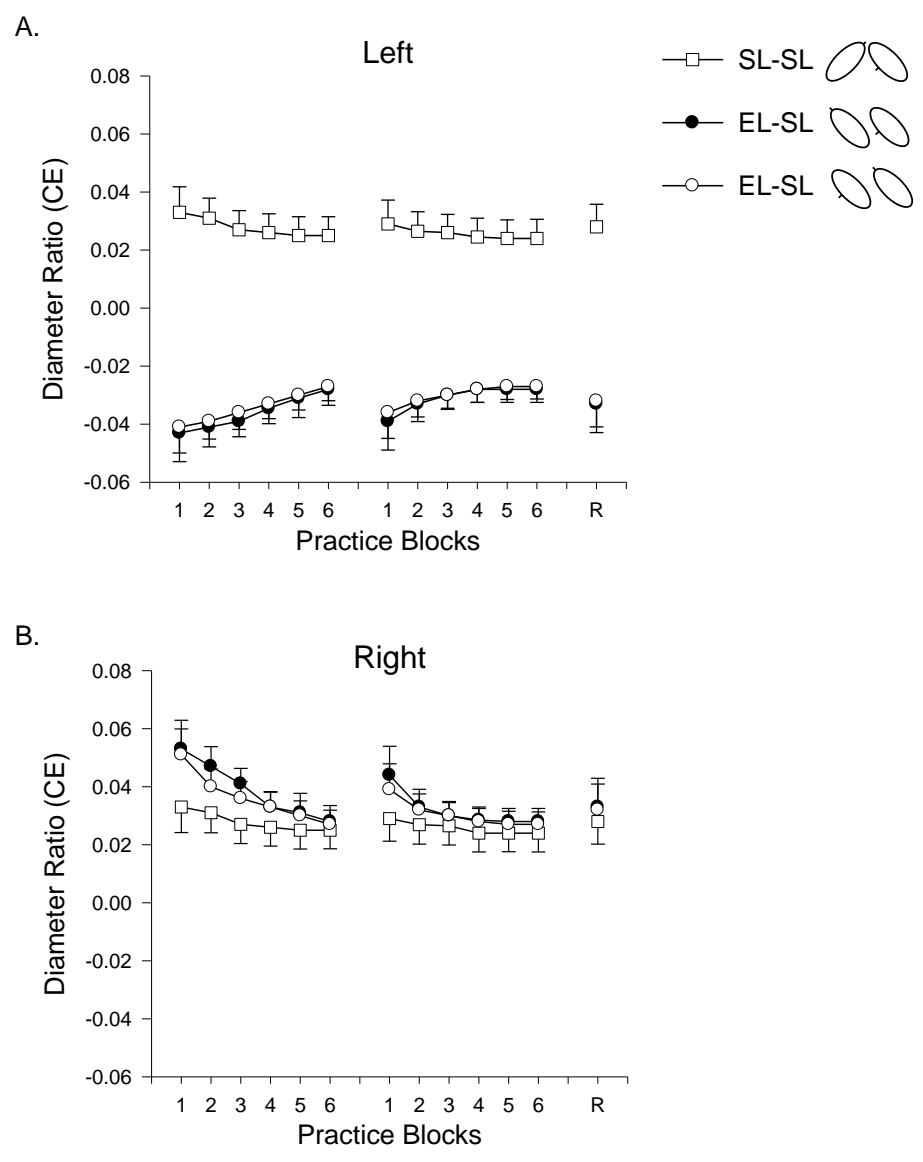
**Figure 12. Relative Phase Visual Feedback**

Representative interlimb endpoint Lissajous plots of right arm endpoint displacement (y-axis) as a function of left arm endpoint displacement (x-axis). Separate plots are shown for early in practice (A) and late in practice (B). The shaded circle represents the to-be-learned  $90^\circ$  relative phase pattern.

### *Diameter Ratio*

The diameter ratio acquisition data were analyzed using a four-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Day (day 1, day 2) x 6 Block (blocks 1-6) x 2 Limb (left, right)) ANOVA with repeated measures on Day, Block, and Limb. Analysis of the error in each arm's diameter ratio yielded a significant Group main effect ( $F_{2,27} = 13.71, p < .01$ ; Figure 13). Post-hoc analysis revealed that movements produced with similar leading joints (SL-SL, open square pattern) resulted in larger diameter ratio values compared with movements produced with different leading joints (open and filled circle patterns). The Limb x Group interaction was also significant ( $F_{2,27} = 21.36, p < .001$ ). Post-hoc tests indicated that when the elbow was the leading joint in the EL-SL conditions, CE was negative for the left-arm, whereas when the elbow was the subordinate joint in the SL-SL condition, CE was positive for the right-arm. All other acquisition main effects and interactions were not statistically significant ( $p > .05$ ).

The diameter ratio retention data were analyzed using a three-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Practice Block (last practice block, retention block) x 2 Limb (left, right)) ANOVA with repeated measures on Practice Block and Limb. Analysis of this data set found that the Practice Block main effect and relevant interactions were not statistically significant ( $p > .05$ ), indicating that the reduction in diameter ratio error obtained throughout the two days of practicing the 90° pattern was retained 24 hours later.



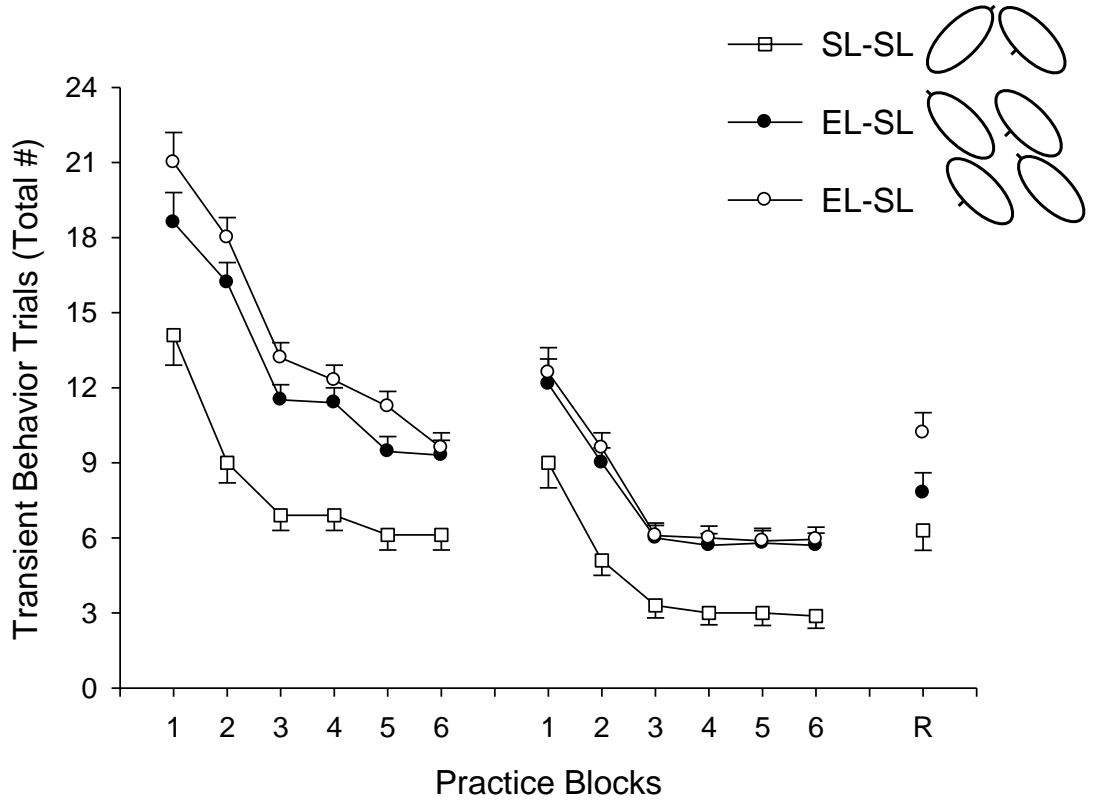
**Figure 13. Diameter Ratio Across Practice Blocks**

Mean (and standard error) diameter ratio constant error is plotted as a function of days and practice blocks for each group: SL-SL RH lead (open square), EL-SL RH lead (filled circle), and EL-SL LH lead (open circle). Separate plots are shown for the left limb (A) and the right limb (B).

*Interlimb Relative Phase: Transient Behavior*

The transient behavior data from the acquisition trials were analyzed using a three-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Day (day 1, day 2) x 6 Block (blocks 1-6)) ANOVA with repeated measures on Day and Block. Analysis of the number of transient behavior trials yielded three significant main effects: 1) Group ( $F_{2,27} = 21.9, p < .05$ ), 2) Day ( $F_{1,27} = 43.4, p < .05$ ), and 3) Block ( $F_{5,135} = 7.67, p < .05$ ). Figure 14 shows the total number of trials which exhibited transient behavior plotted as a function of days and practice blocks for each leading joint group. Post-hoc analysis of the Group main effect revealed that more transient behavior emerged in the groups that practiced the 90° relative phase pattern with different leading joint combinations ( $11.1 \pm 3.3$ ) compared to the group practicing with the same leading joint combination ( $6.10 \pm 2.3$ ) ( $p < .05$ ). On average, day one of practice was characterized by more transient behavior ( $12.0 \pm 3.6$ ) than day two ( $6.1 \pm 2.9$ ), with more transient behavior emerging early in practice (Block 1:  $14.7 \pm 3.8$ ) compared to later in practice (Blocks 5-6:  $6.7 \pm 2.3$ ). All other acquisition interactions were not statistically significant ( $p > .05$ ). By day two, the transient trials in blocks four, five, and six were confined to four out of thirty subjects.





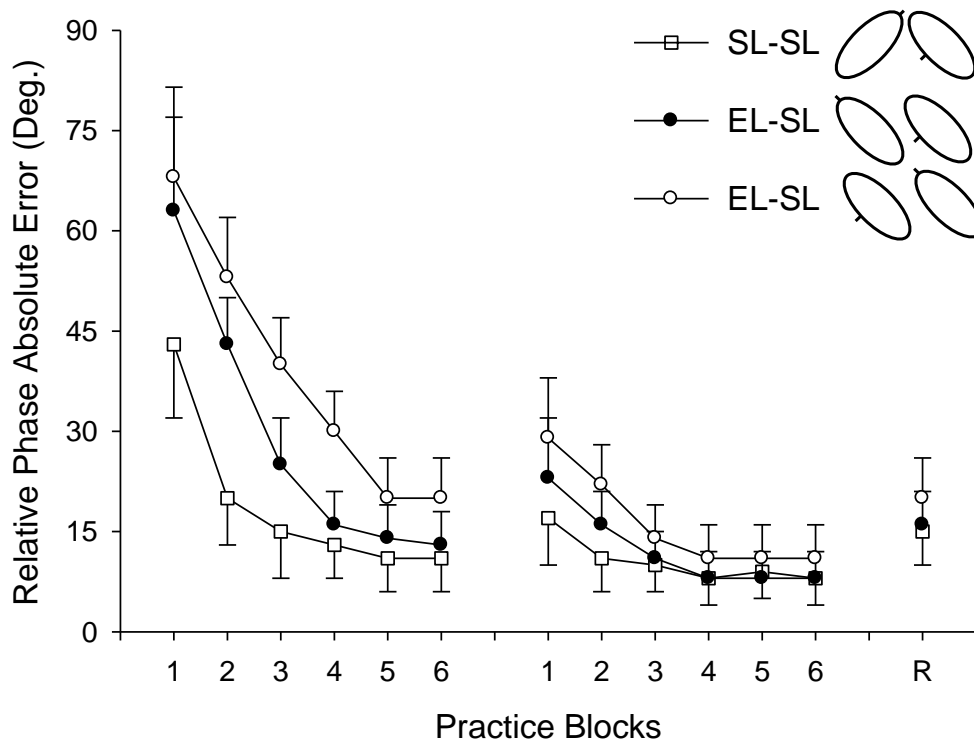
**Figure 14. Transient Behavior During Practice and Retention**

Total number of trials exhibiting transient behavior are plotted as a function of days and practice blocks for each group: SL-SL RH lead (open square), EL-SL RH lead (filled circle), and EL-SL LH lead (open circle).

The transient behavior data from the retention test were analyzed using a two-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Practice Block (last practice block, retention block)) ANOVA with repeated measures on Practice Block. Analysis of transient behavior in the retention data yielded a significant Practice Block main effect ( $F_{2,27} = 11.9, p < .05$ ). Fewer trials with transient behavior were observed for the last practice block compared to the retention block. Transient behavior in the retention blocks differed between groups, as evident by the significant Practice Block x Group interaction ( $F_{2,27} = 15.8, p < .05$ ). The SL-SL group and the EL-SL (LH lead) groups were both characterized with more trials with transient behavior during the retention block compared to the last block of practice. Retention trials with transient behavior were confined to seven out of thirty subjects. Transient behavior trials were not included in the remaining analysis.

#### *Interlimb Relative Phase: Performance Error*

Interlimb relative phase performance error from the acquisition trials were analyzed using a three-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Day (day 1, day 2) x 6 Block (blocks 1-6)) ANOVA with repeated measures on Day and Block. Analysis of interlimb relative phase error yielded significant main effects for Day ( $F_{1,27} = 4.82, p < .05$ ) and Block ( $F_{5,135} = 3.19, p < .05$ ). Plots of each group's relative phase data (absolute error) across practice blocks are portrayed in Figure 15.



**Figure 15. Interlimb Endpoint Relative Phase Absolute Error**

Mean (and standard error) interlimb endpoint relative phase absolute error data are plotted as function of days and practice blocks for each group: SL-SL RH lead (open square), EL-SL RH lead (filled circle), and EL-SL LH lead (open circle).

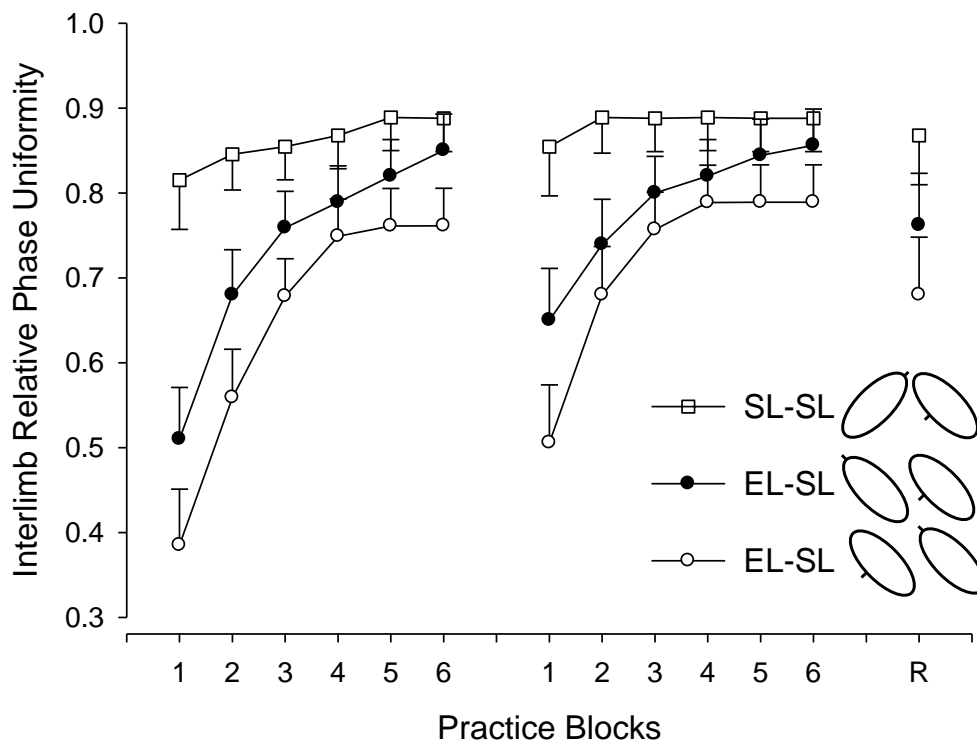
The first day of practice was characterized by larger error in interlimb relative phase ( $28.8 \pm 9.1^\circ$ ) compared to the second day ( $13.0 \pm 6.1^\circ$ ). Post-hoc analysis of the Block main effect indicated that error in interlimb relative phase was significantly larger for block one ( $40.5 \pm 18.4^\circ$ ) compared to blocks two through six ( $12.6 \pm 5.5^\circ$ ). The Day x Block interaction was also significant ( $F_{5,135} = 4.20, p < .05$ ). Follow up post-hoc analysis indicated that error in interlimb relative phase was significantly larger for block one of day one ( $58.1 \pm 12.2^\circ$ ) compared to block one on day two ( $29.9 \pm 5.4^\circ$ ). The Group main effect approached significance ( $F_{2,27} = 13.2, p = .06$ ). Overall, a trend for smaller relative phase error in the group practicing the  $90^\circ$  relative phase pattern with similar leading joints (SL-SL:  $14.6 \pm 9.6^\circ$ ; Figure 15, open square pattern) compared to groups practicing with different leading joints was present (EL-SL LH lead:  $28.4 \pm 16.1^\circ$ ; Figure 15, open circle pattern). The Day x Block x Group interaction was also significant ( $F_{10,135} = 13.2, p < .05$ ). Post-hoc analysis indicated smaller error values in interlimb relative phase for the SL-SL group in blocks one through four of day one compared to both EL-SL groups (RH lead blocks 1-3 and LH lead blocks 1-4). All other acquisition main effects and interactions were not statistically significant ( $p > .05$ ).

The interlimb endpoint relative phase error data from the retention trials were analyzed using a two-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Practice Block (last practice block, retention block)) ANOVA with repeated measures on Practice Block. Analysis of this data set indicated that there was no difference between the last block of practice and the retention block with regard to

absolute error in performance. The practice block main effect and interaction effect was not statistically significant ( $p > .05$ )

*Interlimb Relative Phase: Pattern Stability (Uniformity)*

Interlimb relative phase uniformity data from the acquisition trials analyzed using a three-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Day (day 1, day 2) x 6 Block (blocks 1-6)) ANOVA with repeated measures on Day and Block. Analysis of the uniformity data yielded a significant Group main effect ( $F_{2,27} = 7.97, p < .01$ ) and Block main effect ( $F_{5,135} = 7.97, p < .01$ ; Figure 16). Post-hoc analysis revealed lower uniformity values (indicating less stable coordination) for the groups practicing with different leading joints (EL-SL RH lead and EL-SL LH lead, circles) compared to the group practicing with the same leading joints (square) ( $p < .05$ ). Post-hoc analysis of the significant Block main effect demonstrated that early in practice (Block 1:  $.62 \pm .14$ ) uniformity values were lower than later in practice (Blocks 4-6:  $.82 \pm .04$ ), indicating more stable performance emerged as participants achieved the required  $90^\circ$  relative phase pattern with practice. The overall change in the stability of the produced bimanual coordination pattern appeared to be larger for both EL-SL groups, as evident by a significant Block x Group interaction ( $F_{10,135} = 7.97, p < .01$ ; Figure 16). Post-hoc analysis demonstrated lower uniformity values early in practice for both EL-SL groups (Blocks 1 and 2:  $.53 \pm .1$ ) compared to the SL-SL group (Blocks 1 and 2:  $.82 \pm .08$ ).



**Figure 16. Relative Phase Uniformity During Practice and Retention**

Mean (and standard error) interlimb endpoint relative phase uniformity (pattern stability) is plotted as function of days and practice blocks for each group: SL-SL RH lead (open square), EL-SL RH lead (filled circle), and EL-SL LH lead (open circle).

Thus, the performance of the groups practicing the task with different leading joints had a slightly longer time scale of performance stabilization in comparison to that of the group practicing with similar leading joints (SL-SL). All other acquisition main effects and interactions were not statistically significant ( $p > .05$ ).

Interlimb endpoint relative phase uniformity data from the retention trials were analyzed using a two-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Practice Block (last practice block, retention block)) ANOVA with repeated measures on Practice Block. This analysis did not reveal any difference in the level of uniformity between the last block of practice and the retention block. The practice block main effect and interaction effect were not statistically significant ( $p > .05$ ).

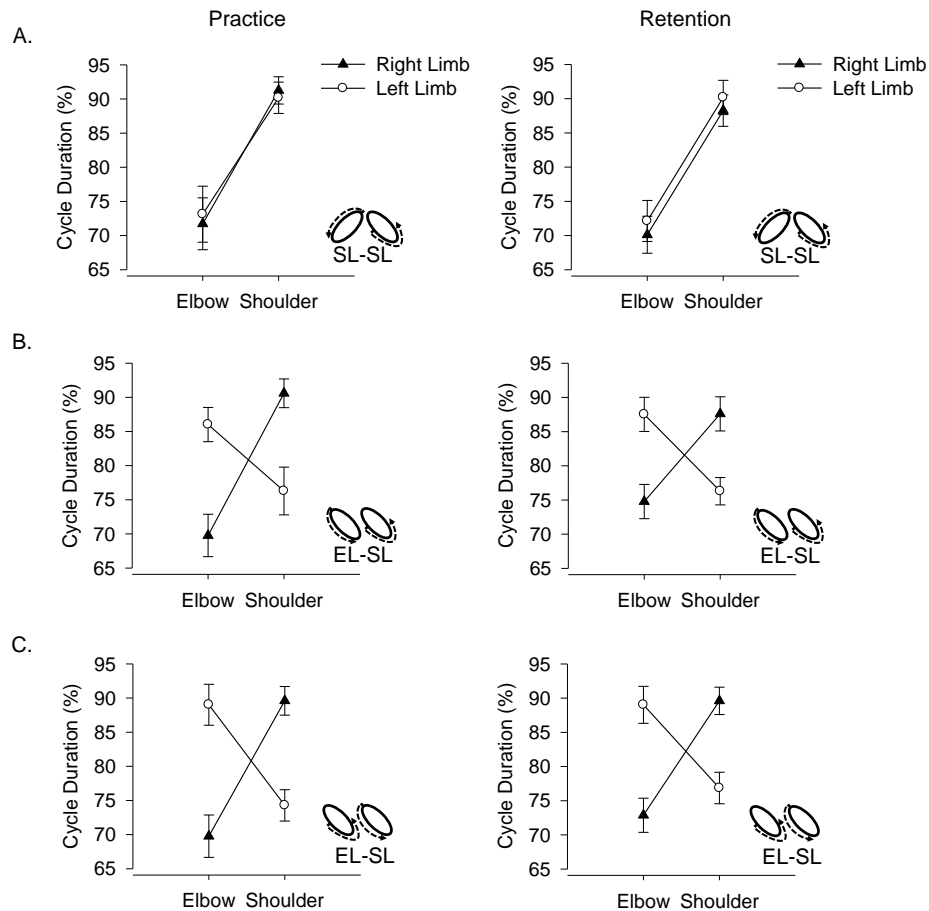
### *Torque Signs*

All three groups learned a novel interlimb relative phase coordination pattern over two days of practice. According to the LJH, the joint characterized by the largest torque sign is acting as the leading joint in a multijoint link. The torque sign data provide compelling evidence that both the elbow and shoulder can act as leading joints within the context of learning this novel interlimb coordination pattern. Torque sign data were analyzed using a five-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Day (day 1, day 2) x 6 Block (blocks 1-6) x 2 Limb (left, right) x 2 Joint (shoulder, elbow)) ANOVA with repeated measures on Day, Block, Limb, and Joint.

The analysis of the torque sign cycle duration data from the acquisition trials yielded a significant Joint main effect ( $F_{1,27} = 19.4, p < .01$ ). There was also a significant Joint x Limb x Group interaction ( $F_{2,27} = 47.6, p < .001$ ). Post-hoc analysis indicated that the portion of cycle duration when MT acted to accelerate the joint was significantly different for the shoulder and elbow for each group. Take for example, the SL-SL group torque sign values (Figure 17A) in which the left and right shoulders exhibited a greater contribution of MT to NT compared to the elbow. Figures 17B and C depict the group data which resulted in *different* leading joint pairings for the left and right limbs (EL-SL RH lead, EL-SL LH lead). In both conditions, the left limb had a greater contribution of elbow MT (than shoulder MT) to NT; while the right limb had a greater contribution of shoulder MT (than elbow MT) to NT. All other acquisition main effects and interactions typically associated with learning, e.g., changes across days and blocks, interactions were not statistically significant ( $p > .05$ ).

The torque impulse retention data were analyzed using a four-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Practice Block (last practice block, retention block) x 2 Limb (left, right) x 2 Joint (shoulder, elbow)) ANOVA with repeated measures on Practice Block, Limb, and Joint. The analysis of this data set did not reveal any differences when comparing the last practice block on day two with the retention block on day three ( $p > .05$ ) (Figure 17, right column). Thus, training on the novel 90° relative phase pattern did not lead to a change in the designation of a joint as leading or subordinate.





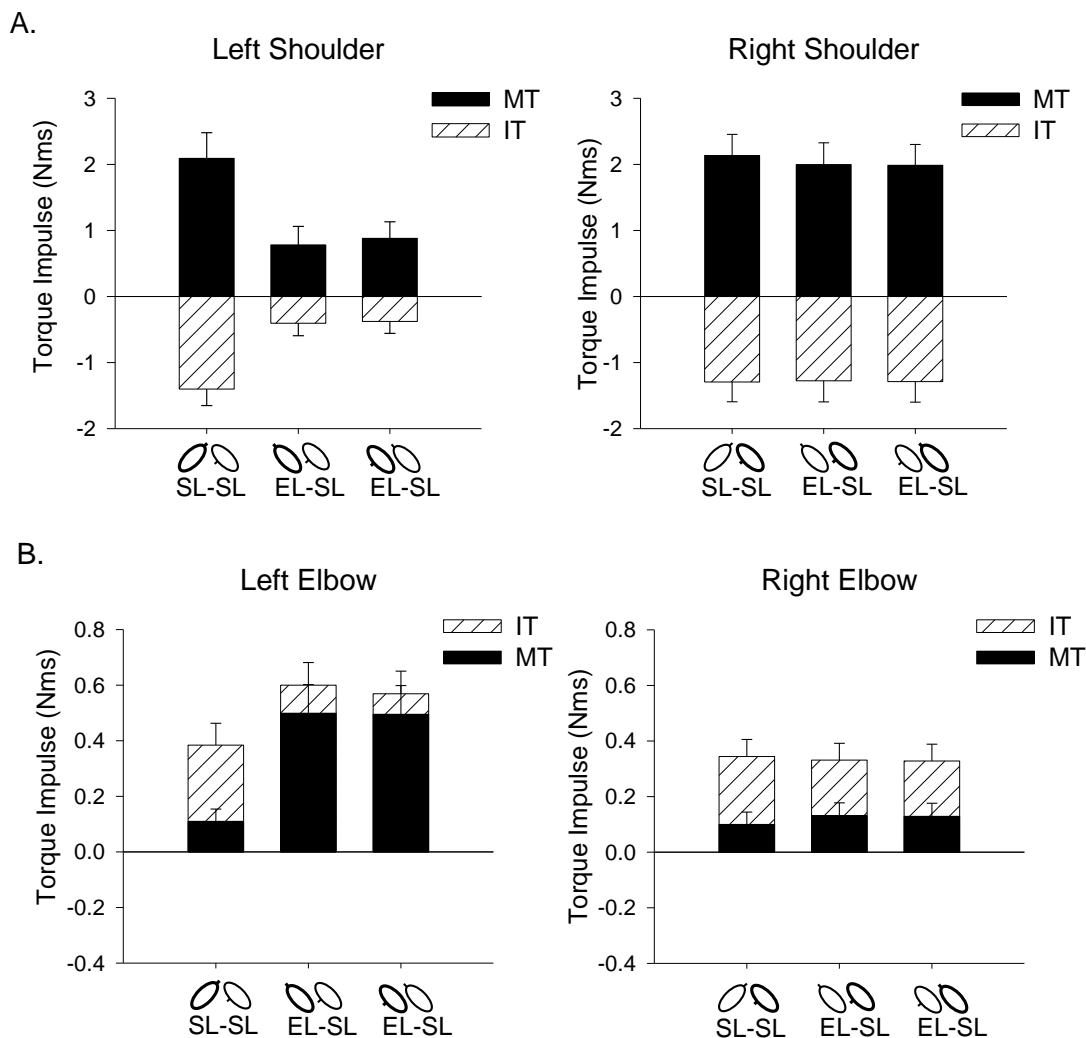
**Figure 17. Practice and Retention Torque Signs**

Mean percentages of cycle duration for the elbow and shoulder joint during which the sign of MT and the sign of NT coincided for the left limb (open circle) and right limb (solid-filled triangle). The left panel depicts data from practice trials and the right panel depicts retention data. A) Mean percentages (and standard error) of torque sign cycle duration for elbow MT and shoulder MT for the left arm-right arm leading joint condition (SL-SL RH lead). B, C) Mean percentages (and standard error) of torque sign cycle duration for elbow MT and shoulder MT for the different left arm-right arm leading joint conditions: EL-SL RH lead (B), EL-SL LH lead (C).

### *Torque Impulses*

Torque impulse at each joint was computed to determine the magnitude of the contribution of MT and IT to a joint's NT. Similar to experiment 1, the torque impulse values, particularly MT, varied in a manner consistent with the torque sign data that indicated different leading joint combinations as function of initial ellipse orientation. Muscle and interaction torque impulse data were analyzed using a five-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Day (day 1, day 2) x 6 Block (blocks 1-6) x 2 Limb (left, right) x 2 Joint (shoulder, elbow)) ANOVA with repeated measures on Day, Block, Limb, and Joint.

Analysis of the MT impulse data from the acquisition trials yielded a significant Joint main effect ( $F_{1,27} = 40.2, p < .001$ ). The Joint x Group interaction ( $F_{2,27} = 4.81, p < .05$ ) and Limb x Group interaction ( $F_{2,27} = 4.43, p < .05$ ) were also significant. The Joint x Limb x Group interaction ( $F_{2,27} = 29.8, p < .001$ ) was also significant. On average, both shoulder MTs and both elbow MTs positively contributed to NT. Post-hoc analysis indicated that the contribution of MT to NT was significantly different for the shoulder and elbow depending on the Group (Figure 18). Take for example shoulder MT (Figure 18A, solid-filled bars) of the left limb. Shoulder MT was larger (greater contribution to NT) for the group producing shoulder leading movements (**SL-SL**) compared to the two groups producing elbow leading movements with the left-arm (**EL-SL**).



**Figure 18. Torque Impulse During Practice and Retention**

A) Mean (and standard error) shoulder MT (solid-filled bars) and shoulder IT (pattern-filled bars) impulses for each limb as produced by each group. B) Mean (and standard error) elbow MT (solid-filled bars) and elbow IT (pattern-filled bars) impulses for each limb as produced by each group. A positive impulse demarks the torque component that predominantly had the same sign as NT; while a negative impulse indicates the torque component that had the opposite sign as NT.

In contrast, elbow MT was larger (greater contribution to NT, Figure 18B, solid-filled bars) for the groups producing elbow-leading movements (EL-SL) compared to the group producing a shoulder-leading movement with the left-arm (SL-SL). Thus, the findings are in support of experiment 1; indicating that when torque sign is used to identify the leading joint, MT contributes significantly more to NT in comparison to when that joint is acting in a subordinate joint role. All other acquisition main effects and interactions were not statistically significant ( $p > .05$ ).

The muscle torque impulse data from the retention trials were analyzed using a four-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Practice Block (last practice block, retention block) x 2 Limb (left, right) x 2 Joint (shoulder, elbow)) ANOVA with repeated measures on Practice Block, Limb, and Joint. This analysis did not find any differences in MT impulse when comparing the last practice block on day two with the retention block on day three. The practice block main effect and interactions were not statistically significant ( $p > .05$ ).

The analysis of the IT impulse data from the acquisition trials yielded a significant Joint main effect ( $F_{1,27} = 54.0, p < .001$ ). The Joint x Group interaction ( $F_{2,27} = 5.95, p < .05$ ) and Limb x Group interaction ( $F_{2,27} = 12.4, p < .01$ ) were also significant. As with the MT impulse data, the Joint x Limb x Group interaction was also significant ( $F_{2,27} = 18.9, p < .01$ ). Overall, right and left shoulder IT negatively contributed to NT; while right and left elbow IT positively contributed to NT. Post-hoc analysis however, indicated that the contribution of IT to NT was significantly different for the shoulder and elbow depending on the condition (Figure 18). In general,

magnitude of IT at the shoulder joint was matched in magnitude of MT. This indicates that elbow motion generated IT at the shoulder which was counterbalanced by shoulder MT, thereby reducing the influence of IT at the shoulder. This contribution was less at the left shoulder for the two groups producing elbow-leading motion at the left limb. One possible reason for this is because the positive and negative contributions canceled each other out (Dounskaia et al., 2002a). For the SL-SL group's left elbow joint exhibited smaller IT magnitude although its contribution to NT was greater, as evident by the relative decrease in MT to counterbalance (Figure 18B). All other acquisition main effects and interactions were not statistically significant ( $p > .05$ ). Similar to MT results, the analysis of the IT data from the retention trials did not find any significant main effects or interaction effects ( $p > .05$ ).

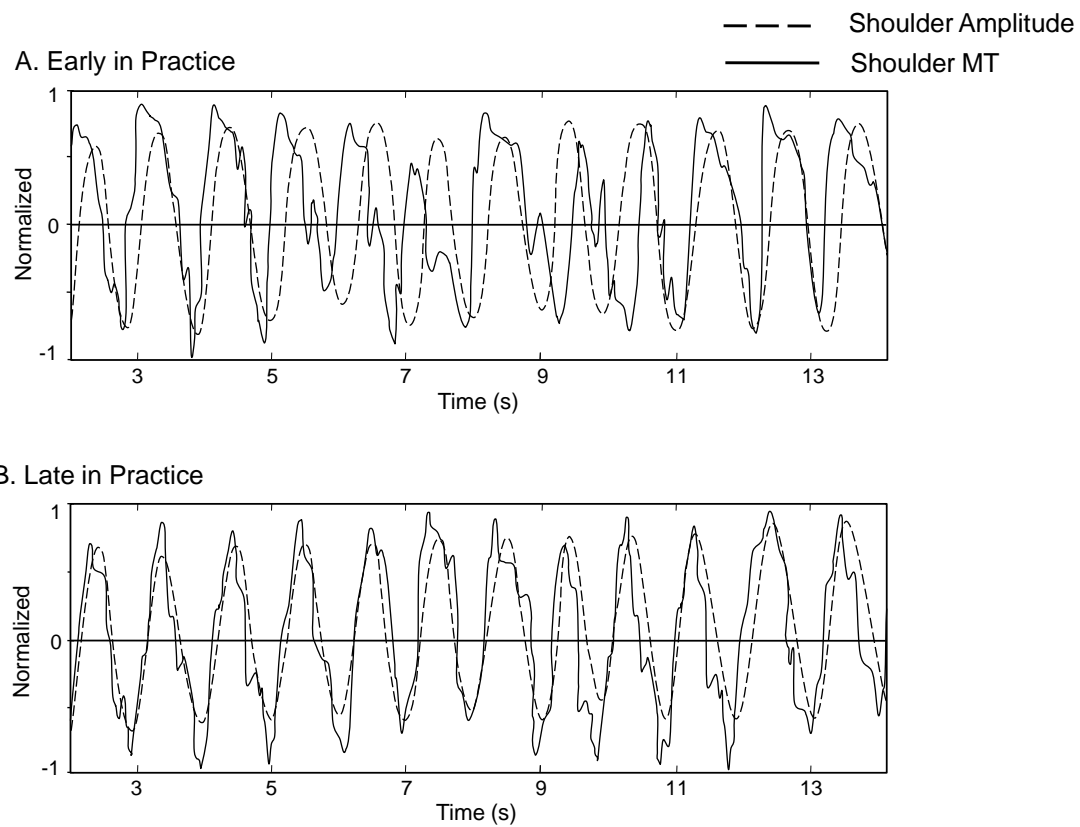
It should be noted that for both MT and IT impulse acquisition data sets, the Day and Block main effects and interactions were not statistically significant. The lack of Day and Block effects suggest that the magnitude of muscle and interaction torque did not change over two days of practice as the novel interlimb bimanual coordination pattern was learned. This is most likely due to the task-induced constraint of tracing a pair of fixed-amplitude templates with the limbs.

Similar to muscle torque, interaction torque impulse data from the retention trials were analyzed using a four-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Practice Block (last practice block, retention block) x 2 Limb (left, right) x 2 Joint (shoulder, elbow)) ANOVA with repeated measures on Practice Block, Limb, and Joint. This analysis did not find any differences in IT impulse when

comparing the last practice block on day two with the retention block on day three. The practice block main effect and interactions were not statistically significant ( $p > .05$ ).

#### *Relative Timing Between MT Peaks and Shoulder and Elbow Amplitude Peaks*

In order for the 90° pattern to be achieved, tuning of the individual joints had to occur; however, torque sign and impulse data did not find changes with practice. Therefore, as an additional attempt to identify contributing factors to learning the interlimb coordination pattern, the intralimb relative timing pattern between joint MT and joint amplitude peaks was examined. Computation of this measure is similar to the measure of relative timing of peak MT previously examined by Dounskaia and colleagues (2002a). The relative timing between MT peaks and joint amplitude peaks was computed by taking the absolute differences in timing of the positive MT peaks and coinciding joint amplitude peaks (Figure 19). Values were then normalized for cycle duration. Each joint's relative time between MT and joint amplitude peaks was analyzed separately. Separate plots for each joint are shown in Figure 20A and B.



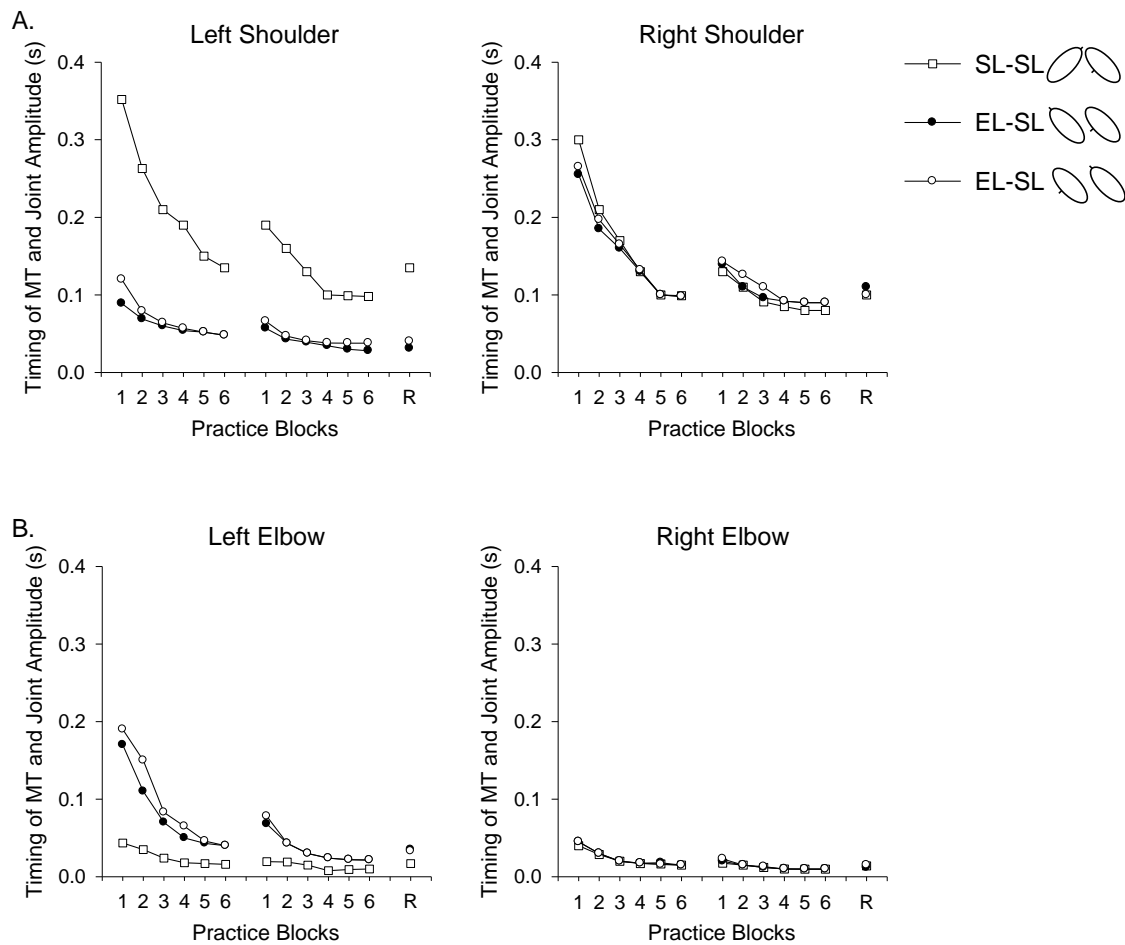
**Figure 19. Sample Data of Timing of MT and Joint Amplitude Peaks**

Sample data of relative timing between MT peaks (dashed grey line) and joint amplitude peaks (solid line) from early in practice (A) and from late in practice (B). The data depicted are from the left shoulder when producing a SL-SL (RH lead) coordination pattern.

The relative timing data between MT peaks and joint amplitude peaks were analyzed using a four-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Day (day 1, day 2) x 6 Block (blocks 1-6) x 2 Limb (left, right)) ANOVA with repeated measures on Day, Block, and Limb.

The analysis of the shoulder relative timing data from the acquisition trials yielded a significant Block main effect ( $F_{5,135} = 7.76, p < .05$ ). Five significant interactions were also found: (1) Limb x Group ( $F_{2,27} = 13.2, p < .05$ ), (2) Block x Group ( $F_{5,135} = 15.5, p < .01$ ), (3) Limb x Block x Group ( $F_{10,135} = 18.6, p < .01$ ), (4) Day x Block x Group ( $F_{10,135} = 9.31, p < .05$ ), and (5) Limb x Day x Block x Group ( $F_{10,135} = 8.83, p < .05$ ). Post-hoc analysis of the Block x Group interaction revealed that early in practice, the SL-SL group had significantly greater time lags between MT and joint amplitude peaks early in a practice session (Block 1: .24) compared to later in a practice session (Blocks 5-6: .10). Post-hoc analysis of the Limb x Block x Group interaction indicated that early in the practice sessions the left shoulder joint of the SL-SL group exhibited a greater time lag between MT and joint amplitude peaks (Blocks 1: .27) compared to both EL-SL groups (RH lead Blocks 1: .07; LH lead Blocks 1: .09). This effect was larger in the Day 1 session compared to the Day two session ( $p < .01$ ) as revealed by post-hoc tests of the Day x Block x Group interaction (Figure 20A). In addition, the relative time between shoulder MT and shoulder joint amplitude peaks differed across limbs early in practice for both of the EL-SL groups.





**Figure 20. Timing of MT Peaks and Joint Amplitude Peaks**

Mean relative timing between MT peaks and joint amplitude peaks are plotted as function of days and practice blocks for each limb; as produced by each group: SL-SL RH lead (open square), EL-SL RH lead (filled circle), and EL-SL LH lead (open circle). Separate plots are shown for the shoulder joint (A) and elbow joint (B).

Early in practice, the *right* shoulder was characterized by a greater time lag between shoulder MT and shoulder joint amplitude peaks (RH lead Day 1 Blocks 1: .09; LH lead Day 1 Blocks 1: .12) compared to the *left* shoulder (RH lead Day 1 Blocks 1: .25; LH lead Day 1 Blocks 1: .26) ( $p < .05$ ). All other acquisition main effects and interactions were not statistically significant ( $p > .05$ ).

The relative timing between shoulder MT peaks and shoulder joint amplitude peaks from the retention trials were analyzed using a three-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Practice Block (last practice block, retention block) x 2 Limb (left, right)) ANOVA with repeated measures on Practice Block, and Limb. For the shoulder data, the analysis did not reveal any significant differences between the retention data and the last practice block ( $p > .05$ ).

The analysis of elbow joint relative timing data from the acquisition trials yielded four significant interactions: (1) Limb x Group ( $F_{2,27} = 23.2, p < .01$ ), (2) Limb x Day x Group ( $F_{2,27} = 28.9, p < .01$ ), (3) Limb x Block x Group ( $F_{10,135} = 14.01, p < .05$ ), and (4) Limb x Block x Day x Group ( $F_{10,135} = 23.9, p < .01$ ). Post-hoc analysis indicated that the left elbow of both EL-SL groups had greater time between MT and joint amplitude peaks compared to the SL-SL group (Figure 20B). Post-hoc analysis also revealed that early in practice in block one of day one, the left elbow of both EL-SL groups demonstrated greater time between MT and joint amplitude peaks (RH lead: .17; LH lead: .19) than the SL-SL group (.04) ( $p < .05$ ) (Figure 20B). The same effect was not found for the right limb. All other acquisition main effects and interactions were not found to be statistically significant ( $p > .05$ ).

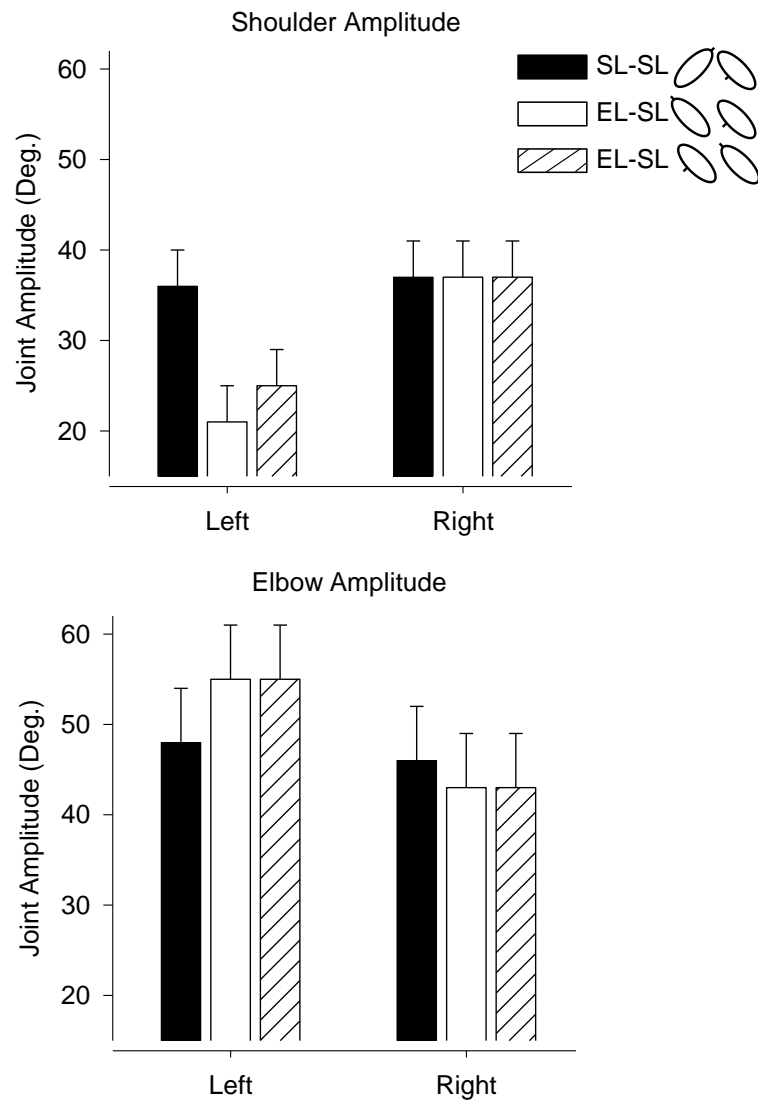
The relative timing between elbow MT peaks and elbow joint amplitude peaks from the retention trials were analyzed using a three-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Practice Block (last practice block, retention block) x 2 Limb (left, right)) ANOVA with repeated measures on Practice Block, and Limb. Similar to the shoulder joint analysis, the elbow joint data also did not reveal any significant differences between retention data and the data from the last practice block ( $p > .05$ ).

To test the for different rates of tuning in the leading joint as a function of leading joint pairs, the data from the first three blocks of practice were fit with a line to assess the rate of change in the relative timing between MT peaks and joint amplitude peaks. For the left shoulder joint, differences in slope indicated a larger value (indicating a greater rate of change) for the SL-SL group (RH lead slope:  $-.08$ ) compared to the slope of both EL-SL groups (LH lead slope:  $-.01$  ; RH lead slope:  $-.02$ ) (Figure 20A, left column). Similarly, the left elbow joint exhibited larger slope values for both of the EL-SL groups (LH lead slope:  $-.050$ ; RH lead slope:  $-.053$ ) compared to the slope of the SL-SL group (RH lead slope:  $-.009$ ) (Figure 20B, left column).

#### *Shoulder and Elbow Joint Amplitudes*

The shoulder joint amplitude data from the acquisition trials were analyzed using a four-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Day (day 1, day 2) x 6 Block (blocks 1-6) x 2 Limb (left, right)) ANOVA with repeated

measures on Day, Block, and Limb. Figure 21A displays mean amplitudes for the shoulder joint. The analysis of the shoulder joint amplitude acquisition data yielded a significant Limb main effect ( $F_{1,27} = 9.47, p < .05$ ). Overall, the left shoulder joint exhibited smaller amplitude ( $26.1^\circ$ ) than the right shoulder joint ( $37.0^\circ$ ). The Limb x Group interaction was also significant ( $F_{2,27} = 19.8, p < .01$ ). Post-hoc analysis of the significant Limb x Group interaction revealed significantly smaller left shoulder amplitudes for the two EL-SL groups compared to the SL-SL group (Figure 21A, compare left limb shoulder black-filled bar with open- and solid-filled bars). Thus, the two groups producing elbow leading movements with the left limb exhibited smaller shoulder amplitudes than the group producing a shoulder leading movement with the same limb. Analysis of the shoulder joint amplitude acquisition data did not yield any significant Day or Block main effects or interactions ( $p > .05$ ). The analysis of shoulder joint amplitude retention data were analyzed using a three-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Practice Block (last practice block, retention block) x 2 Limb (left, right)) ANOVA with repeated measures on Practice Block, and Limb. The shoulder joint amplitude retention analysis did not yield any differences when comparing the last practice block on day two with the retention block on day three ( $p > .05$ ).



**Figure 21. Joint Amplitude**

Mean (and standard error) shoulder joint amplitude (A) and elbow joint amplitude (B) plotted as a function of limb as produced by each group: SL-SL RH lead (solid-filled bars), EL-SL RH lead (open-filled bars), and EL-SL LH lead (pattern-filled bars).

The elbow joint amplitude data from the acquisition trials were analyzed using a four-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Day (day 1, day 2) x 6 Block (blocks 1-6) x 2 Limb (left, right)) ANOVA with repeated measures on Day, Block, and Limb. Figure 21B displays mean amplitudes for the elbow joint. The analysis of the elbow joint amplitude acquisition data yielded a Limb x Group interaction trend ( $F_{2,27} = 5.9, p < .06$ ). Post-hoc analysis of the significant Limb x Group revealed that significantly larger left elbow amplitudes for the two EL-SL groups compared to the SL-SL group (Figure 21B, compare left limb shoulder black-filled bar with open- and solid-filled bars). Thus, the two groups producing elbow leading movements with the left limb exhibited larger shoulder amplitudes than the group producing a shoulder leading movement with the same limb. The analysis of the elbow joint amplitude acquisition data did not yield any significant Day or Block main effects or interactions ( $p > .05$ ).

The analysis of elbow joint amplitude retention data were analyzed using a three-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Practice Block (last practice block, retention block) x 2 Limb (left, right)) ANOVA with repeated measures on Practice Block, and Limb. Similar to the shoulder joint amplitude retention analysis, the elbow data did not yield any differences when comparing the last practice block on day two with the retention block on day three ( $p > .05$ ).

Taken together, the acquisition and retention analyses suggest that joint amplitudes (shoulder and elbow) did not vary as a function of practice with the novel

bimanual coordination pattern. These result, however, are not surprising when the biomechanics of the task are considered. As with the torque sign and torque impulse results, the constraint of the ellipse template size and orientation had to result in smaller shoulder amplitudes and larger elbow amplitudes in the left arm for the different leading joint groups. Thus, the lack of day and block differences is not unexpected.

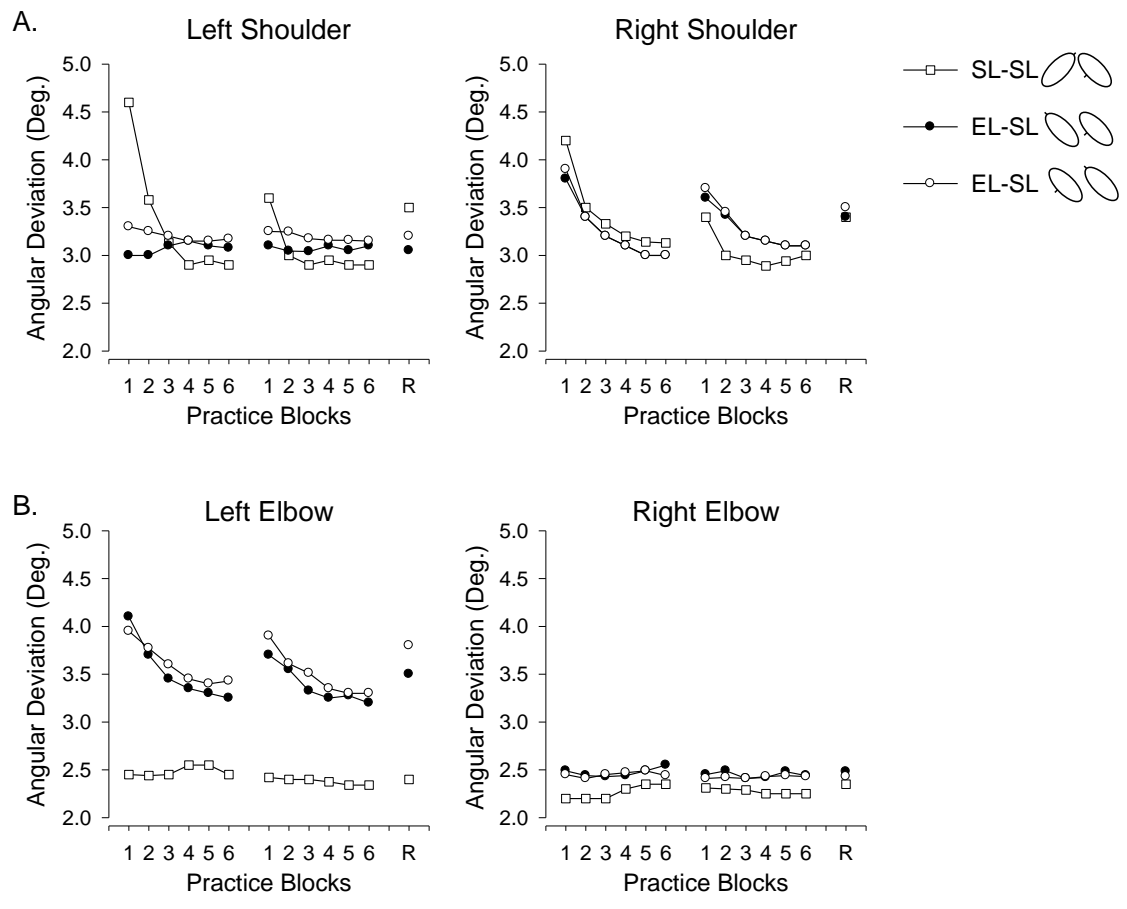
#### *Variability in Joint Amplitudes*

The shoulder and elbow joint amplitude variability data from the acquisition trials were analyzed using a four-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Day (day 1, day 2) x 6 Block (blocks 1-6) x 2 Limb (left, right)) ANOVA with repeated measures on Day, Block, and Limb. The analysis of the variability in shoulder joint amplitude during acquisition yielded a significant Block main effect ( $F_{5,135} = 7.06, p < .05$ ) and four interactions: 1) Block x Group ( $F_{10,135} = 13.4, p < .05$ ), 2) Limb x Block x Group ( $F_{10,135} = 26.1, p < .01$ ), 3) Limb x Day x Block ( $F_{5,135} = 6.24, p < .05$ ), and 4) Limb x Day x Block x Group ( $F_{10,135} = 38.5, p < .001$ ). Post-hoc analysis of the Block x Group interaction revealed that early in the practice sessions, the SL-SL group were characterized by significantly larger variability in angular amplitude (Block 1:  $3.95^\circ$ ) compared to later in the practice sessions (Blocks 4-6:  $2.94^\circ$ ) ( $p < .05$ ). Furthermore, post-hoc analysis of the Limb x Block x Group indicated that early in the practice session the *left* shoulder joint of the SL-SL group exhibited greater variability (Block 1:  $4.10^\circ$ ) compared to both EL-SL

groups (RH lead: 3.05°; LH lead: 3.27°). This effect was larger in the Day one session compared to the Day two session ( $p < .01$ ) (Figure 22A, left limb, Block 1) ( $p < .01$ ) as revealed by post-hoc tests of the Day x Block x Group interaction. Post-hoc analysis also indicated that shoulder angular deviation of the EL-SL groups was different across limbs, early in practice. For example, joint amplitude angular deviation was greater for the left shoulder (Block 1: EL-SL RH lead: 3.05°; EL-SL LH lead: 3.21°) than for the right shoulder (Block 1: EL-SL RH lead: 3.70°; EL-SL LH lead: 3.82°). All other acquisition main effects and interactions were not statistically significant ( $p > .05$ ).

The analysis of elbow joint angular variability from the acquisition trials yielded two significant main effects for Group ( $F_{2,27} = 15.6, p < .05$ ) and Limb ( $F_{1,27} = 10.9, p < .05$ ). Two significant interactions were also found, Limb x Group ( $F_{2,27} = 23.3, p < .01$ ), and Limb x Block x Group ( $F_{10,135} = 12.5, p < .05$ ). Post-hoc analysis of the Limb x Group interaction revealed that for the left limb the SL-SL group demonstrated smaller angular deviation values (2.43°) than either EL-SL groups (RH lead: 3.45°; LH lead: 3.54°) (Figure 22B). Additionally, post-hoc analysis of the Limb x Block x Group interaction indicated that early in practice on block one, angular deviation of the left elbow differed depending on Group, with smaller angular deviation values for the SL-SL group than either of the EL-SL groups ( $p < .05$ ) (Figure 22B, compare square and circle patterns at block one). All other acquisition main effects and interactions were not statistically significant ( $p > .05$ ).





**Figure 22. Joint Amplitude Angular Deviation**

Mean joint amplitude angular deviation is plotted as function of days and practice blocks for each limb; as produced by each group: SL-SL RH lead (open square), EL-SL RH lead (filled circle), and EL-SL LH lead (open circle). Separate plots are shown for the shoulder joint (A) and elbow joint (B).

Shoulder and elbow joint amplitude angular deviation retention data were analyzed using a three-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Practice Block (last practice block, retention block) x 2 Limb (left, right)) ANOVA with repeated measures on Practice Block and Limb. The analysis of the joint amplitude angular variability data (both shoulder and elbow) found no significant differences in variability between the retention data and last acquisition block ( $p > .05$ ).

To test the of different rates of tuning in the leading joint as a function of leading joint pairs, data from the first three blocks of practice were fit with a line to assess the rate of change in the variability of shoulder and elbow joint amplitudes. For the left shoulder, differences in slope indicated a larger value (greater rate of change) for the SL-SL group (RH lead slope:  $-.735$ ) compared to the slope of both EL-SL groups (LH lead slope:  $.05$ ; RH lead slope:  $-.04$ ). Similarly, the left elbow exhibited larger slope values for both of the EL-SL groups (LH lead slope:  $-.325$ ; RH lead slope:  $-.175$ ) compared to the slope of the SL-SL group (RH lead slope:  $-.004$ ).

### *Cycling Frequency*

The cycling frequency data from the acquisition trials were analyzed using a four-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Day (day 1, day 2) x 6 Block (blocks 1-6) x 2 Limb (left, right)) ANOVA with repeated measures on Day, Block, and Limb. This analysis yielded no significant differences for Group, Day, Block, or Limb or any significant interactions between these variables ( $p > .05$ ).

Across practice blocks, group performance did not differ from one another (SL-SL RH lead:  $1.04 \pm .04$  Hz, EL-SL RH lead:  $1.08 \pm .06$  Hz, EL-SL LH lead:  $1.07 \pm .06$  Hz).

The cycling frequency data from the retention trials were analyzed using a three-way (3 Group (SL-SL RH lead, EL-SL RH lead, EL-SL LH lead) x 2 Practice Block (last practice block, retention block) x 2 Limb (left, right)) ANOVA with repeated measures on Practice Block and Limb. This analysis found no change in cycling frequency between the last practice block and the retention block, regardless of limb. The practice block main effect and interactions were not statistically significant ( $p > .05$ ).

### **Summary of Findings and Discussion**

The findings from the current study reinforce the findings from experiment 1, indicating that both the elbow and shoulder can be identified as leading joints depending on initial task conditions. Experiment 2 not only expands classification of leading joints based on principles of the LJH to include a bimanual coordination task, it also demonstrates to some extent how leading joints are tuned with practice of a novel coordination pattern. In doing so, the findings from experiment 2 lend support to the predictions of learning put forth by the LJH. The first prediction is that the acquisition of a novel interlimb joint coordination pattern is influenced by the control of intralimb biomechanical properties. This prediction was tested by having subjects learn novel interlimb coordination patterns requiring different left arm-right arm leading joint combinations. One group of subjects learned an interlimb  $90^\circ$  relative

phase pattern with a right-arm lead that required similar leading joints across limbs (SL-SL). Two other groups learned the same  $90^\circ$  relative phase pattern but with different leading joints (EL-SL), with one group learning the interlimb  $90^\circ$  relative phase with a left-arm lead and the other with a right-arm lead. Support for this prediction came in the form of differences in acquisition of the novel bimanual coordination pattern and endpoint control modulations among groups tracing ellipse templates with different initial leading joint pairs. The second prediction is that the process of acquiring a novel motor skill occurs in a two-step manner. Partial support for this prediction was evident in different rates of change in joint amplitude angular deviation data and the relative timing between MT and joint amplitude of the leading joint earlier in practice. The rate of tuning was also found to be different among leading and subordinate joints. On average, the leading joint experience a greater rate of change within the first three blocks of practice compared to subordinate joint.

### *Identifying Leading Joints*

Similar to experiment 1, analysis of intersegmental dynamics was performed to identify leading joints. As predicted, the SL-SL (RH lead) group exhibited similar control strategies for both limbs. Both left and right shoulders exhibited greater contribution of MT to NT compared to the elbow. In contrast, for the EL-SL groups (RH lead and LH lead) the left elbow was characterized by greater contribution of MT to NT than the shoulder; while the right shoulder was characterized by greater contribution of MT to NT. The two EL-SL groups, which were only different in the

lead limb with regard to the  $90^\circ$  phase, did not differ from one another. This indicates that the limb leading practice strategy did not play a major role in influencing the identification of leading joints. In summary, the current study found joint torque impulse and torque sign differences between groups as were observed for experiment 1 among left-arm and right-arm leading joint conditions.

#### *Performance Changes in Interlimb Relative Phase with Practice*

Following two days of practice, the initial stability difference in interlimb coordination between the similar leading joint group and both of the different leading joint groups diminished and performance equalized among groups. This finding adds support for the hypothesis that performance would be influenced by the biomechanical properties of the limb, since different initial task conditions required different regulations of interactive torques. Throughout practice, the number of trials exhibiting transient behavior decreased, indicating greater stability. With respect to interlimb endpoint relative phase, error was reduced with practice resulting in acquisition of the required  $90^\circ$  relative phase pattern for all groups. Retention of interlimb relative phase was particularly good for each group. While there were differences in interlimb relative phase error between groups early in practice; throughout practice, error was reduced in such a way that the two groups practicing with different leading joints achieved equivalent performance to that of the group practicing with similar leading joints. Similar to previous reports (Lee et al., 1995; Zanone & Kelso, 1992), the current study found decreases in the variability of interlimb coordination patterns with

practice. Such a decrease is taken to represent that coordination has become more stable with practice, but does not necessarily imply that the goal has been achieved. However, the magnitude of interlimb relative phase error was reduced with practice, indicating an improvement in performance with regard to the goal.

The diameter ratio results demonstrated improvements in accuracy in the control of end-effector motion. This occurred despite an initial performance advantage for the similar leading joint group over both of the different leading joint groups. As with the relative phase measures, the two groups producing movements with different leading joints throughout practice did not differ from one another; both decreased in a systematic fashion (at similar rates) until eventually matching performance to that of the similar leading joint group.

#### *Changes in Biomechanics with Practice*

Of particular interest were the findings that neither torque sign nor torque impulse changed with practice. Thus, despite improvements in endpoint control and pattern stability, intersegmental dynamic variables linked to the identification of leading and subordinate joints did not appear to be causing this change. However, the lack of practice effect in these variables is not necessarily surprising, given that initial task constraints and thus joint configurations remained constant throughout practice. Support for the findings of a lack of change in torque magnitude has also been reported (Adamovich, Berkinblit, Fookson, & Poizner, 1999). Adamovich and colleagues (1999) examined pointing movements to kinesthetically defined remembered targets

and analyzed pointing errors, movement kinematics, and joint-angle coordination variables. The results indicated that acquisition of coordinated endpoint position was not related to muscle torque, but was instead related to muscle torque variability during the initial stage of learning. Moreover, the LJI predicts that *tuning* would occur at different rates for the leading and subordinate joint; these measures are also potentially not sensitive enough to reflect tuning.

Since intersegmental dynamics analysis indicated that torque sign and torque impulse did not change with practice, other characteristics of intralimb control were examined in attempts to determine factors contributing to the changes in performance associated with learning. Examination of timing of MT peaks in relation to shoulder and elbow joint amplitude peaks was found to be more fruitful in explaining performance differences. Across practice blocks, relative timing of peak MT in relation to peak joint amplitude decreased, particularly for the leading joint. Interestingly, it appears as though this measure may provide the most direct support to date for the second prediction of the LJI, with regard to differences in the rate of change of the tuning curve for leading and subordinate joints. The results showed that early in practice tuning of the relative timing between MT peaks and amplitude peaks of the leading joint was greater than that of the subordinate joint.

Similar to the initial torque analysis, joint amplitude did not change with practice, indicating that learning did not occur at this level. Examination of joint kinematic variability was also found to be fruitful in explaining performance differences. Further support for the tuning prediction came from examining the

variability of shoulder and elbow amplitude. A trend similar to that found in the relative timing between MT and joint amplitudes indicated a greater initial decrease (tuning) in the variability of joint amplitude of the leading joint. Thus, as the timing pattern between MT peaks and joint amplitude peaks changed with learning, variability in the joint amplitudes produced by MT also decreased. The observed decrease in leading joint amplitude angular deviation with practice indicates stabilization in the production of joint angular motion to achieve the task of tracing the fixed diameter of the ellipse templates. This also indicates that intralimb variables were tuned in such a way as to stabilize individual limb motion within the context of improving overall interlimb coordination pattern stability.

Overall, it was demonstrated that differences in leading joint pairs influenced the acquisition of a novel multijoint coordination pattern. One explanation as to why the leading joint combination influenced learning could be that biomechanical differences linked to limb control are based on which joint is functioning as the leading joint. While the findings demonstrate the importance of considering the influence of intralimb coordination constraints, they also indicate that biomechanical constraints can be overcome, thus diminishing the initial advantage of the movements produced with similar leading joints. Furthermore, it was shown that despite improvements of interlimb coordination pattern stability and endpoint control, joint amplitude and torque sign and impulse were not changed. Rather, timing control appeared to be playing a larger role in the modulation of intralimb control when learning a novel interlimb timing or relative phase pattern.



*Biomechanical Properties Influence Learning*

Taken together, the current set of findings demonstrate that the group producing movements with similar leading joints not only had an initial advantage but also achieved stable performance earlier in learning than the group producing movements with different leading joints, regardless of the phase offset requirements (RH vs. LH lead). Thus, intralimb biomechanical properties (in this case, imposed by initial task constraints) influence interlimb learning. One possible explanation for the SL-SL group stabilizing performance quicker may be found in part in the second prediction of the LJH that states the leading joint is tuned first, followed by tuning of the subordinate joint later in practice. Based on this idea it could be predicted that learning would emerge more easily for the similar leading joint group. This is expected because tuning of the same joint in both arms is occurring at the same point in time for this group; whereas the other groups are not only coordinating different leading joints, but also different leading joints are being tuned at any given point in time.

## CHAPTER IV

### OVERALL CONCLUSION

The aim of this dissertation was to expand our understanding of the influence of intralimb segmental or joint dynamics on the production of bimanual coordination patterns and endpoint accuracy. The Leading Joint Hypothesis, a strategy for control of multijoint movements which takes into account intralimb segmental dynamics provided a theoretical framework for this work. This work is the first of its kind to apply principles of the LJH to a bimanual coordination task and the learning of a novel bimanual coordination pattern.

One of the benefits of the LJH is that it is capable of categorizing movement types based on leading joint control strategies associated with initial task constraints. Experiment 1 applied the principles of the leading joint categorization of movements to individual limb control embedded within a bimanual task. Interestingly, it was shown that bimanual asymmetric coordination patterns produced with similar leading joints not only exhibited greater interlimb stability but also demonstrated greater endpoint accuracy of the individual limbs, than asymmetric patterns produced with different leading joints. The finding that pairings of leading joint combinations are constrained in different ways and associated with differences in interlimb stability and endpoint control, emphasizes the importance of considering the influence of within-limb segmental joint dynamics' on the ability to produce stable bimanual coordination patterns. In terms of bimanual coordination, the findings add support to the growing

body of literature (Buchanan & Ryu, 2005; Tseng & Scholz, 2005; Tseng et al., 2006) which has focused on understanding the influence of intralimb coordination on interlimb stability. The current findings highlight the importance of not only examining bimanual multijoint tasks but also specifically tasks that require coordination of limbs with different joint configurations.

While experiment 1 highlighted the advantage of coordinating limbs with similar leading joints over coordinating limbs with different leading joints; experiment 2 sought to understand if the associated differences in performance (due to initial task constraints) could be reduced with training. The findings from experiment 2 during the first stages of practice support those of experiment 1 by demonstrating a similar relationship between groups as was observed between conditions of experiment 1. In experiment 2, the group learning the novel coordination pattern with similar leading joints exhibited greater interlimb stability during initial trials than the two groups learning coordination patterns with different leading joints; demonstrating a similar advantage of conditions produced with similar leading joints over conditions produced with different leading joints in experiment 1. The results expand on the understanding of changes in intralimb coordination with learning. As with experiment 1, the second study also found stability of interlimb coordination patterns and endpoint control to be influenced by whether tracing actions were produced with similar or different leading joints, particularly during early practice. During the first block of practice the general trend of the relationship between groups was in line with the differences among left arm-right arm leading joint conditions of experiment 1. Interestingly, however,

throughout the two days of practice, performance of the groups learning the novel coordination pattern with different leading joints improved to match more closely that of the group learning the pattern with similar leading joints. The findings suggest that initial deficits in stability of interlimb coordination and accuracy of endpoint control due to initial task constraints, can be overcome with practice. With regard to the learning predictions put forth by the LJM, the results offer support by demonstrating an influence of biomechanical properties on the acquisition of a novel coordination pattern and some differences in the tuning time course of leading joints, although support for a slower tuner of the subordinate joints was not that strong.

The notion that tuning could occur at a single joint and thereby enhance the stability of an individual limb's motion that in turn can be associated with stabilizing interlimb coordination underscores the existence of different levels of movement organization and how they are adapted with practice.

In experiment 2, the goal was to learn a novel interlimb relative phasing between the arms. Relative phase is thought to function as an informational variable which distinguishes changes in stability emerging with practice (Kelso, 1984). The degree of interlimb relative phase offset and the variability of interlimb relative phase both decreased with practice. By the end of practice, all three groups established equivalent stability. Walter, Swinnen, and Dounskaia (2002) examined the acquisition of the ability to trace continuously a circle and ellipse template concurrently with the two arms in order to shed light on the levels of movement organization during which interlimb interference emerges. The study's findings revealed that even when the goal

of the multilimb task is not explicitly conceived with respect to the relative motion of the limbs, to the subject, the task was conceived with regard to the relative motion between the limbs. This finding led the authors to conclude that establishing interlimb stability appears to be a priority of the CNS. The findings help to substantiate the view that interlimb relative phase is represented at the highest level of a hierarchical control structure governing bimanual coordination.

Taken together, the findings indicate a heterarchical organization which links interlimb coordination (relative phase) with leading and subordinate joint control. At the highest level is the global variable of interlimb control, relative phase. At a second level, leading and subordinate joints are selected. This represents a control strategy which drives individual limbs in achieving interlimb coordination. With regard to learning, the selection of intralimb joints influences the rate of learning of the interlimb coordination pattern. On a third level, the selected joints of individual limbs are tuned to achieve the required interlimb coordination pattern.

In summary, the findings from both experiments expand our understanding of the influence of intralimb coordination dynamics on endpoint control, interlimb stability, and acquisition of novel coordination patterns.

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## APPENDIX A

### *Computation of Torque Components*

Net Torque (NT) at a particular joint is comprised of two components: muscle torque (MT) and interaction torque (IT). MT is thought represent *active* torque, because it takes into account the active component due to muscle contraction and the viscoelastic properties of muscle, tendons, ligaments, and other periarticular tissue at the joint. IT is thought to represent *passive* torque because it originates from the motion of the adjacent limb segments. Thus, IT is dependent on motion at both joints. Accordingly, torque components are bounded by the following relationship:

$$NT = MT + IT.$$

### *Torques at the shoulder:*

$$NTS = I_p \ddot{\phi}_p$$

$$ITS = -[I_a + m_a(l_p^2 + 2r_{al_p} \cos \theta)] \ddot{\phi}_p - [I_a + r_{al_p} m_a \cos \theta] \ddot{\theta} + r_{al_p} m_a \sin \theta \dot{\theta}^2 + 2r_{al_p} m_a \sin \theta \dot{\theta} \dot{\phi}_p$$

$$MTS = NTS - ITS$$

### *Torques at the elbow:*

$$NTE = I_a \ddot{\theta}$$

$$ITE = -(I_a + r_{al_p} m_a \cos \theta) \ddot{\phi}_p - r_{al_p} m_a \sin \theta \dot{\phi}_p^2$$

$$MTE = NT - IT$$

The symbol  $\ddot{\cdot}$  represents joint acceleration and the symbol  $\dot{\cdot}$  represents joint velocity. The variables  $\varphi_p$  and  $\varphi_d$  represent the absolute joint angles characterizing the position of the proximal (upper arm) and distal segments (forearm and hand) relative to the horizontal plane passing through their proximal ends. The variable  $\theta$  represents the relative angle ( $\theta = \varphi_d - \varphi_p$ ) between the proximal and distal segments that is equal to zero when the arm is extended. The variables  $m_p$  and  $m_d$  are the proximal and distal masses,  $r_p$  and  $r_d$  are the distances between the proximal end of each segment and its mass center, and  $I_p$  and  $I_d$  are the moments of inertia about the axes passing through the proximal ends of the segments with  $l_p$  the proximal segment length.

The mass of the distal segment was computed as the sum of  $m_d = m_f + m_h$  where  $m_f$  and  $m_h$  are the mass of the forearm and hand respectively. The distance  $r_d$  was calculated with the formula for computation of the mass center of a system of material points:

$$r_d = [r_f m_f + (l_f + r_h) m_h] / (m_f + m_h)$$

with  $l_f$  length of the forearm,  $r_f$  the distance from the elbow joint to the forearm mass center, and  $r_h$  the distance from the wrist joint to the hand mass center.  $I_d$  was computed as follows:

$$I_d = I_f^c + I_h^c + r_f^2 m_f + (l_f + r_h)^2 m_h$$

with  $I_f^c$  and  $I_h^c$  the moments of inertia of the forearm and hand about the axes passing through the corresponding centers of mass.

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